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Review Article

Designed ABA receptor agonists: a New Tool to Improve Crop Quality

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ABSTRACT

Unfriendly environments like drought, cold or any other properties stress lead to a certain reduction of crop yield and quality. Abscisic acid (ABA), as an important plant hormone, plays a very important role in plant growth and resisting plant stress responses. The discovery of ABA crystal structure is a very critical event and provide a very important role for ABA signaling pathways to be exposed to us more clearly. In this process, the screening of ABA receptor agonists played a decisive role in the analysis of ABA crystal structure. Further, various ABA receptor agonists have been screened out, and their functions have also been analyzed. Together, structures studies suggest a detailed mechanism for ABA and receptor binding and regulation of downstream ABA signal pathway, which provide a thought for improve crop yield and quality through the rational utilize the designed ABA agonists.

Keywords: abscisic acid; receptor; agonists; crop quality; pyrabactin

INTRODUCTION

Crop tolerance and quality improvement are regulated by plant hormones and growth regulators, which is an eternal theme in agriculture [1], [2]. Any single strategy, such as appropriate moisture, sufficient light, and included a method of genome editing (GE) to remove or add a gene, has limited improvement in crop traits. In addition to the current global environment, fresh water supplies are alarmingly decreasing and drought, salinity, cold, and other abiotic stresses are responsible for major crop harvest losses world-wide [3], [4], [5]. Therefore, an effective improvement of crop yield is bound to be an interdisciplinary technology combine with geography, physiology, genetics and other aspects about plants and environment.

ABA is plant hormone that plays crucial roles in seed maturation and germination, stomatal closure, and osmotic stress-responsive gene expression and in developmental processes. Stresses, such as drought, salinity, cold and pathogen, induce strong expression of ABA biosynthetic genes, and lead to a high ABA levels in plants [6], [7], [8]. The upregulated ABA levels regulate plants adapt to the adverse conditions through ABA-regulated signal way, especially ABA-dependent gene expression, including the ABA receptors, protein phosphatases type-2C(PP2Cs), Snf1-related kinase 2s(SnRK2s), and AREB/ABF regulon [9], [10], [11], [12]. ABA receptor agonists based on mimics of the phytohormone ABA, which have given a characteristic of potent water savings and drought protection activity for increasing yield [13], [14], [15]. Therefore, according to its function in plants physiology, the control of ABA agonists regulated signal way has the potential to be a new tool for studying functions and improving plant agronomic traits and stress resistance.

ABA-REGULATED SIGNAL WAY

ABA, identified in plants in the 1960s, is an important plant endogenous hormone with a sesquiterpene structure [8], [16], [17]. A series of studies showed ABA plays a critical role in many vital physiology processes, including seed dormancy, seedling growth, leaf senescence , control of vegetative growth and regulating plant responses to environmental stresses such as drought, cold, extreme heat, salinity, waterlogging, anoxia,

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ammonium poisoning, pathogen infection and the parasitism of other plants [18], [19], [20]. Further, studies revealed that the pyrabactin resistance1/PYR1-like/regulatory components of ABA receptor (PYR1/PYL/RCAR) proteins, the most widely recognized ABA receptor family among various types of ABA receptors, has emerged as ABA sensors able to inhibit the activity of specific protein phosphatases type-2C (PP2Cs) in responses to ABA, and then activating the sucrose non-fermenting 1-related protein kinase (SnRK) subfamily 2 (SnRK2s) [21], [22]. The PP2Cs ABI1 and its close structural homolog ABI2, emerged as a hub in the network of ABA signal transduction [23], [24], [25].

In ABA signal pathway, ABA binds in the PYR/ PYL ABA receptors cavity, a conformational change enables the receptors to bind to PP2C active sites [26], [27]. Thus, the structural data show a structure of PYLs-ABA-PP2C, the core complex in ABA signal pathway [28], [29]. Further, the physiological substrate of PP2C, SnRK2 peptide show the accumulation of activated kinases, which phosphorylate downstream effectors to initiate protective responses such as stomatal closure and gene expression reprogramming [30]. In this process, amplifying the receptor of ABA signals can better improve water use and photosynthesis efficiency in crop plants.

ABA RECEPTOR CRYSTAL STRUCTURES

Since the crystal structure of ABA receptor was resolved and reported, various ABA receptors and related crystal structures have been reported in a rapid explosion manner [28], [29], [31], [32]. Recently studies show that more than 70 crystal structures of PYLs family have been reported. In addition, Structural studies mainly focus on structures of ABA-bound PYLs or PYLs-ABA-PP2C, which provides more evidence for learning the ABA signaling pathway [28], [29], [31], [32], [33]. PYR/PYL/RCAR receptors belong to a branch of START/Bet v I proteins superfamily, which share a common fold enclosing large hydrophobic ligand binding pocket. This structure can bind a chemically diverse set of lipids, hormones, and antibiotics [34].

The structure of ABA-bound PYLs comprises a large C-terminal α-helix (α3) is enfolded by a seven-strand anti-parallel β-sheet and two small α-helices, which is the basis for forming a large open ABA binding pocket [28], [29], [31], [32]. This structure is the basis of ABA combination, and it is also main evidence for the transformation of pyrabactin.

ABA RECEPTOR AGONISTS

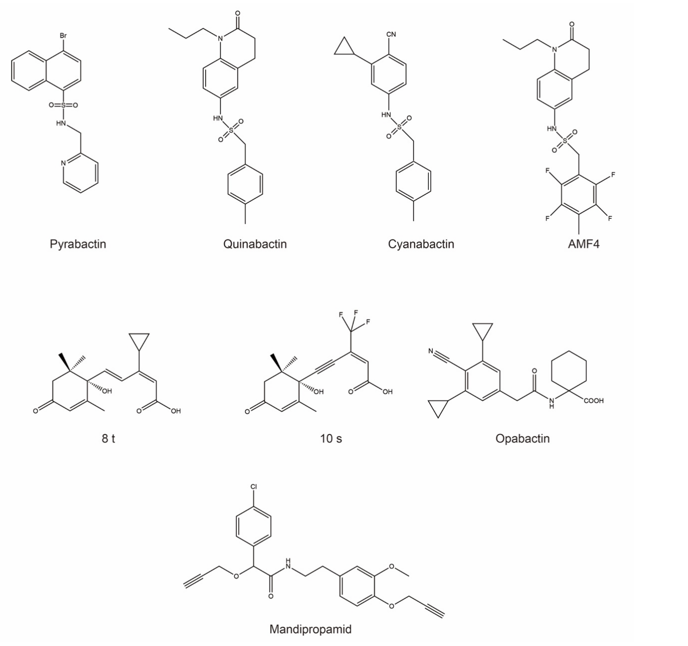
Pyrabactin is a synthetic sulfonamide that directly accelerates the discovery of ABA receptor PYLs [35], [36]. Although its skeleton is not similar to ABA, a similar interaction between ABA-PYL was found in the binding mode of pyrabactin-PYL [26], [37]. This similar banding mode indicated that ABA receptor agonists harbor the potential to improve the crop quality under stresses by activating the ABA signal pathway [13]. Further, the identification of ABA physiology, especially manipulate ABA response on plant stress, which would represent a very useful tool to design ABA receptor agonists [13].

Recent studies have reported a variety of ABA agonists (Figure 1), pyrabactin and its ramification [13], [38]. PYLs agonists derived from this molecule generally require one end to be hydrophilic and the other end to be lipophilic. The polar group at one end of the molecule interacts with the polar residue inside the ligand binding pocket, and the other hydrophobic group interacts with the gate. Additionally, another sulfonamide ABA agonist-AMI was screened out with the method of high-throughput [15], [37], [39]. It has a special potential in promoting the binding of receptors to downstream proteins. Its inhibitory ability on the downstream protein HAB1 is 8.7 times that of ABA and 7.6 times that of pyrabactin. At the same time, it can selectively bind dimeric PYLs and successfully inhibit downstream phosphatase HAB1. These findings raise the possibility that physiological ABA agonists may exist to a new tool to improve crop quality.

SUMMARY AND OUTLOOK

In this review, we focused on the structural analyses understanding of the comprehensive ABA signaling network, in which PYR/PYL/RCARs, group-A PP2Cs, and SnRK2s serve as the core components. However, how to use ABA-regulated plant stress resistance in actual production to increase crop yield remain to be limited. Unexpected, some research groups combined high-throughput screening, virtual screening, x-ray crystallography, and structure-guided design to develop a series of ABA agonists. Recently, a study of opabactin (OP), which is an ABA mimic, showed that OP enhances drought tolerance and hyperactivates ABA transcriptional responses. Further, the ABA agonist inhibits the activity of HAB1 specifically through dimeric PYR/PYL/RCARs. Based on these studies, promising combinations of PYR/PYL/RCARs and ABA agonists, which sought as next-generation agrochemicals that can manipulating plant water use in crop growth and yield.

Figure 1: Representative ABA agonists.



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