



## Original article

## Progress of ethylene action mechanism and its application on plant type formation in crops

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## ABSTRACT

**Background:** The plant hormone ethylene exerts a huge influence in the whole life cycle of plants, especially stress-resistance responses. With the development of functional genomics, that the action mechanism of ethylene takes part in mediated plant architecture has been clarified gradually, such as plant roots, stems, leaves, fiber elongation and so on. Accordingly, the application of ethylene on crops chemical control and genetic improvement is greatly expanded. From the view of ethylene mediated plant architecture in crops, here reviewed advances in ethylene biosynthesis and signal transduction pathway, stress-resistance responses and the yield potential enhance of crops in recently 20 years. On these grounds, the objectives of this paper were to provide scientific reference and a useful clue for the crop creation of ideal plant type.

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## 1. Introduction

Ethylene (CH<sub>2</sub>=CH<sub>2</sub>) is one of the earliest discovered plant hormone, one that is widely used as a plant growth regulator for small molecule gases, that has been widely used in agricultural production practices such as control of chemicals used in crops (Burg, 1973; Kepinski and Leyser, 2003). In 1901, a Russian scientist first discovered that the gas ethylene emitted by the gas lamps on the streets would lead to unusual growth of plants and later used the “triple reaction” produced by the growth of pea seedlings in the dark to verify his findings (Neljubow, 1901). In 1934, the Briton scientist Gane, became the first man to obtain the exact chemical evidence that the plant’s own tissues could produce endogenous ethylene (Gane, 1934). In 1965, ethylene was gradually recognized as a plant hormone under the proposal of American Burg and other researcher (Burg, 1973; Mattoo and White, 2018).

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Ethylene has been found in a wide range of plants so far, including angiosperms, gymnosperms, ferns and even mosses to regulate their growth and development as well as responds to a variety of biological and non-biological processes such as promoting germination, inhibiting root elongation, stimulating the senescence of flowers and leaves and fruit ripening (Xu and Xue, 2012; Mattoo and White, 2018). The well-known plant growth regulator, Ethephon (Ethephon or Ethrel), of which the chemical name is 2-chloroethylphosphonic acid, can release ethylene (Ethylene) in plants to stimulate the bleeding, inhibit stem elongation, promote boll cracking, degumming, ripening, dislocation, and regulating gender conversion (Hattori et al., 2009; Qin and Zhu, 2011; Xu and Xue, 2012). Recent years, studies on ethylene’s involvement in the regulation of fiber elongation (Qin and Zhu, 2011), stem elongation (Zhang et al., 2019), photooxidative stress (Lieberman et al., 1966; Guo and Ecker, 2004) and other physiological processes have made new progress, further expanding the application of ethylene on crops (Yamauchi et al., 2016; Kuroha et al., 2018).

The objectives of present study were to (1) briefly describe the existing research results of synthesis and signal transduction pathway of ethylene based on the involvement of ethylene in the regulation of plants such as maize and rice; (2) discuss the action mechanism of ethylene in the development of major crop types; (3) and explore useful clues and references for crop re-creation of ideal plant architecture (chemical control and genetic improve-

ment) by combining existing results and latest developments of application of ethylene to help major plants grow, resistant stress under adverse circumstances.

## 2. Ethylene synthesis and its metabolism regulation

Many plant tissues produce ethylene in a concentration that in most cases is low. Only until the new detection technology in the 1960 s, especially the application of gas chromatography, did people's understanding of ethylene synthesis and metabolism start to deepen (Lieberman et al., 1966; Bleecker and Kende, 2000). Bradford (from the University of California, Davis) clarified and explained the synthesis transduction pathway of ethylene through a series of ingenious experiments in apples, and summarized it as a signal reaction chain Methionine (Met) → S-adenosyl-L-methionine (SAM) → 1-aminocyclopropane-1-carboxylic acid (ACC) → ethylene. Among them, ethylene is derived from the third and fourth carbon of methionine. In the whole cycle, methionine binds to adenosine to form S-adenosylmethionine, which can then produce 5'-methylthioadenosine (MTA), and after re-adenylation & hydrolysis reaction, could regenerate methionine, which ensures that the trace methionine content in plants can also effectively maintain the ethylene reaction uninterrupted (Lieberman et al., 1966; Bleecker and Kende, 2000; Chen and Zhang, 2006; Bradford, 2008). And this major discovery, thanks to Professor Yang Xiangfa's excellent work, was named as The Yang Cycle.

During the synthesis of ethylene, the activities of three enzymes are regulated: SAM synthetase (SAMS), ACC synthetase (ACS), and ACC oxidase (ACO). SAMS is a multi-gene family protein, and the SAM it generates is also involved in biochemical pathways such as polyamines (Li et al., 2005). The expression of SAMS changes greatly when stimulated in varied environment; ACS is the key enzyme that limits the speed of the whole pathway. ACS exists in the cytoplasm in the form of monomers, dimers or even trimers, with the highest activity in the presence of monomers. Biochemical assays, amino acid sequence analysis and X-rays show that all forms of ACS are an enzyme that relies on pyridoxal phosphate (PLP) coenzymes and is very similar to aspartate transferase and tyrosine aminotransferase, for they are all based on pyridoxal phosphate as a prosthetic group, and therefore can be inhibited by aminoethoxyvinyl glycine (AVG), aminoxyacetic acid (AOA) and its analogues (Yamagami et al., 2003). Recent studies have shown that there are 12 ACS family genes in Arabidopsis, the inactive ACS1, the unfunctional gene - ACS3, ACS10 and ACS12 that encode a specific aminotransferase, and there are 9 ACS family protein genes that actually could encode (Yamagami et al., 2003; Li et al., 2005). Further, GUS detection and Northern detection revealed that these functional ACS family protein genes were expressed in roots, stems, leaves, flowers and fruits and could regulate post the transcription, but the content of ACS2 rose up to a high level as the plants grew (Argueso et al., 2007). Chung et al. (2002) have also confirmed that differences in the phosphorylation-regulated loci and gene expression of these different ACS gene family members are the basis for ACS's different responses to internal and external factors regulations. During the final step when ACO catalyzes ethylene synthesis reaction, it could limit the rate at which synthesis of ethylene takes place. The study also found that ACO is widely distributed in various tissues of plants, and its function depends on the effects of ascorbic acid, Fe<sup>2+</sup>, O<sub>2</sub>, and therefore various chelating agents, such as EDTA, can inhibit its activity, but there is still no critical evidence for its cytoplasmic localization (Chung et al., 2002; Tsuchisaka et al., 2009). In Arabidopsis, ACO is a multi-gene family with 5 family members, and its expression patterns are different, but all are enhanced by the induction of ethylene in the stem. Rauf et al.

(2013)'s reports confirmed the coordinated regulation by ACO5 and NAC transcription factors on the movement of Arabidopsis leaves to adapt to immersion stress.

The current progress have shown that the synthesis and metabolism of plant ethylene is closely correlated to precise regulation by environmental factors such as light and temperature, with many regulatory mechanisms involving the above-mentioned three key enzymes, especially regarding the changes in the activity of rate-limiting enzyme ACS. Argueso et al. (2007) reported that the expression of multiple ACS genes (ACS2, ACS4, ACS5) is induced by injury, which increases the synthesis of ethylene. In plant growth, ethylene can inhibit the expression of ACS gene to limit the production of itself. The ethylene synthesis in wheat leaves can be accelerated by increasing the ACC via light, and it is also confirmed that phytochrome participates in the regulation of ethylene synthesis pathway (Zhong et al., 2012). Wang et al. (2005) further illustrates in the root tip of Arabidopsis thaliana seedlings growing under light in different situations, such as freezing condition, high temperature and hypoxia, the expression of different ACS genes could be induced or suppressed. Ecker Laboratory used ethylene's overexpression mutant *eto1*, *eto2*, and *eto3*, which were screened by positive genetics, and the excess ethylene was produced by stabilizing ACS (Chae et al., 2003). Gene *ETO1* encodes a protein containing a peptide-binding structure, which recognizes ACS via the C-terminus of this structure and ubiquitination, allowing *ETO1* to interact with ACS5 and inhibiting its activity, thus leading to reduction of ethylene biosynthesis. Excess expression of *At ETO1* relieves this inhibition and allows for excessive ethylene synthesis. *ETO2* and *ETO3* encode ACS5 and ACS9 proteins respectively. And by increasing their own stability, it would lead to excessive ethylene synthesis in plants. As mentioned results above indicate, the regulation of the stability of ACS's activity is one of the important ways of ethylene synthesis and metabolic regulation mechanisms, and this regulation is at least partially achieved by the C-terminal structure of the protein.

Other hormonal signals can also regulate the synthesis and metabolism of ethylene through the adjustment of ACS. For example, auxin signal is also capable of promoting ethylene synthesis in the roots and leaves of Arabidopsis thaliana, and can also increase the transcription level of *At ACS4* gene. Besides, Brassinolide also can synergize with auxin to promote ethylene synthesis (De et al., 2005). Staswick and Tiryaki (2004) also confirmed that jasmonic acid can bind to the precursor of ethylene synthesis, ACC, to participate in the regulation of ethylene synthesis.

## 3. Ethylene signal transduction pathways and its linear model

Scholar's understanding of ethylene signal transduction pathways is mostly derived from the genetics and molecular biology of mutants of Arabidopsis thaliana. The initial screening of ethylene mutants is based on the simulated "triple reactions" of Arabidopsis thaliana seedlings, with its phenotype described by researchers as follows: exogenous ethylene causes the Arabidopsis thaliana seedlings in the dark to experience inhibited root and hypocotyl elongation, thickened hypocotyl lateral growth, intensified apical cotyledons and other obvious morphological changes (Bleecker et al. 1988; Staswick and Tiryaki, 2004). With exogenous ethylene applied, the "triple reaction" of the wild type was weakened or even disappeared, and partially or even completely ethylene-insensitive mutants occurred, such as *etr1/2* (Ethylene resistant 1/2), *ein2* (Ethylene insensitive 2), *ein3-6*, *hls1* (Hookless 1), *eir1* (Ethylene insensitive root 1); the second type of mutant is a constitutive triple-reaction mutant, which even in the absence of ethylene, could still trigger a triple reaction, including the mutant *eto1-3* (Ethylene over-exproduction 1-3) and the ethylene

signal constitutive mutant *ctr1* (Constitutive triple response 1) as a result of ethylene excess, which could exert an influence on the size of the plants and the outlook of the flowers. The standard triple-reaction featuring method for mutant screening has reached its limits, meanwhile other screening methods have developed to some extent. For example, by screening at a low concentration of ethylene, the *eer1* (Enhanced-ethylene-response 1) mutant, exhibiting an enhanced ethylene reaction, would be produced the *eer1* (Enhanced-ethylene-response 1) mutant (Ecker, 1995); and using an ethylene antagonist, the *ran* mutant (Response to antagonist), a mutant responsive to the antagonist, could be obtained the *ran* mutant (Response to antagonist) (Xiong et al., 2017; Alonso et al., 2003). After the isolation and identification of aforementioned mutants, based on the positional-cloning of related genes, the upstream and downstream relationship of signal components were determined by genetic engineering and genetic epistasis analysis, and the initial Linear signal transduction pathway in simulated Arabidopsis was obtained (Ecker, 1995). The most upstream sensor in this pathway is the ethylene signal receptor, which is named as *ETR1/2*, *ERS1/2* and *EIN4* in simulated Arabidopsis, and the ethylene molecule would bind to the receptor located on endoplasmic reticulum with the monovalent copper ions ( $\text{Cu}^+$ ), leading to inactivation of the cytoplasmic receptor and its downstream negatively regulated CTR1 complex. As the inactivated receptor CTR1 complex no longer phosphorylates its downstream positive regulator *EIN2*, *EIN2*, not degraded, activates the primary transcription factor *EIN3/EIL1* inside the nucleus in the ethylene signal transduction pathway. *EIN3/EIL1* then activates the expression of downstream target genes such as *ERF1*, *EBF1/2* and *HLS1* at the transcriptional level, and many downstream ethylene-responsive genes are activated at the transcriptional level, thereby producing a series of ethylene responses.

In recent years, as genetics, molecular biology and various other relevant disciplines have achieved rapid development, some new research has further enriched the linear model of ethylene signal transduction pathway, including pathway-related mitogen-activated protein kinase (MAPK), transcription feedback regulation, mRNA degradation and protein regulation mechanisms. The five ethylene receptors in Arabidopsis are all two-component systems, indicating that any one of them with a dominant mutation could decrease the sensitivity of plant ethylene, and any one of its receptors with gene deletion or mutations would be similar to the wild type (Ecker, 1995). It can be seen that the negatively regulated ethylene reaction of ethylene receptors has excessive functionality for its activity is maintained in the absence of ethylene or at a low concentration of ethylene and its activity is lost in the presence of ethylene. According to similarity of protein sequence and structure characteristics, ethylene receptors can be divided into two types: type I (*ETR1* and *ERS1*), which has three hydrophobic transmembrane structures at its N-terminus and a highly conserved histidine kinase structure at its C-terminus; type II (*ETR2*, *ERS2*, and *EIN4*), which has four hydrophobic transmembrane structures at its N-terminus, and a not so conserved histidine kinase structure at its C-terminus. Research results indicated these two types of receptors have functions that could complement each other but also are to a certain degree independent from each other (Ecker, 1995; Xiong et al., 2017; Alonso et al., 2003). Further biochemical tests showed that the ethylene receptor structure includes signal receptor structure at the N-terminus, histidine kinase structure at C-terminus and the reaction regulation structure, and the reaction regulation structure can be further divided into ethylene-binding substructure and GAF substructure. In the hydrophobic region at N-terminus, with the transport of P-type ATPase active protein-RAN1 (Response to antagonist 1), monovalent copper ions ( $\text{Cu}^+$ ), acting as a cofactor, bind to ethylene (Alonso et al., 1999). In addition, the membrane protein *RTE1* (Reversionto-ethylene sensitivity

1), conserved in an evolutionary term, whose transcriptional activity is regulated by ethylene, regulates ethylene reaction by interacting with ethylene receptors (Binder et al., 2010). *EIN2*, a positive regulator that first cloned in 1999, encodes a transmembrane protein made of 1294 amino acids (Bisson et al., 2009). Recent transient expression systems of tobacco leaves and transfer experiments of fluorescence resonance energy have confirmed that *EIN2* is located on the endoplasmic reticulum membrane, and its Ser 645 and Ser 924 sites at C-terminus are phosphorylated by CTR1 which cleaves and wanders into the nucleus, thereby activating the downstream ethylene signal transduction pathway. The latest study suggested that the C-terminus could also depress the ubiquitination of the core transcription factors of *EBF1/2*, including *EIN3/EIL1*, thus promoting their accumulation (Bisson et al., 2009; Binder et al., 2010). There are six *EIN3/EIL1* family members in simulated Arabidopsis, namely *EIN3* and *EIL1-5*. Plants overexpressing *EIN3* or *EIL1* demonstrated a constitutive ethylene response; the mutant *EIN3* or *EIL1* with incomplete functions showed partial ethylene insensitivity, while the double mutant *ein3 eil1* showed complete ethylene insensitivity, indicating functional redundancy between *EIN3* gene families (Resnick et al., 2006). As existing studies have shown, most biological processes related to the action mechanisms of ethylene could happen owing to the regulation of downstream target genes by transcription factors of *EIN3/EIL1*, many of which are involved in reactions such as ethylene reaction (Bisson et al., 2009), photomorphogenesis (Chao et al., 1997; Zhao and Guo, 2011; Zhong et al., 2012), root development (Malheiros et al., 2019), auxin synthesis and transport (He et al., 2011), cytokinin response (Shi et al., 2012), salicylic acid synthesis (Chen et al., 2009), cold stimulation (Shi et al., 2012), salt stress (Zhang et al., 2011) and so on. These studies indicate that the transcription factors of *EIN3/EIL1* have an important role in the ethylene signal transduction pathway and is more likely to be one of the important nodes in network regulation at the transcriptional level in plants.

#### 4. Ethylene synthesis and signal transduction pathways in Rice, maize and cotton

Except for taking ethylene as an important stress hormone produced in adverse circumstance, researchers have expanded their study on the stress resistances of ethylene in mechanical damage, drought, high salt and pathogen infection to field crops from the Linear Model of Signal Transduction Pathway based on the mutants of simulated ethylene reaction of Arabidopsis thaliana. And it is shown that the more intuitive phenotype of ethylene on the field crops is the change on the agronomic traits of the plant type. In terms of cotton, the laboratory of Professor Zhu Yuxian from Peking University (Gou et al., 2007; Qin et al., 2011; Wang et al., 2015) conducted in-depth research on the effect of ethylene on fiber elongation, and the results of the research showed that exogenous ethylene treatment can promote fiber elongation of the cotton, while the AVG, an inhibitor synthesized by ethylene, significantly suppressed its elongation. And studies based on chip technology also confirmed that ethylene synthesis-related genes were significantly increased during the elongation of upland cotton fibers during the first 5–10 days (Gou et al., 2007). Recent advances indicate that ethylene in cotton promotes elongation of fibers by increasing the expression of sucrose synthase, tubulin and patulin genes, and saturated ultralong-chain fatty acids can also promote elongation of cotton fibers, for the latter could activate the pathway of ethylene synthesis (Qin et al., 2011; Wang et al., 2015).

Rice (*Oryza sativa* L.) is a monocotyledonous plant different from the dicotyledonous plant Arabidopsis thaliana in both growth and development. It has a small size of genome of only 389 Mbp, with approximately 32,000 genes. Thanks to comparative geno-

mics and reverse genetics methods, genes related to ethylene synthesis and anabolism, including *ACS*, *ACO*, *SAM*, and *ETO* as well as the homologous genes of their receptors in the signal transduction pathway, such as *CTR1*, *EIN2*, *EIL* and *ERF* genes, have been identified (Jun et al., 2004; Watanabe et al., 2004). Among the genes identified in ethylene anabolism, *SAM* has five family members, with the function of the *SAM3-4* not well understood; the *ACS* family has six members, the *OsACS6* of which is considered to have less activity than *ACS* (Zarembinski and Theologis, 1997); the *ACO* family members have seven members and exert an influence at the transcriptional level; *OsACO5* can be up-regulated via exogenous ETH and GA, but down-regulated by exogenous ABA; *OsACO6* is considered to be a pseudogene (Ruduš et al., 2013); in the ethylene signal transduction pathway have been identified 5 genes of type I (*OsERS1* and *OsERS2*) and type II (*OsETR2*, *OsETR3* and *OsETR4*) (Jun et al., 2004). However, no ETR1 receptors were found in rice. Surprisingly, such receptors were not found in maize and wheat (Gallie and Young, 2004), either. And the implication in the biological sense has not yet been confirmed. Among the five receptors of rice, only the expression of *OsETR2* was significantly induced by endogenous and exogenous ethylene, and was up-regulated by flooding, indole-3lactic acid (IAA) and gibberellin (GA) which suggested that the receptor may be involved in the response of rice to hypoxia stress (Watanabe et al., 2004; Kuroha et al., 2018). The results of overexpression and gene knockout showed that *OsETR2* control the expression of *GI*, *RCN1* and *RAmy3D*, inducing ethylene to regulate the flower bud differentiation and starch accumulation in stems (Watanabe et al., 2004; Kuroha et al., 2018). The homologous gene of *EIN2* in the ethylene signal transduction pathway, *OsEIN2*, has been identified in rice, which is constitutively expressed in many tissues and organs of rice and the expression of which is not affected by exogenous ACC or Ag<sup>+</sup>. Rice with antisense gene *OsEIN2* has seedling with a slightly shorter height, which was consistent with the Ag<sup>+</sup>- treated wild-type phenotype that is, the *OsEIN2* antisense gene showed an ethylene-insensitive phenotype. Some scholars believed that *OsEIN2* is a positive regulator of rice ethylene response (Watanabe et al., 2004). In Arabidopsis, the *EIN2* mutant, owing to the loss of function, showed a strong fully ethylene-insensitive phenotype (Alonso et al., 2003; Binder et al., 2010). In comparison, the ethylene reaction phenotype of rice *OsEIN2* is weaker than that of Arabidopsis *EIN2*. Therefore, the exact function of *OsEIN2* to regulate ethylene reaction in rice needs to be further proved. Further studies revealed that there are three other homologous gene sequences of *EIN2* in the rice genome, which are located at Os07g06190, Os07g06300 and Os03g49400. Therefore, Ma et al. (2010) assumed that the weaker ethylene reaction phenotype of the above-mentioned *OsEIN2* antisense gene strain may be the result of functional redundancy between the members of the rice *EIN2* family, or it is also possible that there is an ethylene signal transduction pathway other than *EIN2* in rice. Six homologous genes of *EIL* in the ethylene signal transduction pathway have been found in rice, namely *OsEIL1-6* (Watanabe et al., 2004). Among them, *OsEIL1* has the highest homology with Arabidopsis thaliana *EIN3*. Previous studies have shown that *OsEIL1* may be involved in rice ethylene signal transduction and positively regulates rice ethylene reaction, but the role played by all homologous sequences in the ethylene signal transduction pathway of rice needs to be further verified. In addition, *RTE1*, *EBF*, *MHZ1* and transcription factors of *ERF* were identified or initially located, including *OsERF1*, *OsSub1A*, *OsSnorkel1* (*SK1*), *OsSnorkel2* (*SK2*), *OsEATB*, etc. And relevant experimental evidence indicates that these genes regulate plant formation including leaf type and stem extension (Hattori et al., 2009; Xu et al., 2006; Qi et al., 2011). Therefore, more sophisticated experiments to explain the molecular functions and genetic interactions would become the key to sort out ethylene synthesis, signal trans-

duction pathways and their action mechanisms in plant type formation in rice.

In the past 20 years, reports on ethylene synthesis, signal transduction pathways and their action mechanisms on plant type formation have been mostly covered regarding dicotyledonous plants, such as Arabidopsis thaliana and monocotyledonous plant rice. Comparatively, there is little relevant research targeting maize, the largest food crop here in the world. Maize is a diploid (ancient tetraploid) plant that originated from Mexico and Guatemala and evolved from teosintes, it has 2,500 Mbp genome, which equivalent to humans and 20 times of Arabidopsis and 6 times for rice. It is estimated that maize has more than 39,000 genes (Schnable et al., 2009). Compared with Arabidopsis and rice, there are relatively less gene correlation regarding ethylene anabolism in maize, and these genes are similar to rice in terms of quantity, structure and function prediction. Mu-transposon insertion test confirmed only 3 *ACS* genes and 4 *ACO* genes (Gallie and Young, 2004). There are two types of ethylene receptors identified in maize, namely type I (*ZmERS1a* and *ZmERS1b*) and type II (*ZmETR2a* and *ZmETR2b*), which is similar to the family of receptor types in rice, suggesting that in monocotyledonous plants, the structures of the ethylene receptors have shared features (Watanabe et al., 2004; Gallie and Young, 2004; Gallie, 2015). Recent research shows that the maize receptor gene is also highly conserved compared to that of Arabidopsis, and further experiments show that its function depends on the conservation of monovalent copper ion (Cu<sup>+</sup>) as a cofactor and ethylene binding site Cys6 (Chen and Gallie, 2010; Zdarska et al., 2019). The homologous genes of *EIN3*, *ERF3*, *EBF1*, *EBF2* and *EIN5* in maize in the ethylene signal transduction pathway have been cloned one after another and even patented (US 8,129,586 and US 8614368), and the ethylene signal transduction pathway in maize is predicted to be used to improve plant type regulation, stress tolerance and yield of various plants in the future.

## 5. Ethylene-regulated plant type formation in rice and maize

The plant type formation of higher plants consists of the occurrence of organs related to plant morphology during their whole growth cycle, especially the formation, shape and location of branches, leaves and flowers. The diversity of the morphological structures of plants depends on the number, formation time and development of phytomers made up by internodes, leaves and secondary meristems (McSteen and Leyser, 2005). The development of secondary meristems is influenced by intrinsic genetic factors, developmental stages and external environmental signals, such as light, temperature, humidity and planting density. The comprehensive regulation by these factors gives the plants developmental plasticity and adaptability to environment. The first green revolution was based on the improvement of the plant type: The large-scale cultivation and planting of semi-dwarf varieties of wheat and rice have greatly increased grain yield and prevented widespread famine in a timely fashion (Peng et al., 1999). Plant hormones are at the center of the network system consisting of many regulatory signals and play an important role in the plant type formation (Qi, 2011; Zhang et al., 2019). A number of studies have shown that IAA, GA, Brassinolide (BR), Cytokinin (CTK) have a promotional effects in assisting plant type formation such as *Lazy1*, *GAI*, *D8* and *BR11* while ethylene and abscisic acid (ABA) exert inhibitory effects (Xu and Xue, 2012).

A number of domestic and foreign studies have also reported that exogenous ethylene regulates the development of a variety of gramineous cereal crops such as rice, maize, wheat and oats to improve lodging resistance (Rajala and Peltonen-Sainio, 2002; Zhang et al., 2019). A large number of studies have shown that the elongation growth of rice coleoptiles is induced by ethylene,

which exerts the opposite effect in the triple reaction of *Arabidopsis thaliana* by inhibiting its hypocotyl elongation. A rice-specific ethylene reaction can also be used for the screening of ethylene-responsive mutants like in the triple reaction of *Arabidopsis thaliana* (Fukao and Bailey-Serres, 2008; Yamauchi et al., 2016). For semi-aquatic plants like rice, the existing research on the action mechanism of ethylene mostly focuses on the adaptation to a series of anoxic environments, such as coleoptile elongation, adventitious root development, aerenchymal tissue development and stalk elongation promoted to escape immersion (escape mechanism) or inhibition of stem elongation to tolerate immersion (tolerance mechanism) (Fukao and Bailey-Serres, 2008). Previous studies have shown that ethylene is the initial regulator of water-induced elongation growth (Jackson, 2007). Under flooding conditions, oxygen stress promotes the expression of *ACS1*, *ACS5*, *ACO1* and *ACO3* as well as *ARD1* (Acireductone dioxygenase 1) in Young's cycle, which increases the endogenous ethylene synthesis in the flooded tissues, and then induces the expression of *OsETR2* to activate the amplification of ethylene, thus regulating the interaction between GA and ABA and promoting cell division and elongation activity to resist hypoxic stress (Magneschi and Perata, 2009). Further experiments have also found that after treatment of internodes or seedlings of rice by ethylene or its precursor ACC, a similar flooding-induced elongation reaction could be initiated, and applying ethylene inhibitors such as  $Ag^+$  would inhibit elongation (Young, 2004). Recent reports also indicate that the ERF genes in the rice ethylene signal transduction pathway, including *OsSnorkel1* (*SK1*) and *OsSnorkel2* (*SK2*), respond to ethylene signaling-mediated rapid internode elongation in deep-water rice by GA response (Hattori et al., 2009). *OsSub1A*, the same ERF gene, by inhibiting the production of ethylene through negative feedback, mediates the immersion tolerance response of dryland rice (Xu et al., 2006). These studies have shown that the increase in ethylene in deep rice not only increases its sensitivity to GA, but also promotes the synthesis of GA. Besides, it also accelerates the degradation of ABA that antagonizes GA, thereby exacerbating GA's promotional effect on cell division and elongation. Qi et al. (2011) recently cloned *OsEATB* of AP2/ARF, a rice gene from Japonica rice 93–11. Ectopic expression experiments showed that overexpression of *OsEATB* reduced endogenous GA levels, and the interaction between ethylene it mediates and GA may be attributed for the differences in internode elongation. Further analysis of expression patterns indicated that the gene was also negatively regulated by ethylene, ABA and abiotic stress (Gao et al., 2017a). During internode elongation, *OsEATB* hindered gibberellin response induced by ethylene by down-regulating the expression of GA biosynthetic gene kauriense synthase A. *OsEATB* affects the plant yield by regulating plant type traits such as plant height and tiller number. Further experiments have confirmed that when rice matures, *OsEATB* reduces plant height and grain ear length but promotes the capability of plants to tiller and branch their spikelets (Gao et al., 2017b).

Research regarding maize type formation mediated by ethylene has mostly focused on production practices, owing to the fact that production quantity and area space of maize tops the charts among all food crops. For example, ethylene-based plant growth regulators such as ethephon, EDHA (the compound of ethephon and DA-6) and phosphonates (e.g. DHEAP), could be applied to control the plant height and ear position of maize so as to establish related agronomic traits to enhance lodging resistance and increase yield potential (Rajala and Peltonen-Sainio, 2002; Zhang et al., 2017; Wang et al., 2017; Wang et al., 2018; Amirian et al., 2019; Zhang et al., 2019). In recent years, there have been new advances in the ethylene-regulated formation of maize roots. Young et al. (2004) have shown that *ZmACS6* is an important regulator of maize root elongation in soil. Geisler-Lee et al. (2009) used quantitative RT-PCR and RNA in situ hybridization to detect the expression of

*ACO* gene in the root cell structures of maize root crown, native phloem screen, companion and epigenetic phloem screen, and that of *ACS* gene in maize root cap, cortex and cortical cells, and they further elucidated the mechanism of ethylene biosynthesis during the formation of aerenchyma in maize roots under 4% hypoxic conditions. Habben et al. (2014) conducted studies suggesting that the down-regulation of *ACS* limits the biosynthesis rate of ethylene, and further field evaluation experiments show that the highest transgenic results under this line of thought can increase maize yield by 580 kg/hm<sup>2</sup> under drought-featuring stress conditions.

## 6. Prospects

As an important stress hormone, ethylene's chemical nature, the enzymatic process of biosynthesis and the biological effects at traditional plant physiological levels have been accumulated. With the help of molecular genetics and biochemistry, the current research on the recognition and signal transduction pathway of ethylene is also in a rapid development stage (Lopez-Gonzalez et al., 2019). However, much remains unclear, with respect to the signal transduction pathways from *CTR1* to *EIN2* in different plant species, the relationship between the MAPK pathway and the ethylene pathway, whether or not *EBF1/2* and *EIN3/EIL1* maintain an unobstructed ethylene pathway under different physiological conditions and in different tissues and thus exert biological effects. Similar doubts are also seen in pattern plants like *Arabidopsis*. In addition, many transcriptional regulators of all hormones, including DELLA proteins and JAZ (An et al., 2012), can inhibit the transcriptional activity of *EIN3/EIL1*, which indicates the complexity of the synergy between ethylene and other hormones (Merchante et al., 2013).

Previous studies have clearly shown that ethylene plays an important regulatory role in plant type formation, which is achieved at least via indirect hormone interaction. However, at present, understanding of ethylene synthesis and its signal transduction pathways in plant type formation has mainly been derived from research on *Arabidopsis thaliana*, a type of dicotyledonous plant. In monocotyledonous plants, especially those represented by gramineous crops, direct experimental evidence is still relatively insufficient. To date, research on rice is currently at a rapid development stage, and has gradually progressed from the physiological level, including lodging resistance and stress tolerance to the molecular mechanism of stem type and leaf elongation. Further, the research on maize and wheat mainly focuses on the mechanism of underground root structure formation, as it is likely that the differences between long-term artificial selection and evolutionary mechanism have rendered the existing genome larger and more complex (Rajala and Peltonen-Sainio, 2002; Geisler-Lee et al., 2009; Habben et al., 2014; Zhang et al., 2019). The revelation here is that on the one hand, the action mechanism of core components of ethylene synthesis and signal transduction pathway is sophisticated and could be varied in different crop plant types; on the other hand, comparative genomics studies have shown that different species have formed after many years of evolution the collinearity of gene sequences, rendering many signal transduction pathways and functional genes genetically conserved, which has also been validated by the recent research on the formation of maize plant types in previous studies. Therefore, an in-depth exploration into ethylene-regulated plant type formation of maize and rice and the environmental adaptability-related gene loci, designed to clarify the action mechanism at the molecular level, will help accelerate the realization of the "second green revolution", further enhancing the potential of crop yield, and provide a strong theoretical support and scientific basis for the cultivation of crops with high resistance to high density and adversity and the cultivation of ideal plant types.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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