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·专题论坛·

# 水稻中乙烯生物合成关键酶OsACS和OsACO调控机制研究进展

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**摘要** 乙烯在调控水稻(*Oryza sativa*)生长发育及胁迫响应中具有重要作用。乙烯生物合成的第1步是甲硫氨酸转化为*S*-腺苷甲硫氨酸(SAM), 然后在ACC合酶(ACS)的催化下合成乙烯前体物质ACC, 最后通过ACC氧化酶(ACO)生成乙烯。该文综述了水稻乙烯生物合成途径中2个关键酶OsACS和OsACO在转录及翻译后的调控机制, 提出了一些未解决的问题, 并展望了未来的研究方向, 以期加深人们对乙烯生物合成复杂机制的理解。

**关键词** 乙烯, 生物合成, ACS, ACO, 调控机制, 水稻

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水稻(*Oryza sativa*)是世界上最重要的粮食作物之一, 其产量和生产力极易受到各种生物及非生物胁迫的显著影响(袁明等, 2014)。作为一种气态植物内源激素, 乙烯在水稻生长发育及胁迫响应中均发挥重要调控作用。在不同生长阶段及环境下, 水稻的乙烯释放量会发生变化, 以调控其自身的生理过程以应对环境胁迫。由于ACS和ACO是催化乙烯生物合成的关键酶, 因此揭示OsACS和OsACO的调控机制对于精细调节水稻体内乙烯的生物合成, 进而提高水稻生产力及抗逆性均具有重要的科学意义和应用价值。本文对水稻*OsACS*和*OsACO*基因家族进行了系统总结和分类, 并重点论述两者在转录水平和翻译后水平的调控机制。

## 1 水稻中乙烯生物合成通路

在高等植物中, 乙烯的生物合成通路已得到阐明(图1)。简单来说, 乙烯的生物合成始于甲硫氨酸(methionine, Met), Met在*S*-腺苷甲硫氨酸(*S*-adenosyl methionine, SAM)合成酶(SAM synthetase, SAMS)的作用下合成SAM。然后在1-甲基环丙烷-1-羧酸(1-aminocyclopropane-1-carboxylic acid, ACC)合酶(ACC synthase, ACS)的作用下合成ACC和副产物5′-甲硫基腺苷(5′-methylthioadenosine, MTA), 这是乙烯合成的主要限速步骤, 且ACS被认为是关键限速酶(Tsuchisaka and Theologis, 2004; Lee et al., 2017)。最后, ACC被ACC氧化酶(ACC oxidase, ACO)氧化, 生成乙烯、$CO_2$和氰化物。同时, 副产物MTA通过杨氏循环(Yang cycle)重新转化为甲硫氨酸, 以确保乙烯生物合成的持续进行, 且不需要合成新的甲硫氨酸(Zhou et al., 2020; Park et al., 2021)。基于水稻OsACS和OsACO与拟南芥序列的相似性及其功能验证, 可知水稻中乙烯合成途径具有一定的保守性(Zhou et al., 2020)。目前在水稻中已鉴定出多个乙烯合成通路基因, 其中多数研究集中在关键酶OsACS和OsACO上。

### 1.1 水稻*OsACS*基因家族

ACS是一种磷酸吡哆醛(pyrodoxal-5′-phosphate, PLP)依赖酶, 由于其是催化乙烯生物合成过程中的

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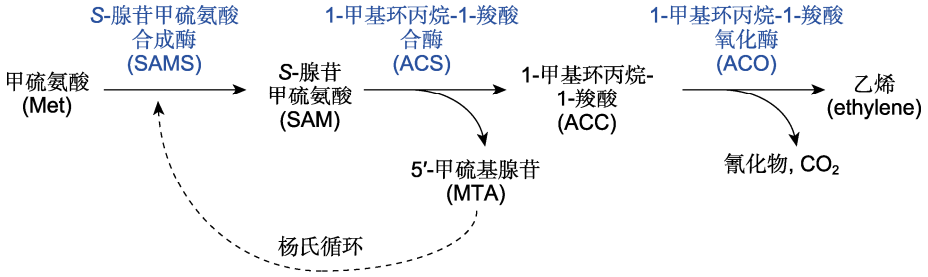


**图1** 乙烯生物合成途径(参考Park et al., 2021)

**Figure 1** Ethylene biosynthesis pathway (refer to Park et al., 2021)

关键限速酶，因此大多数关于乙烯合成调控的研究都集中在该酶上(Argueso et al., 2007)。在拟南芥中，根据蛋白质C端调控序列的特征，可将*ACS*家族分为3种不同的亚型，即Type I、Type II和Type III (Pattyn et al., 2021)。每种亚型的ACS蛋白由较短的N端、保守的催化结构域及含有调控序列的C端组成(Yoon, 2015)。Type I型ACS蛋白具有最长的C端结构域，包含1个钙依赖蛋白激酶(calcium-dependent protein kinase, CDPK)磷酸化位点和3个丝裂原活化蛋白激酶(mitogen-activated protein kinase, MAPK)磷酸化位点。Type II型ACS蛋白的C端有1个CDPK磷酸化位点和1个TOE (Target of ETO1)位点。其中, TOE是E3连接酶ETO1 (ETHYLENE OVERPRODUCER 1)及其2个同源物(EOL1和EOL2)的结合位点(Wang et al., 2004)。ETO1及EOL1/2通过TOE结构与Type II型AtACS蛋白特异性互作，导致其被26S蛋白酶体降解(Yoshida et al., 2005; Christians et al., 2009)。相反，Type III型蛋白的N端能够被环型E3连接酶XBAT32泛素化，随后被26S蛋白酶体降解，其C端的调控机制尚未见报道(Lyzenga et al., 2012)。水稻*OsACS*是多基因家族(Booker and DeLong, 2015)，目前在水稻基因组中共发现了6个*OsACS*基因(Iwai et al., 2006)，包括*OsACS1* (*Os03g0727600*)、*OsACS2* (*Os04g0578000*)、*OsACS3* (*Os05g0196600*)、*OsACS4* (*Os05g0319200*)、*OsACS5* (*Os01g0192900*)和*OsACS6* (*Os06g0130400*)。进化分析显示, OsACS6与拟南芥(*Arabidopsis thaliana*) AtACS10和AtACS12的序列相似度很高，推测其可能具有氨基转移酶活性，而不具有ACC合酶活性，其余5个OsACSs均具有ACS活性(Matsushima et al., 2016)。通过构建拟南芥、大麦(*Hordeum vulgare*)、番茄(*Solanum lycopersicum*)与水稻ACS蛋白的系统发生树，对比拟南芥与水稻ACS蛋白结构域，可将水稻*OsACS*家族分为3种亚型，即Type I–III (图2, 图3)。OsACS2与拟南芥Type I型AtACS的蛋白结构相似，在所有OsACSs中具有最长的C端结构域。OsACS1与拟南芥Type II型ACS的结构相关性较高，虽然其TOE序列与拟南芥及番茄典型的Type II型ACS上的TOE序列有所不同(图4)，但Yoshida等(2006)将OsACS1的C端16个氨基酸残基(包含TOE序列)与GFP进行融合，构成GFP-TOE$^{OsACS1}$转入水稻愈伤组织，发现其GFP荧光强度比对照(GFP空载)显著减弱，表明TOE$^{OsACS1}$能够被水稻内源OsEOLs靶向降解，推测OsACS1的TOE序列与拟南芥及番茄的Type II型ACS的TOE序列具有功能保守性。此外，OsACS3、OsACS4和OsACS5与拟南芥Type III型ACS蛋白相似，其C端较短，目前还未在其C端发现已知的调控结构域(Lee and Yoon, 2018)。

### 1.2 水稻*OsACO*基因家族

ACO是非血红素含铁蛋白质，属于2-酮戊二酸依赖的双加氧酶(2OGD)超家族成员。其以$Fe^{2+}$为辅助因子，需要共底物2-酮戊二酸介导分子氧的活化来氧化底物，且其含有9个保守的氨基酸残基(Kawai et al., 2014)。在水稻中，*OsACO*是多基因家族，目前已在水稻基因组中发现了7个*OsACO*基因，包括*OsACO1* (*Os09g0451400*)、*OsACO2* (*Os09g0451000*)、*OsACO3* (*Os02g0771600*)、*OsACO4* (*Os11g0186900*)、*OsACO5* (*Os05g0149400*)、*OsACO6* (*Os05g0149300*)和*OsACO7* (*Os01g0580500*)。有趣的是，不同于其它物种的*ACO*基因，大多数水稻的*OsACO*s基因结构并不是典型的4个外显子结构(Ou-

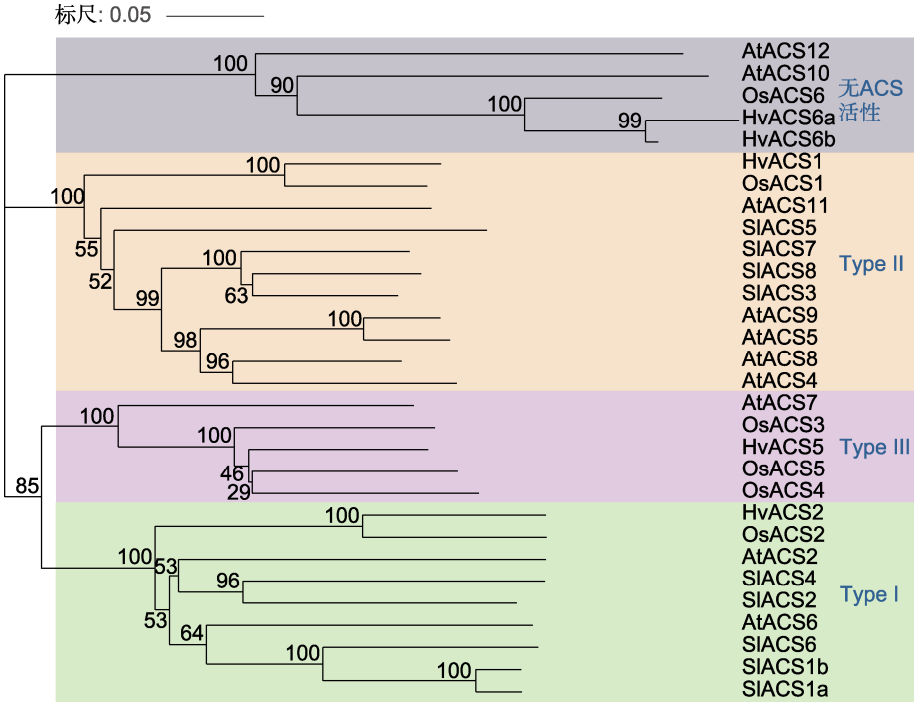


**图2** 水稻(Os)、大麦(Hv)、拟南芥(At)和番茄(Sl) 1-甲基环丙烷-1-羧酸合酶(ACS)蛋白序列的系统发生树

**Figure 2** Phylogenetic tree of the ACC synthase (ACS) protein sequences of *Oryza sativa* (Os), *Hordeum vulgare* (Hv), *Arabidopsis thaliana* (At) and *Solanum lycopersicum* (Sl)

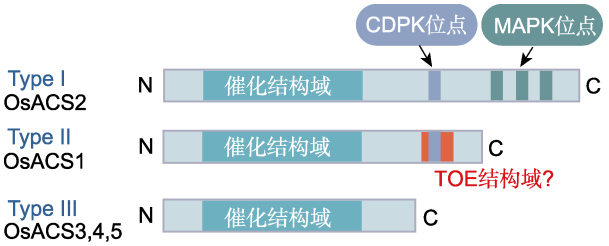


**图3** 水稻3种亚型的ACS蛋白结构(参考Lee and Yoon, 2018)
CDPK: 钙依赖蛋白激酶; MAPK: 丝裂原活化蛋白激酶。ACS同图2。

**Figure 3** The structure of three types of ACS proteins in rice (refer to Lee and Yoon, 2018)
CDPK: Calcium-dependent protein kinase; MAPK: Mitogen-activated protein kinase. ACS is the same as shown in Figure 2.

| | | | |
|---|---|---|---|
| OsACS1/462-487 | 462 | RSVSCPLAIKWALRLTPSIADRKAER | 487 |
| SlACS7/447-465 | 447 | KKK---SFSKWVFRLSFNERQR---- | 465 |
| SlACS3/449-469 | 449 | KKK---SFSKWVFRLSFNDRQRER-- | 469 |
| SlACS8/453-471 | 453 | KKK---LFAKWGFRLSFNDRER---- | 471 |
| AtACS5/449-470 | 449 | RKK---TVSNWVFRVSWTDRVPDER- | 470 |
| AtACS9/449-470 | 449 | RKR---TVSNWVFRVSWTDRVPDER- | 470 |
| AtACS4/450-474 | 450 | RKKTMSNVSNWVFRLSFHDREAEER- | 474 |
| AtACS8/448-469 | 448 | RKM---KVSNWVFRLSFHDREPEER- | 469 |

**图4** 水稻(Os)、拟南芥(At)和番茄(Sl)中Type II型ACS的C端氨基酸序列比对
基本不变的TOE基序结构WVFRLSF/W序列标为红色, OsACS1中可能存在的保守TOE基序用红色方框标出。ACS同图2。

**Figure 4** Sequence alignment of C-terminal amino acids of Type II ACSs from *Oryza sativa* (Os), *Arabidopsis thaliana* (At) and *Solanum lycopersicum* (Sl)
The near invariant TOE motif sequence WVFRLSF/W are shown in red, while the possible conserved TOE motif in OsACS1 is marked with red box. ACS is the same as shown in Figure 2.

yang et al., 2007)。Iwai等(2006)通过序列比对, 发现*OsACO6*是编码截短ACO蛋白的假基因, OsACO4缺少ACO蛋白家族保守的A30和H42残基, OsACO5缺少保守的A30残基, 推测这3个OsACO蛋白可能不行使功能, 但有待进一步验证。通过比对OsACOs氨基酸全长序列可将其分为Type I–III三个亚型(Houben and Van de Poel, 2019), 每个亚型的RXS motif含有不同的X残基, 恰好对应3个不同的亚型。OsACO1、OsACO2和OsACO3属于I型, 其RXS motif为R-M-S序列; OsACO7属于II型, 为R-L/I-S序列; OsACO4和OsACO5属于III型, 为R-R-S序列(图5–图7)。其中, R244和S246是RXS motif中高度保守的2个残基, 对ACC的结合及ACO酶的催化活性具有重要作用(Dilley et al., 2013)。关于3种亚型的ACOs在功能上(如酶活性及蛋白稳定性)是否存在差异仍缺乏相关生

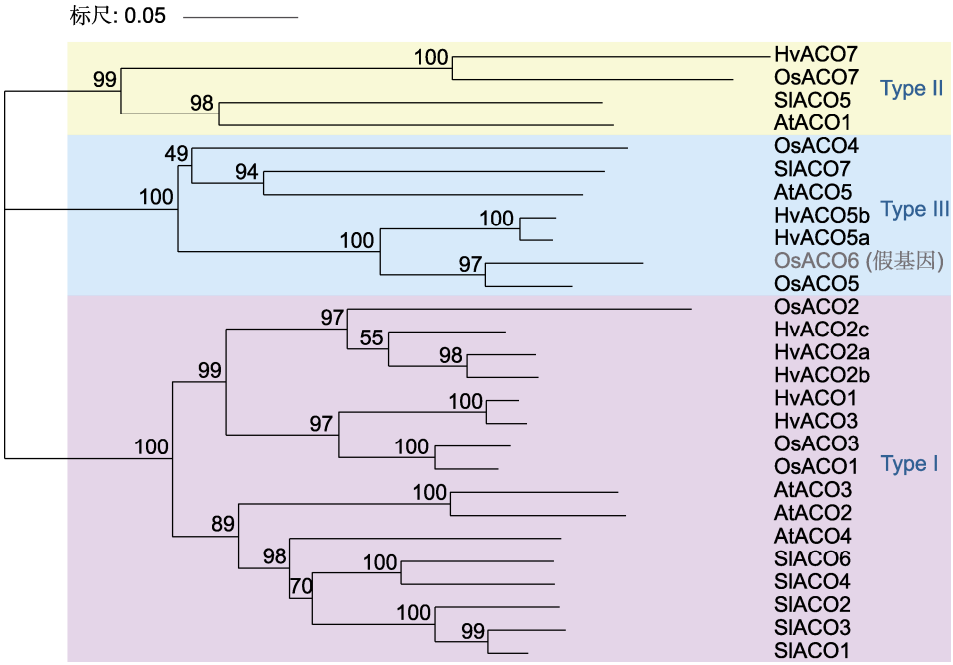


**图5** 水稻(Os)、大麦(Hv)、拟南芥(At)和番茄(Sl) 1-甲基环丙烷-1-羧酸氧化酶(ACO)蛋白序列的系统发生树

**Figure 5** Phylogenetic tree for ACC oxidase (ACO) protein sequences of *Oryza sativa* (Os), *Hordeum vulgare* (Hv), *Arabidopsis thaliana* (At) and *Solanum lycopersicum* (Sl)

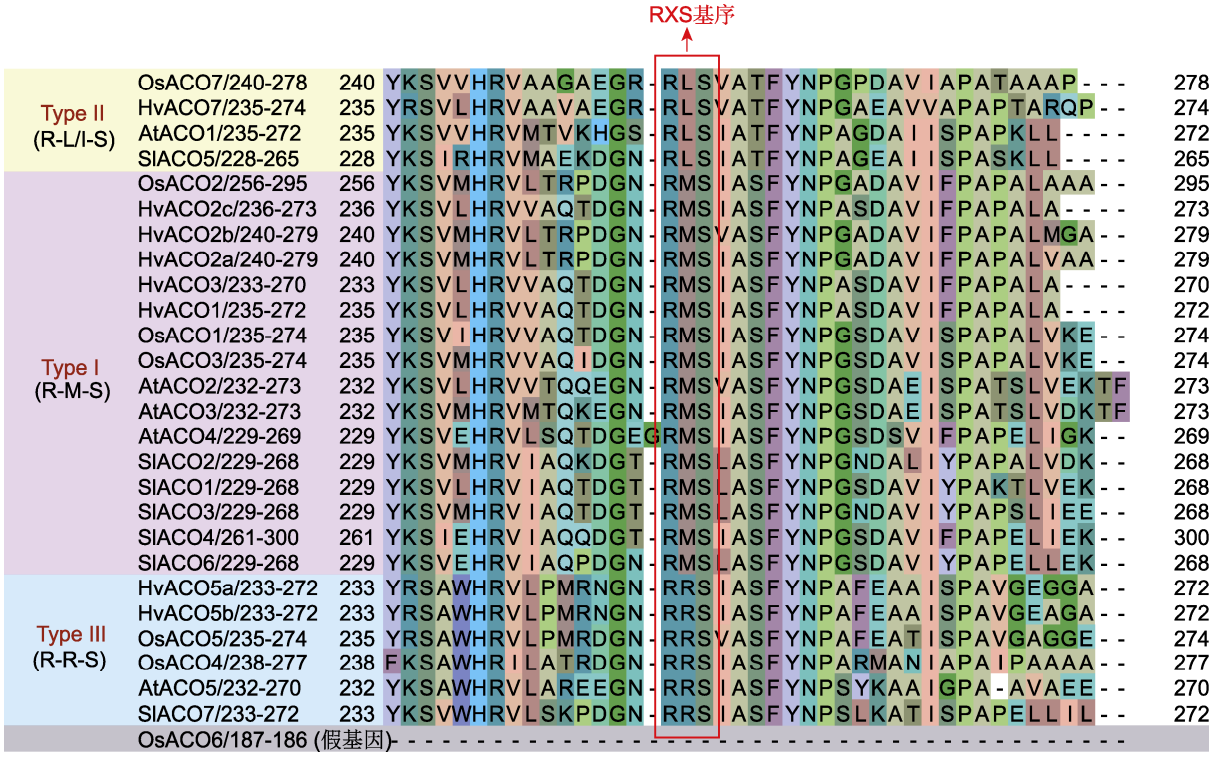


**图6** 水稻(Os)、大麦(Hv)、拟南芥(At)和番茄(Sl) ACO蛋白序列比对
ACO同图5。

**Figure 6** ACO protein sequence alignment of *Oryza sativa* (Os), *Hordeum vulgare* (Hv), *Arabidopsis thaliana* (At) and *Solanum lycopersicum* (Sl)
ACO is the same as shown in Figure 5.

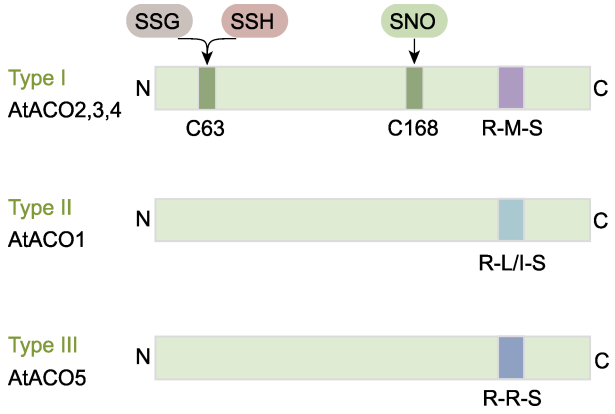


**图7** 拟南芥3种亚型的ACO蛋白结构(参考Pattyn et al., 2021)
C63位点的翻译后修饰包括*S*-谷胱甘肽化(SSG)和*S*-硫巯基化(SSH); C168位点的修饰包括*S*-亚硝基化(SNO)。ACO同图5。

**Figure 7** The structure of three types of ACO proteins in *Arabidopsis thaliana* (refer to Pattyn et al., 2021)
Post-translational modifications at C63 include *S*-glutathionylation (SSG) and *S*-sulfhydration (SSH), while modifications at C168 involve *S*-nitrosylation (SNO). ACO is the same as shown in Figure 5.

理生化及遗传学证据，有待进一步探索(Houben and Van de Poel, 2019)。

在拟南芥中，已发现AtACO2含有2个保守的半胱氨酸残基C63和C168，可能与翻译后修饰有关。AtACO2的C63位点能够被*S*-谷胱甘肽化(*S*-glutathionylation, SSG)修饰 (Datta et al., 2015), C168位点能够被*S*-亚硝基化(*S*-nitrosylation, SNO) (Hu et al., 2015)。此外，与AtACO2同属Type I型的AtACO4存在*S*-硫巯基化(*S*-sulfhydration, SSH)修饰(Aroca et al., 2017)。基于番茄SlACO1和SlACO2已证实C60是SSH修饰位点(Jia et al., 2018)。通过对拟南芥AtACO2、AtACO4与番茄SlACO1和SlACO2进行蛋白序列比对，推测拟南芥Type I型AtACO (以AtACO2为例)的C63可能是SSH修饰的潜在位点(图7)。因此，基于已知的拟南芥Type I型AtACOs翻译后修饰位点(图7)，我们进一步将水稻OsACOs与拟南芥AtACO2进行蛋白序列比对，发现水稻OsACOs的C63位点与拟南芥的保守性较低，但C168位点与拟南芥的保守性较高(图8)，推测其可能是SNO修饰的潜在位点，有待进一步实验验证。

## 2 水稻OsACS调控机制

### 2.1 水稻OsACS转录水平调控

水稻*OsACSs*基因的转录水平受多种转录因子调控。Yoon等(2020)通过ChIP分析发现，锌指同源(ZF-HD)蛋白家族中的OsZHD2直接与*OsACS5*的启动子区域结合并激活其转录，从而诱导乙烯的生物合成。Zhang等(2013)发现转录抑制因子OsERF3依赖其C

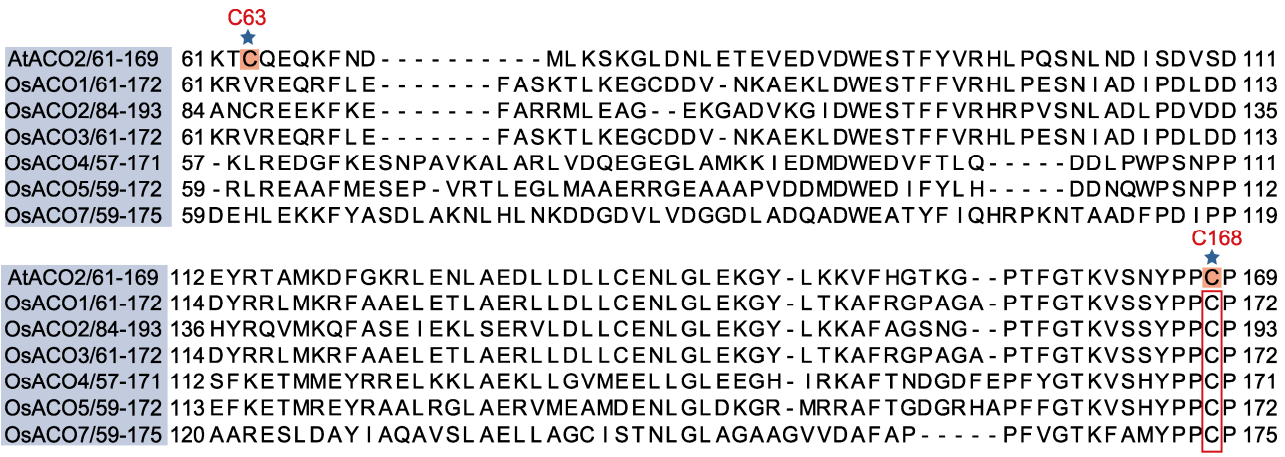


**图8** AtACO2与OsACOs蛋白序列比对
蓝色星号表示拟南芥AtACO2中2个保守的半胱氨酸残基位点C63和C168; 红色方框表示水稻OsACOs与拟南芥保守的半胱氨酸残基位点为C168。

**Figure 8** AtACO2 and OsACOs protein sequence alignment
The blue stars represent the two conserved cysteine residue sites (C63 and C168) in AtACO2, and red box indicates the conserved cysteine residues (C168) of the OsACOs.

端的保守结构EAR-motif (DLNRPPP)负调控*OsACS2*和*OsACS6*的表达，抑制乙烯合成，从而负调控水稻在苗期及分蘖期的抗旱能力。DOF (DNA-binding with one finger)蛋白是植物转录因子中的主要家族之一。水稻OsDOF15转录因子能够识别并结合*OsACS1*启动子区域的AAAG基序从而抑制其转录，负调控水稻中乙烯生物合成，促进水稻主根伸长(Qin et al., 2019)。因此，上述转录因子通过调控*OsACSs*基因的转录水平来影响乙烯的生物合成，进而调控水稻生长发育及胁迫响应相关的生理过程。

### 2.2 水稻OsACS翻译后水平调控

ACS蛋白翻译后水平调控在拟南芥中已得到较深入的研究，其中磷酸化和26S蛋白酶体介导的泛素化是2种重要的调控方式。磷酸化对Type I和Type II型ACS蛋白均具有调控作用。例如，拟南芥MPK3/MPK6通过磷酸化Type I型ACS蛋白(AtACS2/6)的C端增强其稳定性，保护AtACS2/6不被26S蛋白酶体降解，从而促进乙烯的合成(Joo et al., 2008; Han et al., 2010)。相反，脱落酸信号通路负调控元件ABI1(磷酸酶PP2C)与AtACS6互作，使其C端去磷酸化而导致活性下降，且负调控MPK6的活性进而影响其下游底物ACS6的稳定性(Ludwików et al., 2014)。此外，重金属Cd胁迫会降低拟南芥磷酸酶PP2A的活性，减弱对ACS6的去磷酸化作用，增强ACS6的稳定性，导致乙烯合成增加，从而抑制植物的生长(Chen et al., 2020)。在水稻中，Li等(2014)发现盐胁迫可诱导凝集素类受体激酶SIT1，并激活其下游MPK3/MPK6信号级联反应，从而促进乙烯的释放，同时发现*OsACS2*的表达显著上调，推测水稻SIT1-MPK3/6级联可能也通过类似拟南芥MKK9-MPK3/6稳定AtACS2/ACS6的机制来提高OsACS的活性以促进乙烯的合成。在拟南芥中，Type II型ACS蛋白含有1个E3泛素连接酶结合位点TOE，酪蛋白激酶CK1.8通过磷酸化TOE结构中的T463位点促进AtACS5与E3泛素连接酶ETO1的相互作用，以加速AtACS5的降解(Tan and Xue, 2014)。此外，拟南芥14-3-3蛋白也通过依赖磷酸化的方式与其它蛋白互作，从而参与调控ACS的稳定性(Freeman and Morrison, 2011)。例如，拟南芥14-3-3蛋白不仅直接与ACS5互作维持ACS5的稳定性，而且与ETO1/EOLs互作使其降解，进而正调控ACS5蛋白活性(Yoon and Kieber, 2013a)。近年来，研究发现拟南芥ACS5蛋白发挥支架作用(scaffold)，连接E3连接酶SINAT (SEVEN-IN-ABSENTIA)与EOL2形成复合体，通过促进这2个E3连接酶相互降解来维持ACS5的稳定性，且BR信号能促进SLNAT上T147位点发生磷酸化，从而招募14-3-3蛋白进一步促进SINAT与EOL2的相互降解以增加ACS5蛋白的积累(Lee et al., 2021)。在水稻中，通过酵母双杂交实验可观察到14-3-3蛋白(OsGF14s)与OsACS1互作，推测Type I和Type II家族OsACS的C端RXSX基序可能是14-3-3的直接结合位点，暗示在水稻中14-3-3可能通过与OsACS结合阻碍ETO1对ACS靶向降解/ACS去磷酸化，具有稳定ACS活性进而促进乙烯合成的作用(Yao et al., 2007)。

泛素化主要对Type II型ACS蛋白起调控作用。拟南芥Type II型ACS蛋白的TOE位点能够被E3连接酶AtETO1 (或其同源蛋白AtEOL1/2)靶向结合，导致AtACS5泛素化修饰后被26S蛋白酶体识别并降解(Wang et al., 2004)。研究发现，外界环境因素(如光照)能够调控ETO1/EOLs蛋白活性，通过降解ETO1/EOLs快速提高ACS5的稳定性(Yoon and Kieber, 2013b)。在水稻中也鉴定到其同源基因*OsETOL1* (*ETHYLENE OVERPRODUCER 1-like*)，与拟南芥相似，*OsETOL1*对水稻中ACC的积累与乙烯的合成起负调控作用(Du et al., 2014)。但不同于拟南芥AtETO1/EOLs对Type II型AtACS的调控，实验证实OsETOL1直接与水稻Type I型OsACS2互作，且过表达*OsETOL1*呈现出与*osacs2*突变体相似的缺陷表型(乙烯释放量降低、抗旱性减弱及育性下降)，推测OsETOL1可能抑制OsACS2的活性，但其具体分子机制及与拟南芥的调控差异尚待进一步研究(Du et al., 2014)。此外，用外源细胞分裂素(cytokinin, CTK)处理拟南芥能从翻译后水平阻断ACS5蛋白被靶向降解进而增强其稳定性，促进乙烯的合成(Chae et al., 2003)。在水稻中发现外源CTK处理能提高乙烯的释放量，但并未影响*OsACSs*基因的表达水平，推测水稻中也存在CTK对OsACS蛋白的翻译后调控，但其调控机制是否与拟南芥相同值得深入探究(Lee and Yoon, 2018)。

拟南芥Type III型ACS蛋白AtACS7的C端无已知调控结构域，但其N端仍能被E3连接酶XBAT32靶向

结合, 从而使其泛素化修饰后被26S蛋白酶体降解(Xiong et al., 2014)。相比拟南芥, 水稻中Type III型ACS含量较高, 其C端结构也与拟南芥相似, 长度较短且无已知的调控位点(Lee and Yoon, 2018)。有关水稻Type III型OsACS蛋白的翻译后调控机制仍有待深入研究。

## 3 水稻OsACO调控机制

### 3.1 水稻OsACO转录水平调控

目前, 已在植物中发现部分转录因子家族调控ACO的表达。在拟南芥中, WRKY家族的转录激活因子WRKY29能够识别并结合*AtACO5*启动子区的保守结构域W-box (TTGAC(C/T)), 从而激活*AtACO5*的表达(Wang et al., 2023)。NAC家族的III类转录因子SHYG (SPEEDY HYPONASTIC GROWTH)能够与*AtACO5*的启动子结合, 激活其转录(Rauf et al., 2013)。近年来, 也有研究表明, 水稻中NAC转录因子家族在调控ACO转录水平上发挥重要作用。Yu等(2021)通过ChIP技术及酵母单杂交实验证实, 转录因子OsNAC2能够直接与*OsACO3*的启动子结合, 促进乙烯的生物合成。此外, 转录因子OsBIHD1含有植物抗性基因*Pik-H4*的同源结构域, 通过直接与*OsACO3*启动子结合的方式上调*OsACO3*的表达水平, 激活乙烯依赖防御途径(Liu et al., 2017)。*OsACO1*的启动子区域含有GCC box (AGCCGCC), OsEBL1可能与该位点结合从而激活其转录(Iwamoto and Takano, 2011)。除转录因子外, 非编码RNA对水稻ACO的转录调控也具有重要作用。Ahmadizadeh等(2020)利用软件预测水稻中osa-miR5809和osa-miR531可能与OsACOs靶向结合, 从而抑制其转录, 但仍需通过实验进一步验证其调控功能。

### 3.2 水稻OsACO翻译后水平调控

目前, 关于植物中ACO蛋白翻译后水平调控的研究较少。研究表明, NatB介导的ACO2蛋白N端的乙酰化修饰(N-terminal acetylation, NTA)可增强拟南芥AtACO2的稳定性, 从而促进乙烯合成(Liu et al., 2021)。前文已总结了拟南芥AtACO半胱氨酸(Cys)残基通过特异性氧化还原进行翻译后修饰的相关研究。AtACO2的C63位点发生*S*-谷胱甘肽化(SSG)修饰(Datta et al., 2015), 其C168位点发生*S*-亚硝基化(SNO)修饰(Hu et al., 2015)。但这些翻译后修饰对AtACO蛋白的稳定性及活性的影响有待深入研究。近期, 在番茄中发现SlACOh4 (ACO homolog 4)的C172位点也能被*S*-亚硝基化并提高其活性, 从而促进乙烯合成以维持植物体内$K^+/Na^+$稳态, 进而提高耐盐性(Liu et al., 2023)。在水稻中, 对于OsACO翻译后调控机制仍知之甚少。鉴于水稻中C168位点与拟南芥的保守性较高(图7), 推测其可能是潜在的SNO修饰位点, 可作为后续深入研究的切入点。

## 4 研究展望

在高等植物中, 乙烯的生物合成途径虽然较为简单, 但其调控机制极为复杂, 受到包括转录及翻译后水平多个层次的调控。虽然在拟南芥中对乙烯合成的调控机制已有广泛的研究并取得了显著进展, 但是在水稻中的研究却相对有限。ACS作为乙烯合成通路的关键限速酶, 对其在转录以及翻译后调控的研究较为深入。Ahmadizadeh等(2020)通过生物信息学分析, 发现水稻ACS蛋白存在糖基化位点, 这可能作为一种新的翻译后修饰方式, 有待进一步研究; 而绝大多数ACO蛋白无糖基化位点, 磷酸化位点也较少, 其磷酸化程度低于ACS蛋白, 因此关于ACO的翻译后修饰方式仍需进一步探索。鉴于在水稻中构建的*osetol1*突变体可过量积累ACC进而促进乙烯的释放, 后续可考虑以*osetol1*突变体为材料, 通过正向遗传学手段(如EMS诱变)筛选出乙烯合成缺失突变体, 基于其本身可稳定ACS酶活性以维持ACC含量处于较高水平, 将更容易筛选出调控ACC转化为乙烯的关键酶OsACO的关键基因。近年来, 研究发现乙烯前体物质ACC也可以作为独立于乙烯的信号分子参与调控多种生理过程。例如, 在高等植物中, ACC能够独立调控拟南芥根细胞壁代谢(Xu, 2008)、早期营养器官生长(Vanderstraeten et al., 2019)、气孔发育(Yin et al., 2019)以及胚珠对花粉管的吸引(Mou et al., 2020); 调控番茄花粉管伸长(Althiab-Almasaud et al., 2021)及抗病(Tsolakidou et al., 2019); 在低等植物中, ACC能够独立调控苔类植物*Riella helicophylla*的芽孢柱细胞伸长(Stange and Osborne, 1989)和水生红藻植物*Pyropia yezoensis*的生殖器官发育(Uji et al.,

2020), 以及抑制地钱(*Marchantia polymorpha*)叶状体及芽孢的生长(Li et al., 2020)。因此, ACS作为催化ACC合成的酶, 对其调控机制的研究不仅拓宽了对乙烯合成通路的认识, 而且能够推动ACC作为独立于乙烯的信号分子研究取得更多成果。此外, Van de Poel等(2012, 2014a, 2014b)发现在番茄特定的生长发育阶段, ACO也作为乙烯合成的关键限速酶调控乙烯合成。这说明ACO的调控机制可能比预期更复杂。目前, 我们对于水稻OsACS和OsACO调控机制的认识仍是冰山一角。鉴于乙烯对水稻生长发育及逆境响应等生理过程起重要作用, 故对这2种关键酶的调控机制进行深入研究具有重要科学意义及应用价值。

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# Research Progress on the Regulatory Mechanisms of OsACS and OsACO in Rice Ethylene Biosynthesis

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**Abstract** Ethylene plays a pivotal role in regulating the growth, development and stress responses of rice (*Oryza sativa*). The first step of ethylene biosynthesis is the conversion of methionine to SAM, followed by the synthesis of the ethylene precursor ACC under the catalysis of ACC synthase, which is ultimately converted to ethylene by ACC oxidase. In this review, we provide an overview of the latest research progress, especially focusing on the transcriptional and post-translational regulatory mechanisms of two key enzymes involved in the rice ethylene biosynthesis pathway, OsACS and OsACO. Finally, we present several unsolved questions and insights into future research directions to enhance our understanding of the complex mechanism of ethylene biosynthesis.

**Key words** ethylene, biosynthesis, 1-aminocyclopropane-1-carboxylate synthase (ACS), 1-aminocyclopropane-1-carboxylate oxidase (ACO), regulatory mechanism, *Oryza sativa*

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杭州师范大学生命与环境科学学院薛大伟课题组主要从事植物抗逆、植物与环境互作、植物激素合成及信号转导的分子机理研究，目前在植物响应非生物胁迫的基因功能及分子机制等相关研究领域取得了一定成果。该团队利用遗传学、分子生物学、细胞生物学和生物信息学等手段筛选出多个调控植物胁迫响应相关基因。研究成果发表在*Nature Genetics*、*Nature Communications*、*Plant Biotechnology Journal*及*Plant Cell and Environment*等国际著名学术期刊上。