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Evolution of Abscisic Acid Signaling Module and Its Perception

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We hereby review the perception and responses to the stress hormone Abscisic acid (ABA), along the trajectory of 500M years of plant evolution, whose understanding may resolve how plants acquired this signaling pathway essential for the colonization of land. ABA levels rise in response to abiotic stresses, coordinating physiological and metabolic responses, helping plants survive stressful environments. In land plants, ABA signaling cascade leads to growth arrest and large-scale changes in transcript levels, required for coping with environmental stressors. This response is regulated by a PYRABACTIN RESISTANCE 1-like (PYL)–PROTEIN PHOSPHATASE 2C (PP2C)–SNF1-RELATED PROTEIN KINASE 2 (SnRK2) module, that initiates phosphor-activation of transcription factors and ion channels. The enzymatic portions of this module (phosphatase and kinase) are functionally conserved from streptophyte algae to angiosperms, whereas the regulatory component –the PYL receptors, putatively evolved in the common ancestor of *Zygnematophyceae* and embryophyte as a constitutive, ABA-independent protein, further evolving into a ligand-activated receptor at the embryophyta. This evolutionary process peaked with the appearance of the strictly ABA-dependent subfamily III stress-triggered angiosperms' dimeric PYL receptors. The emerging picture is that the ancestor of land plants and its predecessors synthesized ABA, as its biosynthetic pathway is conserved between ancestral and current day algae. Despite this ability, it was only the common ancestor of land plants which acquired the hormonal-modulation of PYL activity by ABA. This raises several questions regarding both ABA's function in ABA-non-responsive organisms, and the evolutionary aspects of the ABA signal transduction pathway.

Keywords: abscisic acid, pyrabactin resistance 1 (PYR)/PYR1-like (PYL)/regulatory components of ABA receptor (RCAR), plant signaling, PP2C group A, SnRK2, plant evolution

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INTRODUCTION

Understanding the evolution of Abscisic acid (ABA) signaling may resolve the puzzle of how plants acquired a major stress signaling pathway that was essential for the colonization of land by ancestral plants. Early land plants, are believed to have been derived from a single common aquatic algal ancestor and had to cope with new challenges, unique to the terrestrial environment (see review by de Vries and Archibald, 2018). Desiccation tolerance was a key adaptive trait for aquatic organisms transitioning to terrestrial environment. This trait has been largely lost in vegetative tissues of trichophytes (see review by

Cuming, 2019). Instead, angiosperm adaptation to land was dependent on the ability to regulate the intake and loss of water to the environment (see review by Anderegg, 2015). One major mean by which angiosperms maintain their water balance is the regulation of evapotranspiration *via* the stomata pores. A plant's daily transpiration rhythm is regulated by many internal and external factors, coordinating stomata aperture during its diurnal cycle. The production of the phytohormone ABA in case of an abiotic stress—overwrites transpiration rhythms and results in a rapid closure of the stomata (see review by Brodribb and McAdam, 2017). In the absence of ABA, as in the case of auxotrophic ABA mutants, the ability to close stomata in response to environmental cues is impaired, and as a result, the ability to endure harmful environments is compromised, ultimately deteriorating plant's growth and development (Koornneef et al., 1982; Taylor et al., 1988). Thus, ABA's regulation of land plant water balance is vital for a sessile plant, whose surroundings are in constant change.

The hormone ABA acts through a conserved signal transduction pathway. This pathway is comprised of a PYRABACTIN RESISTANCE 1-Like (PYL)–PROTEIN PHOSPHATASE 2C (PP2C) and SNF1-RELATED PROTEIN KINASE 2 (SnRK2). The binding of ABA to a soluble PYL protein triggers a conformational change that allows the receptors to bind and inhibit the PP2C that normally represses ABA signaling (Melcher et al., 2009; Miyazono et al., 2009; Nishimura et al., 2009; Park et al., 2009; Yin et al., 2009; Melcher et al., 2010; Peterson et al., 2010). This formation of PYL–ABA–PP2C complex, releases SnRK2 from the otherwise inhibitory complex with PP2C, initiating phosphorylation of transcription factors and ion channels, involved in ABA output responses (Fujii et al., 2009; Umezawa et al., 2009; see reviews by Hubbard et al., 2010; Weiner et al., 2010). This review focuses on the physiological and biochemical perception and responses to ABA, along the trajectory of five hundred million years of plant evolution, from streptophyte algae to angiosperms.

ABA "OUTPUT" RESPONSE IN ALGAE

The presence of ABA has been confirmed in many chlorophytes and streptophyte algae species, yet the environment-induced synthesis of ABA was demonstrated solely in few aquatic algae species (Tietz and Kasprik, 1986; Hirsch et al., 1989; Hori et al., 2014). ABA biosynthesis in the chlorophytes *Draparnaldia mutabilis* and *Dunahella parua* is induced by salinity, whereas it is seasonally accumulated in the streptophyte algae *Chara contraria* (Sabbatini et al., 1987; Tietz et al., 1989; Hirsch et al., 1989). Despite the evidences of ABA biosynthesis in these aforementioned species, in the vast majority of explored algae, no such significant cellular or physiological function was documented (Hirsch et al., 1989; Tietz et al., 1989; Negin and Moshelion, 2016). This is true even in cases where algae were treated with high dosage of the phytohormone (Kobayashi et al., 1997; Nagao et al., 2008; Sulochana and Arumugam, 2016). Exceptions to note are the alterations of membrane properties of *Nitella* treated with ABA (Wanless et al., 1973; Ord et al., 1977) and the ABA inhibition of *Chara* oospores germination (Sederias and Colman, 2007). Despite these putative adaptive responses to ABA, the effect on growth and other cellular functions in these studies were triggered by the application of high concentrations of ABA ranging from 40 to 500 μM, far from endogenous physiological hormone levels (Ullrich and Kunz, 1984; Saradhi et al., 2000; Yoshida et al., 2003; Yoshida et al., 2004). Thus, these extreme ABA concentrations, required to elicit such responses, are prone to attribute to toxicity rather than a putative activation of an ABA signaling cascade. Taken together, little evidence manifests a clear physiological function for ABA in chlorophyte and streptophyte algae, despite its obvious presence of in both algae phyla.

ABA "OUTPUT" RESPONSES IN EARLY DIVERGENT LAND PLANTS (BRYOPHYTES, LYCOPHYTES, FERNS)

The presence of endogenous ABA, and the response to exogenous ABA application, are well described in bryophytes, but less so in lycophytes and ferns (see reviews by Hartung, 2010; Takezawa et al., 2011; Brodribb and McAdam, 2017). In bryophytes, ectopic ABA application and the genetic mimicking of ABA signaling affects various developmental processes. In liverworts, exogenous ABA inhibits gemma and thalli growth and the establishment and maintenance of gemma dormancy of *Marchantia polymorpha* (Tougane et al., 2010; Eklund et al., 2018). In mosses, ABA elicits protonemal morphological changes. For example, in *Physcomitrella patens,* ABA induces the formation of thick-walled spherical "brood cell", and it inhibits protonemal differentiation into "leafy" gametophores (Takezawa et al., 2011). The role of ABA in stress tolerance has also been demonstrated in bryophytes. In *M. polymorpha*, the application of ABA improved gemma survival rate following desiccation or freezing, hypothetically resulting from an ABA-induced accumulation of soluble sugars and intracellular rearrangement of vacuoles and chloroplasts (Pence et al., 2005; Hatanaka and Sugawara, 2010; Akter et al., 2014). In addition, the ABA-induced biosynthesis of bisbibenzyls was hypothesized to improve UV irradiation tolerance (Kageyama et al., 2015). Similarly, in a few moss species (*P. patens*, *Funaria hygrometrica*, *Atrichum undulatum* and *Ditrichum cornubicum*) the application of ABA had a positive effect on tolerance to both desiccation and freezing (Takezawa et al., 2011). This adaptation to stress was putatively attributed to the accumulation of protective proteins such as the LATE EMBRYOGENESIS ABUNDANT (LEA), and enzymes associated with osmotic cellular adjustment (Khandelwal et al., 2010; Shinde et al., 2012; Ghosh et al., 2016). Thus, a cellular physiological response to ABA, associated with the adaptation to abiotic stress is evidenced in the first plants habituating land.

The role of ABA in regulating stomata aperture, however, remains ambiguous in earlier divergent plants. Stomata was an "innovation" that facilitated plant terrestrial adaptation. It is

generally present in most bryophyte plants except liverworts (see review by Chater et al., 2017). It is thought that the major function of bryophyte stomata was to allow spore capsule desiccation, as the stomata-deficient *PpSMF1* (SPEECHLESS, MUTE and FAMA) mutant of *P. patens* retained water in its sporangia (Chater et al., 2016). Neither ectopic ABA application, nor the darkening of hornworts, triggered their stomata closure. However, hornworts' stomata did respond to reduction in water potential, emphasizing their potent responsiveness to environmental cues (Pressel et al., 2018). The application of 100 μM of exogenous ABA did affect stomata aperture in both *P. patens* and *F. hygrometrica*, however, when ABA signaling was genetically blocked in *P. patens*, neither stomata aperture, nor spore capsule dehydration phenotypes, were reported, suggesting that the ectopically applied hormone levels might not mock on endogenous ABA titrations (Chater et al., 2011; Shinozawa et al., 2019). Taken together, further studies, involving genetic assays, could better clarify the inductive role of ABA in regulating stomata aperture in bryophytes.

In early vascular plants (lycophytes and ferns) there is an active debate regarding the regulation of stomatal aperture by ABA. Stomatal responses to ABA in these plants could be measured only under specific environmental conditions, suggesting a minor contribution of ABA to the regulation of their aperture (Ruszala et al., 2011; Soni et al., 2012; Hõrak et al., 2017). For example, *Selaginella bryopteris* stomata displayed no response to ABA in non-stress conditions, despite its response to ABA under the combination of high temperatures (35 °C) and highly elevated vapor pressure deficit (of 4.5kPa; Soni et al., 2012). A mild reduction in stomata conductance in *Athyrium filix-femina* and *Dryopteris filix-mas* was recorded when treated with 10 μM foliar ABA spraying, however, the authors reported that this response was primarily dependent on cultivation methods (Hõrak et al., 2017). Additional stomatal conductance studies that were correlated with endogenous measurements of ABA levels showed that leaf hydraulics was the predominant factor that primarily regulated stomatal aperture while neither endogenous, nor exogenous ABA, triggered stomata closure in lycophytes and ferns (Brodribb and McAdam, 2011; McAdam and Brodribb, 2012; McAdam et al., 2016; Cardoso et al., 2019). Overall, due to the residual effect of ABA on stomata closure in the aforementioned studies, it seems that in bryophytes and early divergent vascular plants (lycophytes and ferns), stomatal regulation is primarily a hydraulics-driven process.

THE PP2C-SNRK2 SIGNALING MODULE THROUGHOUT PLANT EVOLUTION

The module of the PP2C-SnRK2 phosphatase-kinase is highly conserved throughout plant evolution, preceding the adoption of a regulatory role for the ABA molecule (Tougane et al., 2010; Chater et al., 2011; Hauser et al., 2011; Ruszala et al., 2011; Komatsu et al., 2013; Lind et al., 2015; McAdam et al., 2016; Shinozawa et al., 2019). The cellular signaling of ABA in land plants initiates phosphorylation events mediated by a conserved family of SnRK2 kinases. Vascular plant SnRK2s are classified into three subclasses (Lind et al., 2015; McAdam et al., 2016). Subclass III SnRK2s are pivotal for ABA signaling in *Arabidopsis*, as in the absence of three such family members, there was an absolute shutdown of ABA signaling and response (Fujii and Zhu, 2009). The other SnRK2 subclasses play an important role in osmostress responses in *Arabidopsis* (Fujii et al., 2011). Streptophyte algae and bryophytes encode only subclass III SnRK2s, suggesting that the latter might be the founding members of the family, while the other two subclasses could have been a more recent adaptation of vascular plants (Umezawa et al., 2010; Lind et al., 2015).

An evolutionarily conserved function of subclass III SnRK2 in ABA signaling from streptophyta through angiosperms was demonstrated in multiple genetic studies (Chater et al., 2011; Ruszala et al., 2011; Shinozawa et al., 2019). In the moss *P. patens*, the deletion of *PpSnRK2A/PpOST1* leads to a reduced stomatal response to ectopic ABA, similar to a homologous single *Arabidopsis snrk2.6/ost1* mutant (Chater et al., 2011). *P. patens* quadruple mutant (*snrk2a/b/c/d*) is ABA-insensitive, and it is brood cell development-deficient, lacking both ABA-induced gene expression and desiccation tolerance. Unfortunately, there was no data available regarding the sporophyte ABA response of this mutant, including its stomata response, nor its sporangium dehydration. This strong *P. patens* insensitive phenotype was similar to the *Arabidopsis* triple *snrk2.2/2.3/2.6* mutant (Shinozawa et al., 2019), displaying complete ABA insensitivity. This conserved function of SnRK2 was further exemplified by algae/angiosperm-moss cross-species complementation (Shinozawa et al., 2019). The expression of either of the *Arabidopsis SnRK2.6* gene or the semi-terrestrial alga *Klebsormidium nitens KnOST1* gene complemented *P. patens snrk2* quadruple mutants (Shinozawa et al., 2019). The expression of *PpOST1* from *P. patens* or *SmOST1* from the lycophyte *Selaginella moellendorffii* in *Arabidopsis snrk2.6/ost1* mutant partially rescued stomata ABA insensitivity phenotype (Chater et al., 2011; Ruszala et al., 2011). Taken together, the plant SnRK2s functional conservation likely preceded land habituation.

Furthermore, the SnRK2 phosphorylation targets are also highly conserved throughout plant evolution. The S-type anion channel SLAC1 and ABRE/ABFs transcription factors are SnRK2 substrates in *Arabidopsis* (Furihata et al., 2006; Fujii et al., 2007; Geiger et al., 2009; Lee et al., 2009). SnRK2s from algae (*K. nitens*), liverworts (*M. polymorpha*), moss (*P. patens*), lycophyte (*S. moellendorffii*) and fern (*Ceratopteris richardii*) could activate *Arabidopsis* SLAC1 in *Xenopus laevis* oocytes (Lind et al., 2015; McAdam et al., 2016). However, these SnRK2s cannot activate their native SLACs, suggesting that SnRK2-SLAC1 module for regulating stomata aperture emerged after divergence of ferns and seed plants

(Lind et al., 2015; McAdam et al., 2016). SnRK2 ortholog from *K. nitens*, *M. polymorpha* and *P. patens* were capable of transducing ABA-induced gene expression *via* bZIP transcription factor ABF2 in *Arabidopsis* protoplasts (Lind et al., 2015). For detailed ABRE/ABFs evolution see Cuming (2019). In addition, PpSnRK2s from *P. patens* and *Arabidopsis* SnRK2.6/OST1 phosphorylated *in vitro* the same ABA-responsive phosphopeptides (Amagai et al., 2018). Thus, not only is the kinase itself highly conserved, but also the cellular targets of class III SnRK2 are highly conserved, both from algae through angiosperms.

Both the positive and the negative regulatory proteins of the SnRK2 kinase are, too, conserved throughout land plant evolution (Lind et al., 2015; Saruhashi et al., 2015; Yasumura et al., 2015; Stevenson et al., 2016; Lin et al., 2020; Takahashi et al., 2020). Post-translational modifications and protein–protein interactions are the two key regulation means of SnRK2 (Belin et al., 2006; Vlad et al., 2009; Soon et al., 2012; Saruhashi et al., 2015; Stevenson et al., 2016; Nguyen et al., 2019; Lin et al., 2020; Soma et al., 2020; Takahashi et al., 2020). The activation of *Arabidopsis* SnRK2s requires phosphorylation of key serine residues in kinase activation loop (Ser171 and Ser175 for AtSnRK2.6/OST1; Vlad et al., 2010; Soon et al., 2012). In the moss *P. patens*, the activation of SnRK2s is mediated by an ABA Non-Responsive/ABA Responsive Kinase/Constitutive Triple-Response-1-Like (ANR/ARK/CTR1L) protein kinase, a member of B3 Raf-like kinases whose orthologues are conserved in streptophyte algae, but considered lost in vascular plants (Saruhashi et al., 2015; Yasumura et al., 2015; Stevenson et al., 2016; Shinozawa et al., 2019). Recent studies indicated that B2, B3 and B4 groups, are also of the Raf-like kinases family, and are essential for ABA-induced phosphorylation and activation of SnRK2s in *Arabidopsis* (Lin et al., 2020; Takahashi et al., 2020). Thus, this regulation by post-translational modification by Raf-like kinases is too, likely conserved from the common ancestor of algae to land plants.

Functional conservation is also the case for the negative PP2C regulators of SnRK2. In *Arabidopsis*, PP2Cs interacts with SnRK2s and inhibits the kinase activity as it dephosphorylates key serine residues in the kinase activation loop, and physically blocking the kinase catalytic site (Belin et al., 2006; Vlad et al., 2009; Soon et al., 2012). In angiosperms, group A PP2C contains multi-genes with redundant function (Leung et al., 1994; Meyer et al., 1994; Leung et al., 1997; Rodriguez et al., 1998; Saez et al., 2004; Schweighofer et al., 2004; Xue et al., 2008; Zhang et al., 2018; Fujioka et al., 2019). High-order of loss-of-function *Arabidopsis* mutant of PP2C displays an increase of ABA sensitivity, and partially constitutive ABA response (Saez et al., 2006; Rubio et al., 2009). Similarly, in the moss, two group A PP2Cs are encoded by *P. Patens* genome, and the disruption of *PpABI1A* gene results in up-regulation of ABA-induced gene expression and enhanced freezing tolerance (Komatsu et al., 2009). The double mutant *ppabi1a/b* plant shows constitutive "brood cell" phenotype, a global activation of ABA-induced gene expression, and an increase in general protein phosphorylation, indicative of unchecked SnRK2 activity (Komatsu et al., 2013; Amagai et al., 2018). Overexpression of MpABI1 in *M. polymorpha* and *P. patens* resulted in an inhibition of ABA-induced gene expression and reduction of sensitivity of ABA-induced morphological changes (Tougane et al., 2010; Eklund et al., 2018). Moreover, moss and liverwort PP2C phosphatases inhibited SnRK2 activation of *Arabidopsis* SLAC1 expressed in *Xenopus* oocyte (Lind et al., 2015). Albeit all genomes of organisms from the green lineage (Chloroplastida) encode group A PP2Cs (Hauser et al., 2011), little is known about the biochemical interactions of these proteins with SnRK2s in algae. Taken together, these data suggest that PP2C-SnRK2 regulation module is conserved, possibly since the last common ancestor of streptophytes. As aforementioned, since algae do not activate signaling responses to ABA but they do actively transduce downstream signaling components homologous to higher plants', it is likely that the function of SnRK2, its regulatory components, and its cellular targets, preceded that of ABA signaling.

THE EVOLUTION OF ABA RECEPTORS IN LAND PLANTS

The regulatory unit controlling the aforementioned SnRK2-PP2C module is the most recent evolutionarily among the apex of ABA-signaling-transducing apparatuses. All land plants comprise ABA receptors whose function is largely conserved (Park et al., 2009; Ma et al., 2009; Gonzalez-Guzman et al., 2014; He et al., 2014; Pri-Tal et al., 2017; Mega et al., 2019; Kai et al., 2019). Biochemically, ABA is perceived by a family of Steroidogenic Acute Regulatory Transfer (START)-domain protein receptor called PYRABACTIN RESISTANCE 1/PYR1-LIKE/REGULATORY COMPONENTS OF ABA RECEPTOR (PYR/PYL/RCAR) (Ma et al., 2009; Park et al., 2009). Structure studies reveal a "gate-latch-lock" mechanism that regulate receptor activity: ABA receptors have an open ligand-binding pocket, flanked by two mobile β-loops: the gate and latch. The binding of ABA in the pocket induces a closure of the gate loop and forms a surface that enables the docking of the PP2C co-receptor. A highly conserved tryptophan of PP2C inserts into the "ABA pocket" to further stabilize the PYL-ABA-PP2C ternary complex (Melcher et al., 2009; Miyazono et al., 2009; Yin et al., 2009; Moreno-Alvero et al., 2017). This formation of the ternary complex releases SnRK2 from PP2C inhibition as the PYL and SnRK2 compete on the same PP2C interface (Soon et al., 2012).

In angiosperms, PYL proteins are clustered into three subfamilies, which differ in their affinity to ABA, and in their oligomeric state, each comprised of multiple genes with a partially redundant function. Subfamily III receptor forms a homodimer, whereas subfamily I and II receptors are monomers (Miyazono et al., 2009; Nishimura et al., 2009; Santiago et al., 2009; Szostkiewicz et al., 2010; Hao et al., 2011; He et al., 2014). Mutations resulting in monomer conformation increase the receptor's affinity to ABA and to the PP2C (Dupeux et al., 2011; Hao et al., 2011). Monomeric ABA receptors, in comparison to dimeric receptors, require lower ABA concentration to elicit PP2C inhibition (Okamoto et al., 2013;

Gonzalez-Guzman et al., 2014; Pri-Tal et al., 2017; Mega et al., 2019). Based on *in vitro* data, some monomeric receptors have "basal activity", thereby able to interact and inhibit PP2C activity in the absence of ABA (Hao et al., 2011; Mosquna et al., 2011; Sun et al., 2019). In contrast, dimeric receptors have negligible basal activity, as ABA is required for dimer dissociation (Dupeux et al., 2011; Hao et al., 2011).

Bryophyte receptors are clustered distinctly from vascular plants according to phylogenetic analyses (Weng et al., 2016; Sun et al., 2019). Among vascular plant receptors, subfamily I is phylogenetically closer to that of bryophytes, and subfamily III likely diverged later, as it is unique to angiosperm (Hauser et al., 2011; Weng et al., 2016; Sun et al., 2019). It has been shown that land plant PYL receptors have evolutionarily conserved function (Bowman et al., 2017; Jahan et al., 2019; Shinozawa et al., 2019; Sun et al., 2019). In liverworts, single receptor MpPYL1 knock-out *M. polymorpha* mutant abolished ABA-induced growth inhibition and gene expression (Jahan et al., 2019). The conserved function of MpPYL1 was further confirmed by ABA binding ability, receptor-mediated PP2C inhibition, the activation of ABA-induced gene expression, and the cross-species complementation of *Arabidopsis* ABA-related mutants compromise in either of biosynthetic-pathways or PYL genes (Bowman et al., 2017; Jahan et al., 2019; Sun et al., 2019). Similarly, ABA receptors from the moss *P. Patens* and the lycophyte *S. moellendorffii* displayed both PP2C inhibition and activation of ABA-induced gene expression (Shinozawa et al., 2019; Sun et al., 2019). As the essence of the function of the receptor is the binding to its target, the PP2C interface, the conservation of these targets might themselves have dictated receptor functional conservation, as the SnRK2 and the receptor compete on the very same interface in PP2C.

THE ALGAL ORIGIN OF ABA RECEPTORS

The majority of algae genomes do not encode PYL-like proteins, but few species comprise PYL-like proteins, whose conserved basal, ABA-independent PP2C inhibition activity, suggests that the regulation of PP2C activity might be the ancestral function of the PYL proteins (Sun et al., 2019). Recent genomic and transcriptomic studies demonstrated that some *Zygnematophyceae* algae genome encode PYL homologous proteins (de Vries et al., 2018; Cheng et al., 2019). Protein sequence analysis of these *Zygnematophyceae* PYLs revealed amino acid differences in ABA-binding residues, otherwise conserved in bona fide ABA receptors (Sun et al., 2019). Biochemical and genetic complementation assays, confirmed that *Zygnema circumcarinatum* PYL-like protein (ZcPYL8) can elicit ABA signaling in *Arabidopsis* as it possesses the ability to inhibit PP2C. Further analysis demonstrated that this protein has basal, ABA-independent PP2C inhibition activity, and it could not bind ABA (Sun et al., 2019). Thus, the analysis of the algal PYL indicate that ABA hormonal modulation *via* ligand activation was acquired after the divergence of the ancestor of streptophyte algae from the common ancestor of land plants (Sun et al., 2019).

Studies describe two intertwined trends in the evolution of the ABA receptors: the rise in gene number due to the increase in genetic complexity; and the reduction in receptor ABA-independent basal activity (Sun et al., 2019). We hereby focus on the reduction in receptor basal activity as former reviews by Umezawa et al. (2010) and Hauser et al. (2011) explored the topic of the increase in genetic complexity. The analysis of ABA-independent receptor inhibition of PP2C by PYLs encoded by early divergent plants, suggests a reduction in receptor ABA-independent, constitutive basal activity, in favor of ABA-dependent activity. For example, basal activity of *M. polymorpha* MpPYL1 was around 50% phosphatase inhibition in the absence of ABA. In comparison, three out of four receptors of *S. moellendorffii* had only 15–30% such basal activity, while the fourth SmPYL2 was fully ABA-dependent (Sun et al., 2019). This evolutionary process peaked with the appearance of the strictly ABA-dependent subfamily III dimeric receptors, which are limited to later divergent angiosperms. Lower basal activity provides a broader range of response, and so is the contrary: high basal activity masks the fine-tuned ABA-triggered response. The reduction of ABA-independent basal constitutive activity, alongside the appearance of the dimeric receptors that dominate the response in angiosperms, suggests that a dampening of the basal activity of the receptors was a driving force for the evolution of ABA responsiveness in land plant PYLs (Sun et al., 2019). Thus, in angiosperms, dimeric PYL receptors have evolved, allowing both "finer-tuning" response to variable levels of ABA, and dominating the adaptive stress response of ABA (Park et al., 2009; Okamoto et al., 2013; Pri-Tal et al., 2017; Vaidya et al., 2017; Vaidya et al., 2019).

CONCLUSIONS AND OPEN QUESTIONS: THE EVOLUTIONARY COURSE OF ABA SIGNALING MODULE

The collective data from recent years allow us to draw a putative picture of plant ABA signaling evolution (**Figure 1**). It is likely that the common ancestor of *Zygnematophyceae* and embryophytes possessed a PP2C-SnRK2 module that was regulated by a PYL-like protein (also reviewed by Fürst-Jansen et al., 2020). It is still unknown how these organisms regulated the activity of the PYL-like proteins, whether it was by transcriptional, translational or post-translational modifications, or possibly, by allosteric modulation of a yet unidentified hypothetical small molecule. The origin of the PYL proteins is also currently unknown, however, one hypothesis suggests that this ancestral START domain protein was obtained from soil bacteria *via* horizontal gene transfer (Cheng et al., 2019).

The ancestor of land plants and his predecessors synthesized ABA, as its biosynthetic pathway is conserved between

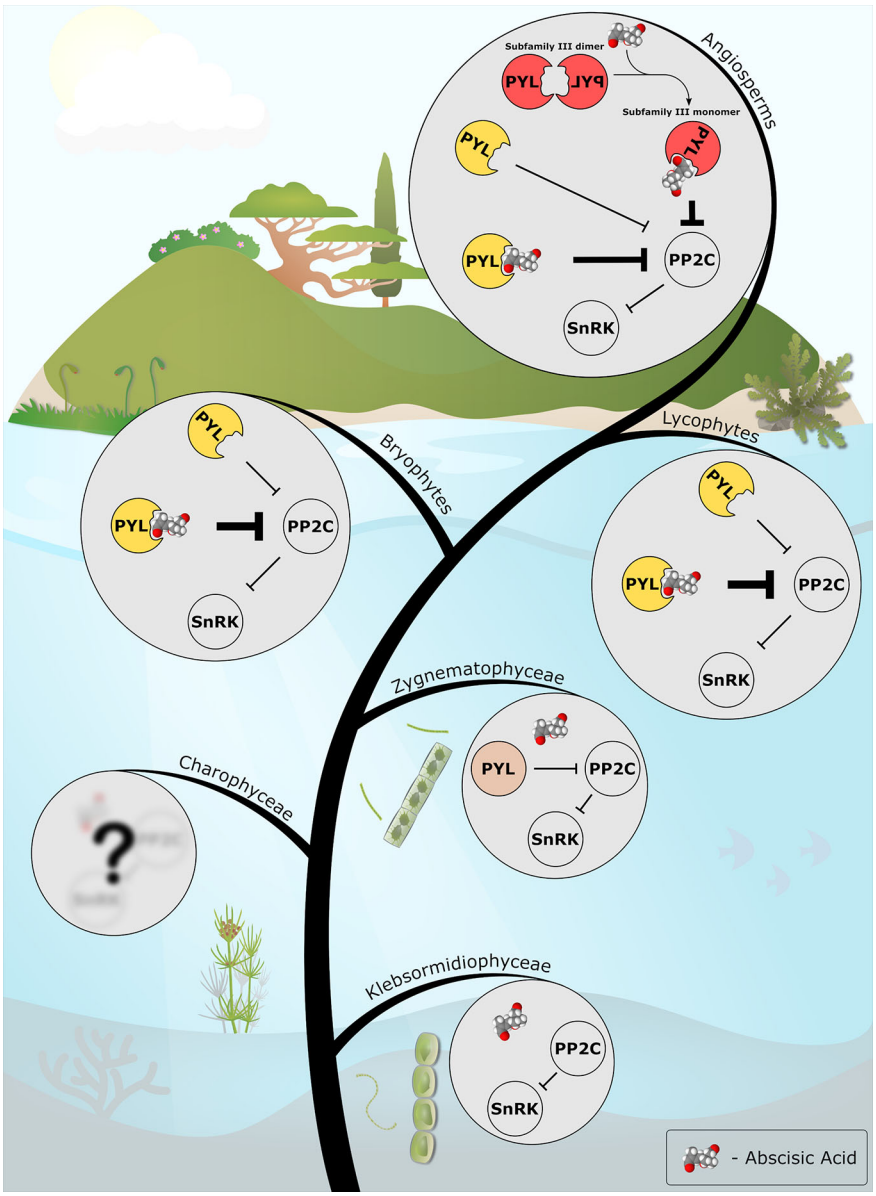

FIGURE 1 | The emerging evolutionary scenario of ABA signaling as described in this review. ABA biosynthesis and PP2C-SnRK2 signaling modules are present in the streptophyte algae (e.g. *Klebsormidiophyceae*). A PYL protein with only basal, ABA-independent, PP2C-inhibition activity (in light brown) evolved in the common ancestor of *Zygnematophyceae* and land plants. Along the course of evolution, the PYL protein of the last common ancestor of land plants (in yellow) gained the ABA-dependent activity, thus recruited ABA into the preexisting signaling cascade. In angiosperms, the appearance of a new subfamily of dimeric PYLs (in red) added another layer of regulation, facilitating ABA-mediated fine-tuning of abiotic stress signaling in plants. ABA molecule is presented as a Van der Waals spheres model. The model was generated with Jmol: an open-source Java viewer for chemical structures in 3D. http://www.jmol.org/.

ancestral and current algae (Hauser et al., 2011; de Vries et al., 2018). Despite this ability to produce ABA, it was only the common ancestor of land plants whom acquired the hormonally modulation of PYL activity by ABA (Sun et al., 2019). This raises several questions regarding ABA's function in ABA-non-responsive organisms, such as modern day algae, and regarding evolutionary aspects of the ABA signal transduction pathway, such as what made ABA in particular a successful stress transducer?

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YS, DM, and AM drafted the manuscript. OP-T contributed to the graphics.

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