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# 生态学报

(SHENGTAI XUEBAO)

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**封面图说:** 带雏鸟的白枕鹤一家——白枕鹤是一种体型略小于丹顶鹤的优美的鹤。体羽蓝灰色,腹部较深,背部较浅,脸颊两侧红色,头和颈的后部及上背为白色,雌雄相似。其虹膜暗褐色,嘴黄绿色,脚红色。白枕鹤常常栖息于开阔平原芦苇沼泽和水草沼泽地带,有时亦出现于农田和海湾地区,尤其是迁徙季节。主要以植物种子、草根、嫩叶和鱼、蛙、软体动物、昆虫等为食。繁殖区在我国北方和西伯利亚东南部。我国白枕鹤多在黑龙江、吉林、内蒙古繁殖,与丹顶鹤的繁殖区几乎重叠,为国家一级保护动物。

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石璐, 李梦莎, 王丽华, 于萍, 李楠, 国静, 阎秀峰. COI1 参与茉莉酸调控拟南芥吲哚族芥子油苷生物合成过程. 生态学报, 2012, 32(17): 5438-5444.

Shi L, Li M S, Wang L H, Yu P, Li N, Guo J, Yan X F. COI1 is involved in jasmonate-induced indolic glucosinolate biosynthesis in *Arabidopsis thaliana*. Acta Ecologica Sinica, 2012, 32(17): 5438-5444.

## COI1 参与茉莉酸调控拟南芥吲哚族芥子油苷生物合成过程

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**摘要:** 芥子油苷是一类具有防御作用的植物次生代谢产物, 外源激素茉莉酸对吲哚族芥子油苷的合成具有强烈的诱导作用, 但茉莉酸调控吲哚族芥子油苷生物合成的分子机制并不清楚。以模式植物拟南芥 (*Arabidopsis thaliana*) 的野生型和 *coi1-22*、*coi1-23* 两种突变体为研究材料, 通过茉莉酸甲酯 (MeJA) 处理, 比较了拟南芥野生型和 *coi1* 突变体植株吲哚族芥子油苷含量、吲哚族芥子油苷合成前体色氨酸的生物合成基因 (*ASA1*、*TSA1* 和 *TSB1*)、吲哚族芥子油苷生物合成基因 (*CYP79B2*、*CYP79B3* 和 *CYP83B1*) 及调控基因 (*MYB34* 和 *MYB51*) 的表达对 MeJA 的响应差异, 由此确定茉莉酸信号通过 COI1 蛋白调控吲哚族芥子油苷生物合成, 即茉莉酸信号通过信号开关 COI1 蛋白作用于转录因子 MYB34 和 MYB51, 进而调控吲哚族芥子油苷合成基因 *CYP79B2*、*CYP79B3*、*CYP83B1* 和前体色氨酸的合成基因 *ASA1*、*TSA1*、*TSB1*。并且推断, COI1 功能缺失后, 茉莉酸信号可能通过其他未知调控因子或调控途径激活 MYB34 转录因子从而调控下游基因表达。

**关键词:** 茉莉酸; COI1; 吲哚族芥子油苷; 拟南芥

## COI1 is involved in jasmonate-induced indolic glucosinolate biosynthesis in *Arabidopsis thaliana*

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**Abstract:** Glucosinolates are a group of sulphur-rich thioglucosides known to play an important role in plant defense. The accumulation of indolic glucosinolates (IGS) is strong induced by jasmonate (JA). Many studies have demonstrated that coronatine-insensitive 1 (COI1) is important in JA signaling, and is involved in almost all the JA-responsive pathways. However, the underlying molecular mechanisms for JA-induced IGS accumulation remain partially understood. In this study, the *coi1-22* and *coi1-23* mutants and wild-type (WT) *Arabidopsis thaliana* plants were used to investigate the role of COI1 in MeJA-induced IGS metabolism.

The effect of MeJA treatment on IGS contents in *coi1-22* and *coi1-23* plants was analyzed. The results showed that the contents of IGS were significantly increased in MeJA-treated WT plants compared with the control, while the IGS levels were not changed notably in MeJA-treated *coi1-22* and *coi1-23* plants, indicating that the accumulation of IGS is insensitive to MeJA treatment in the mutants. Thus, *coi1-22* and *coi1-23* are good materials for studying the mechanisms of JA-induced IGS biosynthesis. Transcription factors are important regulators on the expression of genes. The R2R3-MYB transcription factors ATR1/MYB34 and HIG1/MYB51 have been reported to act as the direct biosynthetic transcriptional activators for

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IGS, and they regulate many IGS biosynthetic genes and the tryptophan (IGS precursor) biosynthetic genes. The expression levels of *MYB34* and *MYB51* in MeJA-treated *coi1-22*, *coi1-23* and WT plants were analyzed. The results showed that in WT plants, the expression levels of *MYB34* and *MYB51* were significantly higher in MeJA-treated plants than the control after 3 h MeJA-treatment, while it is not the case in *coi1-22* and *coi1-23* plants, indicating that the loss of function of COI1 blocks the MeJA-induced *MYB34* and *MYB51* expression. Furthermore, it is interesting to find that the expression levels of *MYB34* in *coi1-22* and *coi1-23* mutants were significantly higher than in the control plants, suggesting that another signal pathway other than COI1 might be involved in JA-regulated *MYB34* expression. Moreover, the expression levels of tryptophan biosynthetic genes *ASA1*, *TSA1* and *TSB1* and IGS biosynthetic genes *CYP79B2*, *CYP79B3* and *CYP83B1* were further analyzed. The results showed that the induced expression of *ASA1*, *TSA1*, *TSB1*, *CYP79B2*, *CYP79B3* and *CYP83B1* was substantially attenuated in two *coi1* mutants after 3 h of MeJA treatment, indicating that the loss of function of COI1 blocks the MeJA-induced tryptophan biosynthetic genes and IGS biosynthetic genes expression, and the expression of *ASA1*, *TSA1*, *TSB1*, *CYP79B2*, *CYP79B3* and *CYP83B1* might be regulated by COI1 via *MYB34* and *MYB51*. Lastly, the expression levels of *ASA1*, *TSA1* and *TSB1* in *coi1-22* and *coi1-23* mutants after 6 h of MeJA treatment and those of *CYP79B2* and *CYP79B3* in *coi1-22* and/or *coi1-23* after 24 h of MeJA treatment were significantly higher than in the control plants, suggesting that another signal pathway other than COI1 might also be involved in the JA-regulated expression of them.

In conclusion, COI1 is involved in JA-regulated biosynthesis of indolic glucosinolates in *A. thaliana*. JA induces the expression of tryptophan biosynthetic genes *ASA1*, *TSA1* and *TSB1* and IGS biosynthetic genes *CYP79B2*, *CYP79B3* and *CYP83B1* through *MYB34* and *MYB51* via COI1. In addition, another pathway might exist in JA-induced IGS biosynthesis when COI1 is not functional.

**Key Words:** jasmonic acid; COI1; indolic glucosinolate; *Arabidopsis thaliana*

芥子油苷 (glucosinolate) 是一类含氮、含硫的植物次生代谢产物, 主要分布于十字花科植物。芥子油苷及其降解产物具有多种生化活性, 介导着植物与环境之间的相互作用, 因而吸引了人们的研究兴趣<sup>[1-4]</sup>。人们对芥子油苷的组成和生物合成已经有了较为清晰的认识, 合成途径中的许多关键酶基因已经克隆并鉴定了功能<sup>[2-4]</sup>。依据侧链氨基酸的来源可将芥子油苷分为脂肪族、芳香族和吲哚族 3 个类群, 其中吲哚族芥子油苷的侧链来源于色氨酸。已有研究表明, 外源茉莉酸对芥子油苷合成具有强烈的诱导作用, 尤其是吲哚族芥子油苷<sup>[5-6]</sup>。

茉莉酸 (jasmonic acid, JA)、茉莉酸甲酯 (methyl jasmonate, MeJA) 以及其他茉莉酸衍生物统称为茉莉酸类化合物 (jasmonates, JAs), 作为植物激素和信号化合物在植物生长、发育特别是抵御生物和非生物胁迫等生物学过程中起着重要的作用<sup>[7-8]</sup>。许多研究表明, COI1 (coronatine-insensitive 1) 蛋白是茉莉酸信号途径的信号开关, 广泛地参与几乎所有的响应茉莉酸的代谢过程, 在茉莉酸信号途径中起关键的调控作用<sup>[9-11]</sup>。拟南芥 *coi1* 功能缺失突变体中, 吲哚族芥子油苷的含量不受茉莉酸诱导<sup>[12-13]</sup>, 暗示 COI1 在茉莉酸调控吲哚族芥子油苷生物合成过程中可能起重要作用, 但 COI1 参与该过程的分子机制尚不清楚。

本文以模式植物拟南芥 (*Arabidopsis thaliana*) 及其 *coi1* 功能缺失突变体为材料, 通过检测 MeJA 处理对吲哚族芥子油苷生物合成基因及调控基因表达的影响, 分析 COI1 在茉莉酸调控吲哚族芥子油苷生物合成过程中的作用。

## 1 材料和方法

### 1.1 植物材料及生长条件

野生型拟南芥为 Columbia-0 (Col-0) 生态型, *coi1* 的 T-DNA 插入突变株 SALK\_095916 和 SALK\_045434 的种子购自 Arabidopsis Biological Resource Center (ABRC), 筛选获得的纯合突变体分别命名为 *coi1-22* 和 *coi1-*

23。经鉴定,两突变体植株体内 *COI1* 基因的表达量分别约为野生型植株的 40% 和 50%,且幼苗对茉莉酸的敏感性均降低,可以作为 *coi1* 突变体材料使用<sup>[14]</sup>。

种子经 75% 酒精消毒 10 min 后,用无菌水冲洗 3—5 次,并于 4 °C 避光条件下处理 3 d 后逐粒播于盛有草炭土与蛭石混合物(体积比 1:2)的花盆中,在人工培养室中培养(温度 22 °C,人工光照 8 L/16 D,光子通量密度约 150  $\mu\text{mol}/\text{m}^2/\text{s}$ ,空气相对湿度 65%)。

## 1.2 MeJA 处理

参照 Anderson 等<sup>[15]</sup>的方法,将生长 4—5 周的拟南芥幼苗置于密封塑料盒,处理组加入体积分数为 0.5% MeJA 的乙醇溶液,使盒内空气中 MeJA 的终浓度为 0.1  $\mu\text{mol}/\text{L}$ ;对照组用等量的 99.5% 乙醇水溶液进行处理。

## 1.3 芥子油苷测定

芥子油苷提取及测定按照 Pang 等<sup>[16]</sup>的方法。

## 1.4 荧光实时定量 PCR

利用 TRIzol 试剂(Invitrogen, USA)提取总 RNA,使用 DNAase(TaKaRa Inc., China)对 RNA 中所含痕量基因组 DNA 进行消化。按照 PrimeScript RT reagent Kit(TaKaRa Inc., China)说明书合成 cDNA 第一链,去离子水稀释 10 倍作为实时荧光定量 PCR 的模板。

荧光实时定量 PCR 使用 SYBR Green Master mix(TaKaRa Inc., China),以 *ACTIN2* 基因作为内参,在 ABI 7500(Applied Biosystems Inc., USA)实时荧光定量 PCR 仪上进行扩增。每个样品 3 次重复。各基因的特异引物序列如下:

*ACTIN2* (At3g18780) 5'-ATTGAGATGCCGAGAAGTCTTGTTC-3', 5'-ACCACCGATCCAGACACTGTACTTCC-3';  
*ASA1* (AT5g05730) 5'-CGAATTCCTCAGTCATGGT-3', 5'-ATGTCTAGCGTTGGTCGTT-3';  
*COI1* (At2g39940) 5'-TCGCGACGGTTGATGATGT-3', 5'-CGACACACCAAAGAAGCCGA-3';  
*CYP79B2* (AT4g39950) 5'-GTAACCTCGGAGCATTCGT-3', 5'-TCGCCGGATATCACATCC-3';  
*CYP79B3* (AT2g22330) 5'-AGTCACTTCCGAACACTCA-3', 5'-TCGCAGGTTACCATAATTCC-3';  
*CYP83B1* (AT4g31500) 5'-TCACGCCATATCTACCAGC-3', 5'-TGGACGTCATGACTGGAC-3';  
*MYB34* (AT5g60890) 5'-GTTTAGTCCTGAAGAAGACGACACT-3', 5'-CCTTTTTCGCTTCAACCGCT-3';  
*MYB51* (At1g18570) 5'-CGAATCTTCTCTGCCATGG-3', 5'-TTCAGAAATGTGAGAACCC-3';  
*TSA1* (At3g54640) 5'-CGATCATCTGTAAGCGGAAA-3', 5'-ATGCTCCGGCTTTGATATTC-3';  
*TSB1* (AT5g54810) 5'-CGTCTCGCTCCAAGTCAT-3', 5'-CCAAACCGACCGAACGAA-3'。

## 2 结果与分析

### 2.1 吲哚族芥子油苷含量对 MeJA 的响应

已有研究表明,拟南芥 *COI1* 基因突变后,吲哚族芥子油苷的积累对茉莉酸不敏感<sup>[12-13]</sup>。由于 *coi1-22*、*coi1-23* 为不完全缺失突变体,首先分析两种突变体中吲哚族芥子油苷含量对 MeJA 的响应。

对 MeJA 处理的 *coi1* 突变体及相应野生型植株中吲哚族芥子油苷含量的测定结果显示,在 3 h、6 h 和 24 h,MeJA 处理的野生型植株中吲哚族芥子油苷的含量与对照的相比均显著提高( $P < 0.05$ )。而在 *coi1-22* 和 *coi1-23* 纯合突变体植株中,MeJA 处理的植株中吲哚族芥子油苷的含量与对照的相比均没有显著变化( $P > 0.05$ ),且 *coi1-22* 和 *coi1-23* 纯合突变体植株中吲哚族芥子油苷的含量均低于野生型植株(图 1)。以上结果表明 *coi1-22* 和 *coi1-23* 两种突变体中吲哚族芥子油苷的积累对 MeJA 的敏感性降低。因此,这两种突变体可用于分析茉莉酸调控吲哚族芥子油苷生物合成的机制。

### 2.2 吲哚族芥子油苷合成调节基因表达对 MeJA 的响应

转录因子在基因的表达调控中起关键作用。MYB 家族转录因子成员 MYB34 和 MYB51 是吲哚族芥子油苷生物合成的正向调节因子,调节多种吲哚族芥子油苷生物合成基因及吲哚族芥子油苷合成前体——色氨酸

生物合成基因的表达式<sup>[17-18]</sup>。为分析 COI1 在茉莉酸调控吲哚族芥子油苷合成过程中的作用,有必要比较 *coi1* 突变体和野生型拟南芥中 *MYB34*、*MYB51* 表达对 MeJA 的响应差异。

由于吲哚族芥子油苷含量在 MeJA 处理 3 h 就有了明显的反应,因而应该重点分析 MeJA 处理 3 h 时的基因表达情况。从图 2 的结果可以看出,MeJA 处理 3 h 后,无论是 *MYB34* 还是 *MYB51* 基因,在野生型植株中的表达都显著高于对照(未经 MeJA 处理的)植株,特别是 *MYB51* 基因的表达上调 150 多倍。相比而言,*coi1-22* 和 *coi1-23* 两种突变体植株中,*MYB34* 和 *MYB51* 基因的表达与对照植株没有差异,表明 *MYB34* 和 *MYB51* 基因的表达在 *coi1-22* 和 *coi1-23* 两种突变体中未受 MeJA 的诱导,意味着 COI1 功能缺失阻断了茉莉酸信号诱导 *MYB34* 和 *MYB51* 基因表达的作用。

值得关注的是 *MYB34* 基因的表达情况。在 MeJA 处理 6 h 时,*coi1-22* 和 *coi1-23* 两种突变体中 *MYB34* 基因的表达显著高于对照植株(图 2),这意味着茉莉酸信号不是通过 COI1 作用,而可能是通过其他信号通路诱导了 *MYB34* 基因的表达。

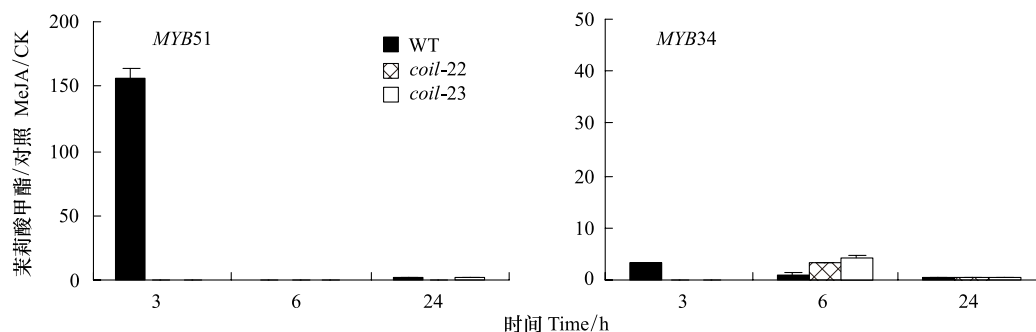


图 2 MeJA 处理对拟南芥 *MYB51* 和 *MYB34* 基因表达的影响(平均值±标准差)

Fig. 2 The effect of MeJA treatment on the expression of *MYB51* and *MYB34* genes in *Arabidopsis thaliana* (Mean±SD)

### 2.3 色氨酸生物合成基因表达对 MeJA 的响应

色氨酸是吲哚族芥子油苷生物合成的前体,也是吲哚族芥子油苷生物合成的限制因子。色氨酸合成受氨基苯甲酸合成酶(AS) $\alpha$ 亚基 ASA1、色氨酸合成酶(TS) $\alpha$ 亚基 TSA1 和 $\beta$ 亚基 TSB1 等催化<sup>[18]</sup>,编码这些酶的基因的表达也受转录因子 *MYB34* 和 *MYB51* 调控<sup>[18]</sup>。比较野生型和 *coi1* 突变体中这些基因的表达对 MeJA 响应的差异,可以辅助分析 COI1 在茉莉酸调控吲哚族芥子油苷生物合成过程中的作用。

从图 3 中 MeJA 处理 3 h 的结果可以看出,在 *coi1-22* 和 *coi1-23* 突变体中 ASA1、TSA1 和 TSB1 基因的表达没有响应 MeJA 的处理,表明 COI1 功能缺失影响了茉莉酸调控 ASA1、TSA1 和 TSB1 基因表达进而影响了色氨酸生物合成的通路,并且 ASA1、TSA1 和 TSB1 基因有可能是通过转录因子 *MYB34* 和 *MYB51* 接受 COI1 调控的。

从 MeJA 处理 6 h 的结果可以看出,在 *coi1-22* 和 *coi1-23* 突变体中 ASA1、TSA1 和 TSB1 基因的表达对 MeJA 处理的响应均显著高于野生型植株(图 3),意味着茉莉酸信号对 ASA1、TSA1 和 TSB1 基因表达调控而对色氨酸合成的调控可能不仅仅是经由 COI1 路径,其他信号通路也有可能在起着联络作用。

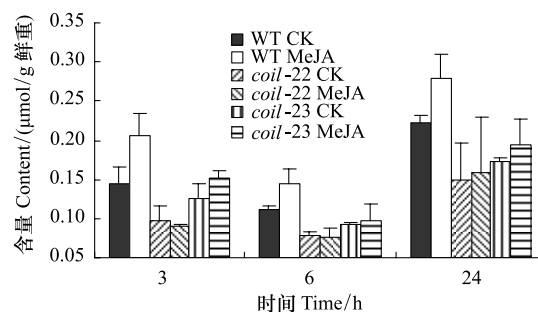


图 1 MeJA 处理对拟南芥吲哚族芥子油苷含量的影响(平均值±标准差)

Fig. 1 The effect of MeJA treatment on the indolic glucosinolates content in *Arabidopsis thaliana* (Mean±SD)

WT:野生型 wild-type CK:对照 control MeJA:茉莉酸甲酯 methyl jasmonate

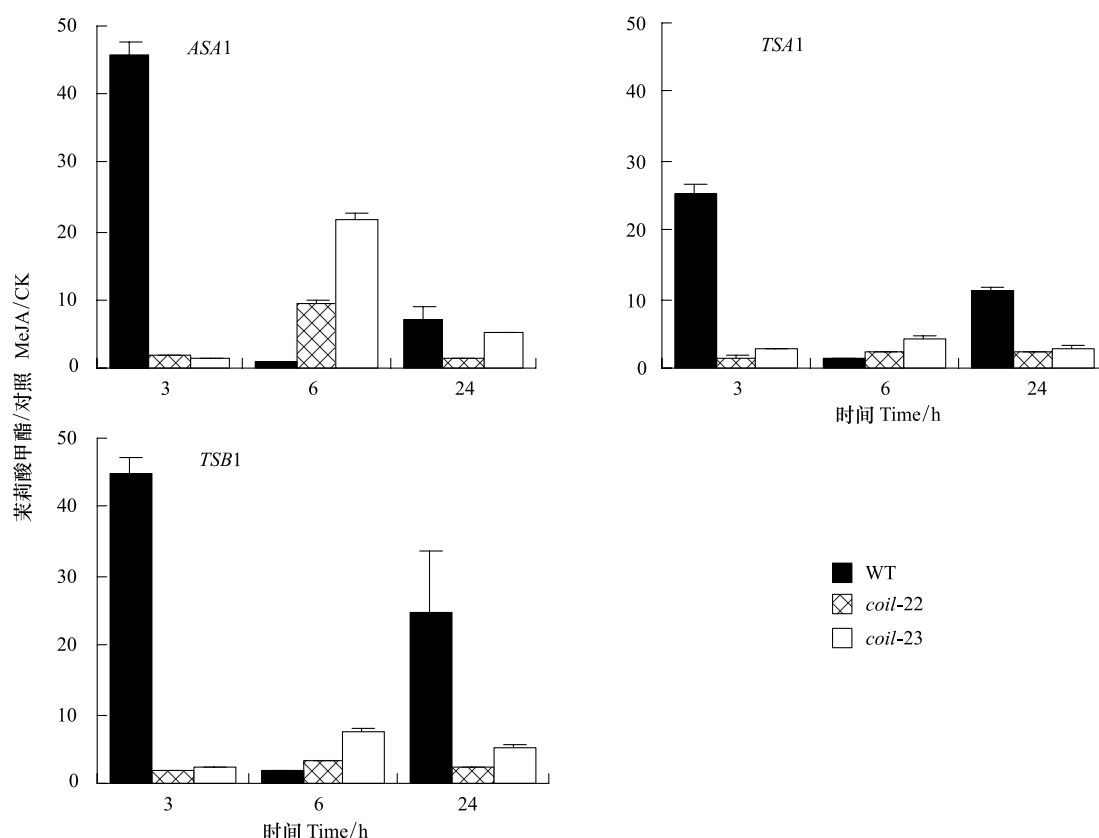


图3 MeJA处理对拟南芥色氨酸生物合成基因表达的影响(平均值±标准差)

Fig. 3 The effect of MeJA treatment on the expression of Trp biosynthesis genes in *Arabidopsis thaliana* (Mean±SD)

#### 2.4 吲哚族芥子油苷生物合成基因表达对 MeJA 的响应

由色氨酸形成吲哚族芥子油苷的核心结构是吲哚族芥子油苷生物合成的重要过程,这一过程由细胞色素P450酶(Cytochrome P450 proteins, *CYP*)*CYP79B2*、*CYP79B3*、*CYP83B1*等催化完成<sup>[4, 17]</sup>。

比较野生型和 *coi1-22*、*coi1-23* 突变体植株中3个吲哚族芥子油苷生物合成基因 *CYP79B2*、*CYP79B3* 和 *CYP83B1* 的表达差异(图4)可知,COI1功能缺失影响了茉莉酸调控 *CYP79B2*、*CYP79B3* 和 *CYP83B1* 基因表达进而影响吲哚族芥子油苷合成的通路,并且 *CYP79B2*、*CYP79B3* 和 *CYP83B1* 基因有可能是通过转录因子 *MYB34* 和 *MYB51* 接受 COI1 调控的。

### 3 结论与讨论

已有研究表明茉莉酸信号调控植物芥子油苷特别是吲哚族芥子油苷的生物合成<sup>[5, 6]</sup>,人们也知道 COI1 蛋白是茉莉酸信号途径的信号开关,参与多种次生代谢产物及代谢基因的调控<sup>[11, 20-22]</sup>。尽管有关拟南芥 *coi1* 功能缺失突变体中吲哚族芥子油苷含量不受茉莉酸诱导的报道<sup>[12-13]</sup>暗示 COI1 在茉莉酸调控吲哚族芥子油苷生物合成过程中可能起重要作用,但 COI1 参与该过程的分子机制并不清楚。

通过比较拟南芥野生型和 *coi1* 突变体植株中吲哚族芥子油苷生物合成基因、前体色氨酸生物合成基因以及转录因子基因对外源 MeJA 的响应差异,可以看出,茉莉酸信号也是通过 COI1 蛋白调控吲哚族芥子油苷生物合成的(图5)。从本文 MeJA 处理3h的吲哚族芥子油苷含量变化和相关生物合成基因、转录因子表达变化以及研究报道 *MYB34*、*MYB51* 转录因子与相关生物合成基因的上下游关系<sup>[18]</sup>推断,茉莉酸信号通过信号开关 COI1 蛋白作用于转录因子 *MYB34*、*MYB51*,进而调控吲哚族芥子油苷合成基因 *CYP79B2*、*CYP79B3*、*CYP83B1* 和前体色氨酸的合成基因 *ASA1*、*TSA1*、*TSB1*。

在 MeJA 处理的 *coi1* 突变体植株中, *MYB34* 基因在处理6h处被显著诱导上调表达(图2),位于其下游的

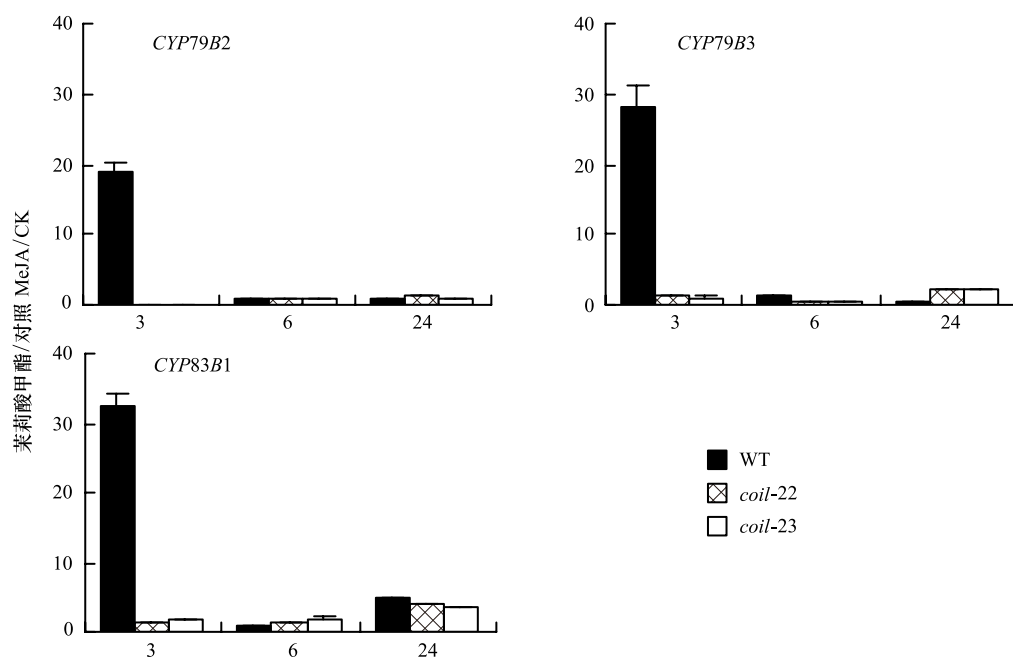


图4 MeJA 处理对拟南芥吲哚族芥子油苷生物合成基因表达的影响(平均值±标准差)

Fig. 4 The effect of MeJA treatment on the expression of indolic glucosinolates biosynthesis genes in *Arabidopsis thaliana* (Mean±SD)

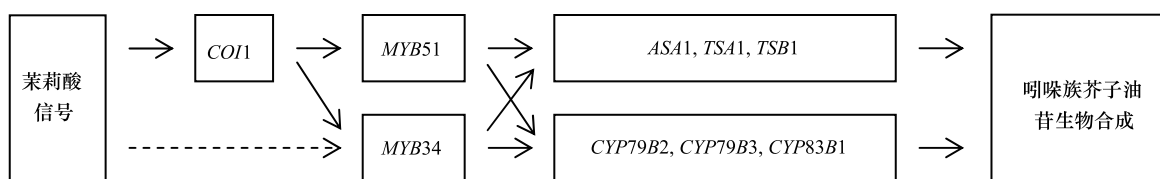


图5 茉莉酸调控吲哚族芥子油苷生物合成的信号途径,虚线表示未知途径

Fig. 5 JA signal transduction pathway mediating indolic glucosinolates biosynthesis, the broken line represents the unknown pathway

色氨酸生物合成基因 *ASA1*、*TSA1*、*TSB1* 和吲哚族芥子油苷生物合成基因 *CYP79B2*、*CYP79B3* 也显著上调(图3、图4)。这暗示 *COI1* 突变后,茉莉酸信号转导途径中存在未知调控因子或调控途径,该因子或途径能够感受 *COI1* 的缺失并激活 *MYB34* 的表达从而调控下游生物合成基因,且在 *COI1* 功能缺失的背景下,*MYB34* 作为重要的调控因子响应茉莉酸信号且诱导下游色氨酸生物合成基因和吲哚族芥子油苷生物合成基因的表达。遗憾的是,在 *coi1-22* 和 *coi1-23* 两个不完全缺失突变体植株中,MeJA 处理 24 h 后吲哚族芥子油苷的合成没有显著增加,表明 *coi1-22* 和 *coi1-23* 中 *MYB34* 调节的下游基因的表达并未对吲哚族芥子油苷的合成产生作用。这与所使用的突变体材料中 *COI1* 的不完全突变有关,所推测的调控因子或调控途径有待于利用完全缺失突变体及深入的分子生物学研究进一步证实。

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