

茉莉酸甲酯诱导保卫细胞气孔关闭的信号转导机制

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摘要 气孔是由植物器官表面成对的保卫细胞围成的小孔, 气孔运动控制气体交换, 与植物逆境应答和生长发育等生物学过程密切相关, 受多种因子调控, 茉莉酸甲酯(MeJA)是其中之一。与ABA类似, MeJA也可诱导气孔关闭, 但是其机理尚不清楚。该文综述了近年来MeJA调控气孔运动的信号转导机制进展, 包括Ca²⁺、胞质pH、活性氧和NO等第二信使对气孔开闭的影响以及COI1、JAR1、RCN1和TGG1/2等信号组分之间的调控关系, 并讨论了保卫细胞中MeJA与ABA信号途径的相互作用。

关键词 茉莉酸甲酯; 保卫细胞; 气孔关闭; 信号转导; 脱落酸

Signal Transduction Mechanism of Stomatal Closure Stimulated by Methyl Jasmonate in Guard Cells

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Abstract Stomata are small pores on the plant surface, bounded by pairs of guard cells. Stomatal movements control gas exchange between the plant and its surroundings and are closely related to growth, development and responses to stresses. Stomatal movements are regulated by multiple factors including methyl jasmonate (MeJA). Similar to abscisic acid (ABA), methyl jasmonate (MeJA) stimulates stomatal closure, but the molecular mechanisms underlying this biological process remain unknown. This review summarizes recent advances in mechanisms of MeJA-induced stomatal closure, involving changes in cytosolic pH, the second messengers Ca²⁺, reactive oxygen species (ROS) and nitric oxide (NO), and key signaling components such as COI1, JAR1, RCN1 and TGG1/2. Signal crosstalk between MeJA and ABA pathways in guard cells is also discussed.

Key words methyl jasmonate; guard cells; stomatal closure; signaling transduction; abscisic acid

1 引言

气孔是存在于植物器官表面的微小孔隙, 由一对保卫细胞包围而成。作为植物与外界进行气体和水分交换的通道, 气孔开闭控制着光合作用所需

CO₂的摄取和蒸腾作用水分的散失^[1]。保卫细胞具有非常灵敏的感受外界和内部信号变化的能力, 环境胁迫、病菌侵染、激素等刺激都可被植物感知, 通过改变保卫细胞膨压而在气孔上做出快速反应, 使气孔

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处于最适宜的开闭状态,最大限度地优化气孔对CO₂的吸收和减少因蒸腾作用导致的水分散失^[2-3]。气孔受到干旱等胁迫后会迅速关闭,这对于植物减少水分损失和更好地适应环境具有重要意义^[4]。深入研究气孔信号转导途径及其调控机理对人们认识植物适应环境的机制有重要的理论意义,也对增强农作物抗逆性、提高产量和品质具有重要的实践意义。

茉莉酸类物质(jasmonates, JAs)以茉莉酸(jasmonic acid, JA)和茉莉酸甲酯(methyl jasmonate, MeJA)为主体,还包括茉莉酸的某些氨基酸结合物、葡萄糖苷和羟化衍生物等,广泛存在于植物体中,对植物的生长发育和抗逆性起重要调节作用^[5]。大量研究表明, JAs作为“伤害激素”在植物抵抗机械伤害和病虫害等方面发挥信号作用^[5-8]。与ABA类似, JAs也在植物诸多生理过程中起作用,如抑制幼苗和根的生长、种子萌发,促进叶片衰老和气孔关闭、花粉发育、叶绿素降解等^[5,9]。其中, MeJA诱导的气孔关闭是植物中普遍存在的重要生理响应过程。迄今,已在包括拟南芥^[10-12]、大麦^[13]、圆叶鸭跖草^[14]、蚕豆^[15]、粉蓝烟草^[16]和兜兰^[17]等多种植物中观察到MeJA诱导气孔关闭的现象。国内外学者对保卫细胞MeJA信号途径进行了研究,结果表明, MeJA诱导的气孔关闭类似于ABA信号途径,也与Ca²⁺通道激活^[11,18-19]、保卫细胞胞质碱化^[10,15,17-18]以及活性氧(reactive oxygen species, ROS)和一氧化氮(nitric oxide, NO)的产生有关^[12,20-21]。已鉴定的信号组分包括NAD(P)H氧化酶AtrbohD/F(*Arabidopsis thaliana* respiratory burst oxidase homolog D/F)^[10]、Snf1(sucrose nonfermenting 1)相关的蛋白激酶OST1(open stomata 1)^[10]、属于蛋白磷酸酶2C(protein phosphatase 2C, PP2C)的ABI1(ABA insensitive 1)和ABI2(ABA insensitive 2)^[11]、蛋白磷酸酶2A(PP2A)的调节亚基RCN1(roots curl in naphthylphthalamic acid 1)^[12]以及硫代葡萄糖苷酶TGG(thioglucoside glucosidases)^[22]。但是,与ABA相比, MeJA诱导气孔关闭的信号机制还很不清楚。本文对近年来该领域取得的进展进行综述,以期为进一步开展相关研究提供参考。

2 保卫细胞中MeJA的信号组分

2.1 胞质[Ca²⁺]

Ca²⁺是保卫细胞内MeJA和ABA信号途径中重要的第二信使。ABA刺激Ca²⁺从液泡和内质网释放,使

[Ca²⁺]_{cyt}升高^[23-24]。[Ca²⁺]_{cyt}升高调节阴离子通道和外向K⁺通道,诱导气孔关闭。MeJA也能促进拟南芥保卫细胞非选择性Ca²⁺流动,引起[Ca²⁺]_{cyt}振荡^[11,18-19]。Ca²⁺通道抑制剂和钙调素抑制剂均抑制MeJA诱导气孔关闭^[10,16],说明[Ca²⁺]_{cyt}升高对MeJA诱导气孔关闭是不可缺少的过程。董发才等^[25]用MeJA处理拟南芥叶片下表皮,引起[Ca²⁺]_{cyt}升高,质膜Ca²⁺通道阻断剂LaCl₃和Ca²⁺螯合剂乙二醇-双-(2-氨基乙醚)四乙酸[ethylene glycol bis(2-aminoethyl) tetraacetic acid, EGTA]均能明显地降低MeJA对气孔关闭的促进作用。由此推测,胞质Ca²⁺可能是MeJA促进气孔关闭的重要信号转导因子。以MeJA信号不敏感突变体*coronatine-insensitive 1(coi1)*为材料的研究表明, MeJA不能诱导*coi1*气孔关闭。药理学和遗传学证据表明, MeJA不能诱导*coi1*保卫细胞[Ca²⁺]_{cyt}升高或S-型阴离子通道变化^[11]。最近的研究表明,钙依赖的蛋白激酶6(calcium-dependent protein kinase6, CPK6)在MeJA介导的保卫细胞信号转导中起正调控作用。CPK6基因功能缺失的拟南芥突变体*cpk6-1*中, MeJA对细胞内非选择性Ca²⁺流的诱导受到阻断, [Ca²⁺]_{cyt}升高受到抑制, MeJA不能激活*cpk6-1*保卫细胞的S-型阴离子通道,因而阻碍了MeJA对气孔关闭的诱导,但ROS和NO的产生未受影响^[26]。除Ca²⁺通道外, MeJA也能增强外向K⁺通道,抑制内向K⁺通道,引发气孔关闭^[27]。

2.2 胞质pH

多项研究表明, MeJA引起的胞内pH升高可能是气孔保卫细胞信号转导的一个组分。Evans^[27]的研究表明, MeJA通过胞质碱化激活蚕豆保卫细胞质膜的外向K⁺通道,导致保卫细胞的膨压降低,引起气孔关闭,这与ABA诱导气孔关闭的机制相似。JA可促进兰花叶片气孔关闭,阻止气孔张开,在JA诱导气孔关闭之前发生胞质碱化现象,而且JA的碱化作用的程度和幅度与兰花和蚕豆对ABA的应答非常相似^[17]。由于信号传导受到破坏, MeJA不能诱导JA信号突变体*coi1*发生胞质碱化和气孔关闭^[18]。刘新等^[15]研究证明,在JA诱导蚕豆气孔关闭的过程中有H⁺信号的参与,外源JA能够引起蚕豆保卫细胞胞质的碱化,并且胞质碱化发生在气孔孔径改变之前。研究还表明,在MeJA和ABA诱导气孔关闭过程中,胞质碱化先于ROS和NO产生^[10,28]。但Islam等^[18]的研究则恰好相反,认为胞质pH升高发生在ROS产生的下游。用丁酸

盐抑制胞质碱化, 导致MeJA和ABA诱导的 $[Ca^{2+}]_{cyt}$ 升高和气孔关闭均受到抑制, 说明胞质pH变化会反馈影响 $[Ca^{2+}]_{cyt}$ ^[18]。这些研究表明, 胞质pH同 Ca^{2+} 一样, 也是保卫细胞MeJA与ABA信号途径的重要第二信使。

2.3 ROS和NO

近年来, ROS和NO作为保卫细胞内重要的第二信使参与气孔运动广受关注^[30-31]。研究表明, ROS和NO都参与了MeJA和ABA诱导的气孔关闭^[10-11, 20, 24, 28-29]。拟南芥中编码NAD(P)H氧化酶的两个基因*AtrbohD*和*AtrbohF*突变, 破坏了MeJA诱导的ROS产生和气孔关闭^[10]。由于信号转导受阻, MeJA不能诱导*coi1*保卫细胞产生ROS和NO, 因此不能诱导气孔关闭^[11]。RCN1是PP2A的一个调节亚基, MeJA和ABA都不能诱导RCN1敲除突变体*rcn1*气孔关闭, ROS和NO产生受阻, 施加 H_2O_2 可以成功诱导气孔关闭, 表明RCN1在位于ROS和NO产生途径的上游发挥作用^[12, 20]。JA可提高蚕豆气孔保卫细胞NO的水平, JA和NO能够诱导蚕豆气孔关闭, NO的清除剂则大大减弱JA诱导的气孔关闭^[15]。薄惠等^[21]的研究表明, 蛋白激酶MEK1/2的专一抑制剂PD98059可抑制MeJA诱导的拟南芥保卫细胞中 H_2O_2 的产生和气孔的关闭。该结果表明, 类属于细胞分裂原活化蛋白激酶激酶(mitogen-activated protein kinase kinase, MAPKK)的蛋白激酶MEK1/2参与了MeJA诱导的拟南芥气孔关闭的信号转导过程, 其作用机制可能是通过调节MeJA诱导保卫细胞产生和积累 H_2O_2 而起作用。拟南芥中两个硫代葡萄糖苷酶基因*TGG1*和*TGG2*也被证明参与MeJA诱导的气孔关闭。MeJA可以诱导*tgg1-3*和*tgg2-1*气孔关闭, 但不能诱导*tgg1-3tgg2-1*双突变体气孔关闭, 并且*TGG1*和*TGG2*位于MeJA信号途径中ROS产生的下游和 $[Ca^{2+}]_{cyt}$ 的上游^[22]。

3 保卫细胞MeJA信号途径

目前, 保卫细胞MeJA诱导气孔关闭的信号途径还未完全阐述清楚, 其可能的机制为, MeJA诱导保卫细胞产生ROS和NO, RCN1调节的PP2A参与调控这个步骤, ROS主要由*AtrbohD/F*编码的NAD(P)H氧化酶催化产生, 但参与该信号途径中NO产生的基因还不确定。ROS和NO促使保卫细胞 $[Ca^{2+}]_{cyt}$ 升高, Ca^{2+} 来源于胞内钙库的释放和 Ca^{2+} 通道介导的质外体。*ABI2*(PP2C)以及*TGG1*和*TGG2*基因的突

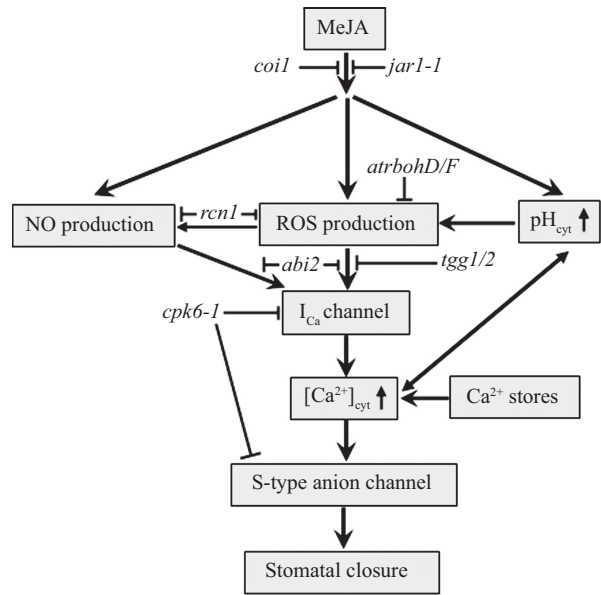


图1 保卫细胞MeJA信号途径模式图(根据参考文献[32-33]修改)

Fig.1 Model of MeJA signaling pathway in guard cells(modified from references [32-33])

变可破坏ROS和NO引起的 $[Ca^{2+}]_{cyt}$ 升高。 $[Ca^{2+}]_{cyt}$ 升高激活S型阴离子通道, 引起气孔关闭, CPK6参与这个过程。胞质pH也是保卫细胞MeJA信号途径的重要组分, 引起 $[Ca^{2+}]_{cyt}$ 变化和ROS产生(图1)。

4 保卫细胞中MeJA和ABA信号途径存在“对话”机制

MeJA和ABA诱导气孔关闭的信号机制不仅类似, 而且大量研究表明, 保卫细胞中这两种信号途径存在“对话”机制^[32-33]。某些信号组分如 $[Ca^{2+}]_{cyt}$ 、胞质pH、ROS和NO, 共同在MeJA和ABA介导的拟南芥保卫细胞信号转导中起作用。用ABA生物合成的抑制剂氟啶酮预处理拟南芥抑制MeJA诱导的气孔关闭, 但不抑制ABA诱导的气孔关闭。ABA缺失突变体*aba2-2*破坏MeJA诱导的气孔关闭, 但不抑制ABA诱导的气孔关闭。究其原因, 氟啶酮和*aba2-2*突变抑制MeJA诱导的 $[Ca^{2+}]_{cyt}$ 升高而不抑制ABA对 $[Ca^{2+}]_{cyt}$ 的诱导。这表明内源ABA参与MeJA诱导的气孔关闭^[34]。对ABA和MeJA信号突变体的研究也揭示了保卫细胞中二者存在相互作用。ABA不敏感突变体*ost1-2*能响应MeJA产生 H_2O_2 并诱导气孔关闭, 但不能响应ABA; MeJA不敏感突变体*jar1-1*(jasmonate resistant 1)和*coi1*能响应ABA产生 H_2O_2 ,

而不能响应MeJA诱导气孔关闭^[10-11]。MeJA虽然可以诱导ABA不敏感突变体*abi2-1*产生ROS和NO,但不能激发S-型阴离子通道和Ca²⁺通道,同样也不能诱导气孔关闭^[11],表明MeJA通过ABA信号途径诱导气孔关闭。本实验室研究表明,对ABA不敏感的磷脂酶D基因缺失突变体*plda*,也不能响应MeJA及时关闭气孔(王俊斌等,待发表)。番茄ABA生物合成突变体*sitiens*不能响应MeJA发生气孔运动,但经过ABA预处理后,MeJA可以诱导*sitiens*气孔关闭^[35],说明ABA对MeJA诱导番茄气孔关闭是非常必要的。

5 展望

目前,已经有较多研究报道MeJA在气孔运动过程中发挥调节作用,无论是诱导气孔关闭还是抑制气孔开放过程都有MeJA参与的证据。如上所述,MeJA和ABA诱导气孔关闭信号转导途径之间有相似之处,两条信号途径也存在“对话”。然而,相比ABA,MeJA调控气孔运动的信号转导途径还不清楚。这一途径中MeJA如何调控下游组分的生理反应和其他信号组分间如何互作等都是需要重点研究解决的问题,有待进一步研究,采用生理和遗传分析方法,结合分子生物学的技术手段,人们对MeJA在植物气孔运动中作用的认识将会更加深入。

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