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植物的环境信号分子茉莉酸及其生物学功能

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摘要:茉莉酸信号分子参与植物生长发育众多生理过程的调控,尤其是作为环境信号分子能有效地介导植物对生物及非生物胁迫的防御反应。迄今已知具有信号分子生理功能的至少包括茉莉酸(jasmonic acid, JA)以及茉莉酸甲酯(methyl jasmonate, MeJA)和茉莉酸-异亮氨酸复合物(jasmonoyl-isoleucine, JA-Ile)等茉莉酸衍生物,统称为茉莉酸类化合物(jasmonates, JAs)。从环境信号分子角度介绍了茉莉酸信号的启动(环境信号感知与转导、茉莉酸类化合物合成)、传递(局部传递、维管束传输、空气传播)和生物学功能(茉莉酸信号受体、调控的转录因子、参与的生物学过程)。

关键词:茉莉酸信号;生物学功能;环境响应

Jasmonic acid signaling in plants and its biological functions in relation to environment

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Abstract: Jasmonates (JAs) are fatty acid-derived signaling molecules involved in the regulation of many physiological and developmental processes in plants, including root growth, tuber development, fruit ripening, senescence, tendril coiling, and pollen development. In addition, Jasmonates are important regulators in plant response to biotic and abiotic stresses, such as ozone exposure, wounding, water deficit and pathogen/pest attack. In plants, Jasmonic acid (JA) can be metabolized into different compounds depending on the chemical modification on the carboxylic acid group, pentenyl side chain or the pentanone ring. Currently, JA, MeJA (a volatile methyl ester, methyl jasmonate) and JA-Ile (predominant amino acid conjugate, jasmonoyl-isoleucine) were known to function as signal molecules in plants. Jasmonic acid and its derivatives are collectively named jasmonates. To date, the physiological functions of the jasmonates are still not completely understood. Details of the jasmonate signaling pathway are currently at the center of active research and exciting results have been produced. In this review, we summarize the current status of our knowledge on plant JA signaling pathway and its biological functions in relation to environment, including the triggering of JA signaling, transportation of the JA signals and the biological functions of JA signaling. In general, activation of JA-mediated signaling pathway is accompanied by the regulation of the biosynthesis of JAs. Signaling compounds can be transported via a local response responsible for a short distance signal transduction, translocation through the vascular system or airborne transportation responsible for a long distance signal transduction in plants. In the past few years, lots of new data on JA signaling have been published, and some of the JA signaling components have been identified and functionally analyzed. Our knowledge of JA biosynthesis, metabolism, transportation and plant response has been greatly enhanced. However, there are several major gaps in our

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understanding of how plants perceive various environmental signals and induce jasmonic acid synthesis. With the development of molecular biology, the discovery and characterization of JA acceptors has paved the way for understanding the core module responsible for JA signaling (COI/JAZ/MYC2). Although we now have a much better understanding of the molecular mechanisms of JA action, many detailed questions remain. For examples, how JA signaling interact with other phytohormones and how plants prioritize growth and development under conditions of environmental stresses. Although JA signaling plays a prominent role in promoting plant defence in plant response to various environmental factors, more and more studies have shown that other phytohormones are also implicated in plant defence signaling pathways, such as salicylic acid (SA), ethylene (ET) and auxin. Cross-talk among multiple signaling pathways is an important mechanism in plant signal transduction networks. However, there is limited knowledge for the complex regulatory networks in relation to plant interaction with the environment. In conclusion, future research needs to focus on the JA perception, mitogen-activated protein kinases (MAPKs) in jasmonic acid signalling, the downstream transcription factors in the JA signaling pathway, the transcription factors regulating plant growth and development, cross-talk among multiple phytohormones signaling pathways, and the diverse actions of JAs in plant growth, development and interaction with the environment.

Key Words: Jasmonic acid signaling; biological function; environmental response

1980 年 Ueda 和 Kato 从苦艾(*Artemisia absinthium*)中分离并鉴定了具有促进衰老生理活性的茉莉酸甲酯(methyl jasmonate, MeJA)[1],从而引发了人们对茉莉酸信号分子的广泛关注。迄今已知,具有信号分子生理功能的至少包括茉莉酸(jasmonic acid, JA)以及茉莉酸甲酯和茉莉酸-异亮氨酸复合物(jasmonoyl-isoleucine, JA-Ile)等茉莉酸衍生物,人们将它们统称为茉莉酸类化合物(jasmonates, JAs)。研究表明,茉莉酸信号分子参与植物生长发育众多生理过程的调控,尤其是作为环境信号分子能有效地介导植物对病原菌、食草动物及非生物胁迫等的防御反应,诱导一系列防御基因的表达、防御反应化学物质的合成,并调节植物的“免疫”和应激反应。本文从环境信号分子角度介绍茉莉酸信号的启动、传递和生物学功能。

1 茉莉酸信号的启动

1.1 信号感知与转导

最近几十年,人们对外界生物胁迫和非生物胁迫信号如何被植物感知并启动茉莉酸信号的生物合成进行了大量的研究,其中在番茄中的研究较多。1991 年 Pearce 等人在番茄(*Lycopersicon esculentum*)中发现了应答昆虫食害等机械损伤的系统素(systemin)[2],这是一种由 18 个氨基酸组成的多肽信号分子,来源于由 200 个氨基酸组成的前体蛋白——前系统素(prosystemin)[3]。番茄受到机械损伤后,前系统素水解为系统素,可通过质外体(apoplast)运输到其他细胞,与细胞表面受体 SR160(富含亮氨酸重复单位的蛋白)结合,最终激活茉莉酸信号途径[4-5]。除了创伤信号外,人们在番茄中还发现病菌与真菌激发子诱发的寡聚糖信号,最终也激活茉莉酸信号途径。推测寡聚糖的作用机制与系统素有相似的途径,但具体的诱导机制还不清楚[6-7]。

近几年,在拟南芥(*Arabidopsis thaliana*)中也发现了与系统素具有相同功能的多肽——由 23 个氨基酸组成的 AtPEP1。与系统素的产生类似,机械损伤或者病原体侵染促使前体蛋白 PROPEP1(由 92 个氨基酸组成)水解为 AtPEP1,AtPEP1 与质膜上的受体 PEPR1(富含亮氨酸重复单位的酶)结合,最终激活茉莉酸信号途径[8]。

系统素、AtPEP1 与受体结合诱发茉莉酸信号途径的过程比较复杂,目前知道最主要的过程是激活质膜上的磷脂酶,之后磷脂酶作用于膜上的磷脂释放亚麻酸(茉莉酸合成前体)[9]。不过,系统素激活磷脂酶活化的机制还不清楚。目前为止,人们发现了几种可以被系统素、AtPEP1 诱导的磷脂酶,包括番茄中的 PLA2 和拟南芥中的 DAD1、DGL、PLD,且这几种磷脂酶作用机制相似[10-12]。

1.2 茉莉酸类化合物的合成

针对茉莉酸类化合物在植物体内的合成,近一二十年人们已经研究了多种单子叶和双子叶植

物,其中对模式植物拟南芥和番茄开展的工作最多。到目前为止,茉莉酸类化合物的生物合成途径已经比较清楚,途径中的各种酶已基本完成功能解析,并且关注茉莉酸合成途径与其他代谢途径关联关系的研究逐渐增多。

关于茉莉酸类化合物生物合成的研究进展,国内学者已有较好的综述[13-14],这里不再详细阐述。在拟南芥中,至少存在两条合成茉莉酸的途径,即从亚麻酸(linolenic acid, 18:3)开始的十八烷途径和从十六碳三烯酸(16:3)开始的十六烷途径。两条途径都涉及叶绿体、过氧化物酶体和细胞质 3 个反应场所,从不饱和脂肪酸到 12-氧植物二烯酸(12-oxo-phytodienoic acid, 12-OPDA)或去甲基-含氧植物二烯酸(dn-OPDA)的合成发生在叶绿体中,而后到茉莉酸的转化发生在过氧化物酶体中,对茉莉酸的修饰在细胞质中完成[15]。

茉莉酸(JA)经各种化学修饰会代谢成不同的结构,但目前为止人们仅发现茉莉酸甲酯(MeJA)、茉莉酸-异亮氨酸复合物(JA-Ile)与顺式-茉莉酸(*cis*-jasmone, CJ)这 3 种茉莉酸衍生物在环境诱导的茉莉酸信号途径中起作用[16]。

2　茉莉酸信号的传递

茉莉酸类化合物在植物响应生物与非生物胁迫的反应中扮演着重要角色,在植物的防御过程中起着调控全局的作用。例如,在由创伤信号引发的防御反应中,通常既有伤口附近的局部防御反应,也有未受伤部位的系统获得性抗性(systemic acquired resistance, SAR),乃至相邻植株产生的诱导防御反应。在这些防御反应中,人们发现了茉莉酸信号的短距离传递和远距离传输(图 1)[17]。

2.1　短距离信号传递

当植物受到机械损伤或昆虫取食后,在损伤部位会造成迅速并且短暂的 JA 或 JA-Ile 的积累,由此激活伤口周围组织防御基因的表达,从而产生局部防御反应。在局部防御反应中,茉莉酸信号的短距离传递可能有两种方式。其一,由创伤反应产生的系统素作为信号物质,通过质外体与韧皮部传递到邻近部位,激活茉莉酸级联反应途径。其二,由系统素诱导产生的 JA 与 JA-Ile 充当了流动信号,被转运到邻近部位进行防御反应[18]。

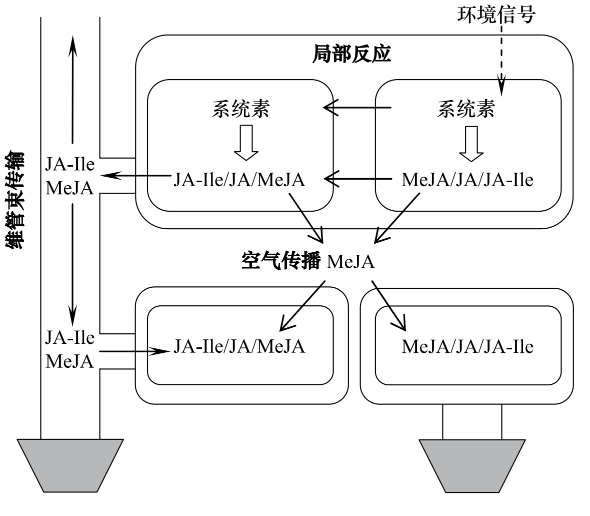

图 1　茉莉酸信号的传递[17]

Fig.1　Transmission of JA signal[17]

2.2　远距离信号传输

目前为止知道,茉莉酸信号的远距离传输方式有维管束传输与空气传播两种。

2.2.1　维管束传输

先前,许多研究者认为系统素在远距离信号传递的过程中发挥直接作用,是一种可移动的信号分子。但是,用拟南芥的茉莉酸不敏感突变体 *jai*1、系统素不敏感突变体 *spr*1、茉莉酸缺失突变体 *spr*2 与 *acx*1*A* 等开展的一系列嫁接实验证明,系统素只是在局部起到信号放大与诱发茉莉酸类化合物合成的作用,之后,茉莉酸类化合物 JA-Ile 在植物体内传输[19]。Thorpe 等则通过同位素标记实验证明,MeJA 可以在维管束中的韧皮部和木质部转移[20]。

一些工作也表明,茉莉酸类化合物并不是简单地沿维管束运输,而是在运输过程中伴随着茉莉酸类化合物的重新合成。在番茄维管束的伴胞和筛管复合体(companion cell-sieveelement complex, CC-SE)中也发现了各种 JA 合成酶(如 LOX、AOS 等)的定位[21],且韧皮部中的筛分子有形成 JA 前体 OPDA 的能力[22]。

近些年 Koo 等[23]通过实验发现,伤诱导导致的全身性 JA、JA-Ile 的产生并非全部由受伤部位转移而来,至少有一部分是重新合成的,并在未受伤部位级联循环产生更多的 JA-Ile。Wang 等也证实了这一结果[24]。

2.2.2　空气传播

实验发现,番茄韧皮部信号的流动速度为每小

时 1—5 cm[25]，但机械损伤后 15 min 内就可在整株检测到 JA 与 JA-Ile 的积累[26]。20 世纪 90 年代 Malone 等的环割实验也证明，即使维管束传输被阻断了，远端叶片中也存在迅速且强烈的防御基因表达[26]。大量的事实表明，除了维管束传输以外，茉莉酸信号还存在其他的远距离传播途径。JA 可被甲基化形成 MeJA。相对于没有载体辅助就难以穿透细胞膜的 JA，MeJA 容易透过细胞膜且有很强的挥发性，可通过空气传播扩散到远距离叶片和相邻的植株而发挥作用[27]。在拟南芥[19]、烟草（*Nicotiana tabacum*）[28]、利马豆（*Phaseolus lunatus*）[29]、山艾树（*Artemisia kawakamii*）[30]等植物中已经证实，MeJA 可以在同一植株的损伤与未损伤叶片之间或相邻植物间通过空气传播。

3 茉莉酸信号的效应

3.1 茉莉酸信号的受体

人们对茉莉酸信号受体的认识经历了复杂的过程。1994 年 Feys 最先确认拟南芥的 COI1 蛋白是茉莉酸敏感蛋白[31]，进一步发现拟南芥 *coi*1 突变体丧失了对茉莉酸的所有反应[32]，证实了这一观点。COI1 是一种泛素连接酶 E3 的组成部分，SCF 型泛素连接酶 E3 包括 S、C、F 3 个组分，其家族所有成员的 S（SKP1 蛋白）和 C（Cullin 蛋白）组分都相同，区分标志是 F 组分（F-box），F-box 蛋白为 COI1 的 SCF 型泛素连接酶 E3 记为 $\mathrm{SCF}^{\mathrm{COI1}}$[33]。COI1 蛋白的发现对于茉莉酸信号途径的研究有着重要意义。

人们曾一度以为 COI1 就是茉莉酸信号在细胞内的受体，直到 JAZ 蛋白家族的发现使人们对茉莉酸信号转导途径有了新的认识。2007 年 Thines 在茉莉酸合成突变体 *opr*3 中发现了 8 个 JAZ 蛋白[34]。在拟南芥中有 12 个 JAZ 蛋白，它们都有 Jas 和 ZIM 两个保守结构域[35]。JAZ 蛋白通过 Jas 结构域与 COI1 相作用，通过 ZIM 结构域与 MYC2 发生作用[36]。因此，许多研究者认为，JAZ 蛋白是 COI1 的靶蛋白，JAZ 蛋白的降解是解除 JA 途径抑制的关键步骤。然而，2010 年 Sheard 等通过晶体结构的分析又对茉莉酸受体提出了不同观点，并证实 COI1-JAZ 复合物是茉莉酸的高亲和受体，即 COI1 与 JAZ 是茉莉酸信号的共同受体[37]。目前认为，当植物受到外界环境刺激后，生成的 JA-Ile 与 COI1-JAZ 复合体直接结合，形成的复合物转移到 26s 蛋白酶体后被降解，同时激活了下游基因的转录（图 2）。

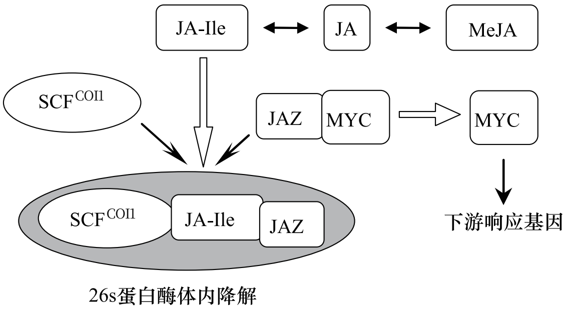

图 2 茉莉酸信号的转导通路

Fig.2 Transduction pathway of JA signal

3.2 茉莉酸信号调控的转录因子

从图 2 看，茉莉酸信号通过 JAZ 蛋白直接启动的是 MYC 类转录因子，不过最新的研究发现，MYB 类转录因子也可以通过与 JAZ 蛋白的结合而被茉莉酸信号激活。此外，受茉莉酸信号调控的还有 NAC、ERF、WRKY 等几类转录因子。茉莉酸信号通过这些转录因子进而调节众多基因的表达、影响植物的生长发育过程特别是植物对环境的响应与适应。也有研究表明，茉莉酸信号还能诱发 MAP 级联反应途径[38]、钙离子通道[39]，以及与乙烯、水杨酸、脱落酸等信号分子互作调控植物生命活动的众多过程[40]。

3.2.1 MYC 类转录因子

在 MYC 类转录因子中，MYC2 蛋白是大家所熟知的调节蛋白。MYC2 属于 bHLH（碱性螺旋-环-螺旋）类转录因子，由 *JIN*1 基因编码。JAZ 蛋白家族中的大多数成员都可与 MYC2 相互作用[41]。很长时间以来，人们认为只有 MYC2 蛋白可以与 JAZ 蛋白直接作用，2011 年 Fernandez-Calvo 等鉴定出另外两种 bHLH 类蛋白——MYC3 与 MYC4，发现它们也可以与 JAZ 蛋白相互作用，并与 MYC2 功能叠加[42]，不过这 3 种 MYC 蛋白在茉莉酸信号途径中的分工以及它们相互之间的作用机制还不是很清楚。

3.2.2 MYB 类转录因子

MYB 类转录因子属于 R2R3-MYB 转录因子家族，在植物应答环境过程中起着重要的调节作用。Dombrecht 等通过 MYC2 突变体 *jin*1 证明，在茉莉酸处理的情况下，MYC2 可以通过调节 MYB51 和 MYB34 的表达量达到负调节色氨酸及吲哚族芥子油苷合成的作用，由此推断 MYB 转录因子在 MYC2

的下游起作用[41]。但近期的研究发现,有一些 MYB 类转录因子可以与 JAZ 蛋白结合,如 MYB75、Glabra1、MYB21 和 MYB24,从而影响植物花青素积累、毛状体形成以及雄蕊成熟等发育过程。这些 MYB 类转录因子与 JAZ 作用的机制与 MYC2 相似,都是通过 JAZ 蛋白的降解来启动下游基因的转录[43-44]。

3.2.3　NAC 类转录因子

NAC 类转录因子在生物与非生物胁迫时也被茉莉酸信号诱导,并且在植物的生长发育过程中起到重要作用。拟南芥 NAC 家族中的 ATAF1、ATAF2 转录因子都受到茉莉酸信号的诱导,茉莉酸信号通过对 ATAF1、ATAF2 的调节提高了植物对干旱、盐胁迫、灰霉病菌及其他一些病原体的抵抗能力,同时对植物的氧化应激反应、开花、角果发育有着重要的调节作用。此外,ATAF1 与 ATAF2 还调节着茉莉酸与水杨酸信号途径之间的相互作用[45-46]。拟南芥中 NAC 家族中的另 2 个转录因子 ANAC019 与 ANAC055 也存在于 MYC2 转录因子的下游,并与 MYC2 起平行作用,可促进种子萌发、细胞分裂、细胞次生壁的合成以及影响脱落酸信号[47]。

3.2.4　ERF 类转录因子

在拟南芥中,ERF 转录因子家族有 122 个成员[48]。近几年基因水平的微阵列实验证实茉莉酸信号可以诱导许多 EFR 转录因子的转录。在拟南芥中,EFR1、EFR2、EFR4 转录因子位于 MYC2 转录因子的下游,同样受到茉莉酸信号的诱导,但 EFR4 却与 EFR1、EFR2 相互抑制[49-50]。此外,茉莉酸信号通过诱导 ORA59 转录因子增加了对灰霉病的抵抗性[51]。在烟草中,OPBP1 转录因子也受到茉莉酸信号的诱导[52]。由于 ERF 转录因子是一类乙烯应答因子,因而也介导着茉莉酸信号途径与乙烯信号途径之间的相互作用[48]。

3.2.5　WRKY 类转录因子

WRKY 类转录因子在植物发育、衰老及应对环境胁迫过程中具有重要调控作用。拟南芥中有 74 个 WRKY 家族成员[53]。近年来的研究表明,有一些 WRKY 类转录因子是受茉莉酸信号调控的,如拟南芥中的 WRKY70[54]、WRKY18[55]、WRKY33[56]、WRKY53[57]、WRKY62[58] 等,它们多与植物的防御功能相关。通过基因敲除、超表达等实验推测它们处于 COI 的下游,且受到 COI 蛋白的抑制作用。在烟草中,2 个 WRKY 类转录因子——NaWRKY3 和 NaWRKY6 可以调节茉莉酸生物合成相关基因(*LOX*、*AOS*、*AOC*、*OPR*)的表达从而提高 JA 和 JA-Ile 的水平,对茉莉酸信号起到反馈作用[59]。此外,WRKY 蛋白也是 MAP 激酶的作用目标[53]。

4　茉莉酸信号参与的生物学过程

4.1　受茉莉酸信号影响的环境应答

大量研究表明,茉莉酸类化合物是与抗性密切相关的植物生长物质,作为内源信号分子参与植物在干旱、盐胁迫、低温等条件下的抗逆反应。

4.1.1　光

植物受光的影响并观察到茉莉酸信号变化的主要体现在两个方面,即植物的光形态建成和 UV-B 对植物的伤害。在拟南芥和水稻中都观察到红光/远红光介导的光形态建成伴随着茉莉酸信号的变化,在蓝光介导的拟南芥光形态建成中也发现茉莉酸信号途径的参与[60-61]。UV-B 辐射的增强能够诱导烟草属和曼陀罗属植物体内茉莉酸的生物合成从而启动茉莉酸信号途径,并且这些过程与植物的化学防御相关联[62-63]。

4.1.2　温度

Zhao 等[64] 对香蕉(*Musa acuminata*)的研究发现,低温处理后内源茉莉酸含量会略有降低,但变化不显著。不过,在寒冷中 MYC 基因会对外源 MeJA 快速反应,并在体内重新合成大量的茉莉酸,抵御寒害。此外,对番茄(*Lycopersicon esculentum*)[65]、石榴(*Punica granatum*)[66]、枇杷(*Eribotrya japonica*)[67]、芒果(*Mangifera indica*)[68]、番石榴(*Psidium guajava*)[69]等植物的研究都表明,外源 MeJA 处理能够诱导热激蛋白家族转录、增加抗氧化剂合成、降低脂氧合酶活性从而增加植物抵御寒害(零上低温)的能力,说明茉莉酸信号途径参与了植物对低温的响应与适应过程。最近对香蕉的研究发现,冷储存后 MeJA 可明显诱导 MYC 家族转录因子以及许多冷敏感基因(*MaCBF*1, *MaCBF*2, *MaCOR*1, *MaKIN*2, *MaRD*2, *MaRD*5 等)的表达,由此减缓寒害对植物的伤害[64]。

目前,有关茉莉酸信号参与植物抗热性的报道相对较少,但在红掌(*Spathiphyllum floribundum*)幼苗

和蝴蝶兰（*Phalaenopsis amabilis*）中已发现外源 MeJA 处理能提高它们的耐热性[70]。

4.1.3 水

已有不少研究发现干旱胁迫中有茉莉酸信号途径的参与。在拟南芥[71]、柑橘（*Citrus paradisi* × *Poncirus trifoliata*）[72]中发现，干旱胁迫后内源茉莉酸含量的增加是快速、瞬时的，而后随着胁迫时间的延长逐渐降低到基础水平。另一方面，外源茉莉酸施加也可以有效地缓解干旱对植物造成的损伤。早期潘瑞炽等用 MeJA 处理提高了花生（*Arachis hypogaea*）幼苗的抗旱性[73]，在水稻（*Oryza sativa*）[74]、大豆（*Glycine max*）[75]、花椰菜（*Brassica oleracea*）[76]中也观察到 MeJA 处理可以通过调整新陈代谢来抵御干旱胁迫。对蚕豆（*Vicia faba*）和大麦（*Hordeum vulgare*）的研究表明，MeJA 可能是通过 K^+ 通道调控气孔运动、从而提高植株抗旱能力的[77-78]。

4.1.4 盐分

在拟南芥[79]、番茄[80]、大麦[81]等植物中都发现，盐处理后内源茉莉酸含量明显增加。而且，在盐敏感的植物中茉莉酸含量增加迅速而又持久，而耐盐植物中茉莉酸含量的变化则不明显[81]。人们也观察到，外源茉莉酸可以提高大豆[82]、胡椒（*Capsicum annuum*）[83]和葡萄藤（*Rupestris riparia*）[84]等植物对盐胁迫的抵御能力。

4.1.5 CO_2浓度

Allhornl 等发现，高浓度 CO_2（500、700、1000 μmol/mol）环境导致利马豆（*Phaseolus lunatus*）向空气中释放茉莉酸类化合物（MeJA 和 *cis*-JA）的量增加[85]。不过，有关 CO_2作用下植物体内茉莉酸信号途径的研究还比较少。

4.1.6 臭氧

经臭氧处理后野生型拟南芥的内源茉莉酸含量明显增加，而用臭氧敏感突变体 *rcd*1（radical-induced cell death 1）[86]、*oji*1（ozone-sensitive and jasmonate-insensitive 1）[87]以及茉莉酸信号突变体 *jar*1[88]开展的实验表明，外源 MeJA 可以抑制由臭氧导致的细胞程序性死亡的传播，而阻断茉莉酸信号则会使植物对臭氧产生更强烈的过敏反应。施加外源 MeJA 也导致杂交杨树（*Populus maximowizii*×*P. trichocarpa*）[89]、番茄[88]对臭氧的敏感性降低。但是，最近对棉花的研究显示，只有在高浓度（685 体积分数）臭氧下，MeJA 才显示出对臭氧损伤扩散的抑制，并伴随着与乙烯的拮抗作用[90]。

4.2 基因芯片和蛋白组学研究结果

近年发展起来的基因芯片和蛋白组学等系统生物学研究手段，可以从全局角度在基因和蛋白质水平上检测植物各种生理过程的反应和变化，从而分析各代谢途径间的相互关系。

Jung 等采用基因芯片技术在 MeJA 处理的拟南芥中鉴定了 137 个表达水平发生变化的基因。其中有 74 个基因上调表达，包括茉莉酸生物合成相关基因、各种防御基因（如 pdf1.2、黑芥子酶结合蛋白的编码基因）、氧化应激基因（氧化酶类、谷胱甘肽转移酶、cyp450 家族的编码基因）、衰老相关基因、细胞壁修饰相关基因、激素代谢相关酶（如负责乙烯合成的 ACC 氧化酶）基因，以及涉及储藏、信号转导、初生和次生代谢相关的基因。63 个基因下调表达，包括光合作用相关基因（Rubisco 酶基因、叶绿素蛋白基因、早期光诱导蛋白基因）、寒冷调节基因、干旱调节基因、防御反应相关基因、植物生长发育相关基因、细胞壁修饰相关基因和一些其他的未知功能基因等[91]。

Chen 等通过蛋白组学方法比较了拟南芥中 MeJA 处理前后各类蛋白含量变化，发现了 186 个差异表达的蛋白。这些蛋白涉及到植物的光合作用、碳水化合物代谢、激素代谢、次生代谢、产物运输、胁迫和防御以及基因转录等[92]。

基因芯片和蛋白组学的研究结果进一步证实了茉莉酸信号途径所涉及的植物生理代谢过程的广泛性。

5 展望

近年来，关于植物环境信号分子——茉莉酸的研究取得了较大的进展，但由于植物对环境的反应是一个多种信号相互作用的复杂体系，茉莉酸信号在植物-环境关系中的作用机制还有待进一步阐明。

有关茉莉酸信号的合成、传递等一系列转导途径已经较为清晰，但是对于不同的环境信号如何被植物感知并启动茉莉酸合成的研究还不系统。由于细胞膜上受体以及激酶种类较多，且不同的生物以及非生物信号会刺激不同的酶活化，同时伴随着钙离子通道、钾离子通道开放等一系列复杂的反应，所

以环境信号的感知尚有很大的研究空间。

茉莉酸受体的研究已取得较大进展，茉莉酸信号转导模式也已经建立，但这一调控过程中还有许多细节不甚清楚。如，茉莉酸信号如何诱导下游转录因子转录，以及这些下游转录因子间如何相互作用共同调控植物生长发育等，都是一系列有待解决的问题。

随着对激素信号网络作用机制研究的不断深入，人们发现水杨酸、乙烯、生长素等植物激素会与茉莉酸信号相互作用，以调节植物适应环境。目前对植物接受环境信号后的复杂调控网络及生物代谢过程的认识还很有限。

References：

[1] Udea J, Kato J. Isolation and identification of a senescence promoting substance from worm wood (*Artemisia absinthiun* L.). Plant Physiology, 1980, 66(2): 246-249.

[2] Pearce G, Strydom D, Johnson S, Ryan C A. A polypeptide from tomato leaves induces wound-inducible proteinase inhibitor proteins. Science, 1991, 253(5022): 895-897.

[3] McGurl B, Pearee G, Orozeo-Cardenas M, Ryan C A. Structure, expression, and antisense inhibition of the systemin precursor gene. Science, 1992, 255(5051): 1570-1573.

[4] Scheer J M, Ryan C A. The systemin receptor SR160 from *Lycopersicon peruvianum* is a member of the LRR receptor kinase family. Proceedings of the National Academy of Sciences of the United States of America, 2002, 99(14): 9585-9590.

[5] Ryan C A, Pearce G. Systemins: A functionally defined family of peptide signals that regulate defensive genes in solanaceae species. Proceedings of the National Academy of Sciences of the United States of America, 2003, 100(S2): 14577-14580.

[6] Farmer E E, Ryan C A. Octadecanoid precursors of jasmonic acid activate the synthesis of wound-inducible proteinase inhibitors. The Plant Cell, 1992, 4(2): 129-134.

[7] Narvάez-Vάsqueza J, Florin-Christensen J, Ryan C A. Positional specificity of a phospholipase A activity induced by wounding, systemin, and oligosaccharide elicitors in tomato leaves. The Plant Cell, 1999, 11(11): 2249-2260.

[8] Yamaguchi Y, Huffaker A, Bryan A C, Tax F E, Ryan C A. PEPR2 is a second receptor for the Pep1 and Pep2 peptides and contributes to defense responses in *Arabidopsis*. The Plant Cell, 2010, 22(2): 508-522.

[9] Ryan C A. The systemin signaling pathway: differential activation of plant defensive genes. Biochimica et Biophysica Acta, 2000, 1477(1/2): 112-121.

[10] Dombrowski J E, Pearce G, Ryan C A. Proteinase inhibitor-inducing activity of the prohormone prosystemin resides exclusively in the C-terminal systemin domain. Proceedings of the National Academy of Sciences of the United States of America, 1999, 96(22): 12947-12952.

[11] Ellinger D, Sting N, Kubigsteltig I I, Bals T, Juenger M, Pollmann S, Berger S, Schuenemann D, Mueller M J. DGL and DAD1 lipases are not essential for wound- and pathogeninduced jasmonate biosynthesis: redundant lipases contribute to jasmonate formation. Plant Physiology, 2010, 153(1): 114-127.

[12] Wang X. Lipid signaling. Current Opinion in Plant Biology, 2004, 7(3): 329-336.

[13] Wasternack C. Jasmonates: An update on biosynthesis, signal transduction and action in plant stress response, growth and development. Annals of Botany, 2007, 100(4): 681-697.

[14] Jiang J K, Pi Y, Hou S, Tang K X. Jasmonate biosynthetic pathway: its physiological role and potential application in plant secondary metabolic engineering. Chinese Bulletin of Botany, 2010, 45(2): 137-148.

[15] Schilmiller A L, Koo A J, Howe G A. Functional diversification of acyl-coenzyme A oxidases in jasmonic acid biosynthesis and action. Plant Physiology, 2007, 143(2): 812-824.

[16] Bruce T J, Matthes M C, Chamberlain K, Woodcock C M, Mohib A, Webster B, Smart L E, Birkett M A, Pickett J A, Napier J A. *Cis*-Jasmone induces *Arabidopsis* genes that affect the chemical ecology of multitrophic interactions with aphids and their parasitoids. Proceedings of the National Academy of Sciences of the United States of America, 2008, 105(12): 4553-4558.

[17] Ryan C A, Moura D S. Systemic wound signaling in plants: a new perception. Proceedings of the National Academy of Sciences of the United States of America, 2002, 99(10): 6519-6520.

[18] Schilmiller A L, Howe G A. Systemic signaling in the wound response. Current Opinion in Plant Biology, 2005, 8(4): 369-377.

[19] Heil M, Ton J. Long-distance signalling in plant defence. Trends in Plant Science, 2008, 13(6): 264-272.

[20] Thorpe M R, Ferrieri A P, Herth M M, Ferrieri R A. ^{11}C-imaging: methyl jasmonate moves in both phloem and xylem, promotes transport of jasmonate, and of photoassimilate even after proton transport is decoupled. Planta, 2007, 226(2): 541-551.

[21] Hause B, Stenzel I, Miersch O, Maucher H, Kramell R, Ziegler J, Wasternack C. Tissue-specific oxylipin signature of tomato flowers: allene oxide cyclase is highly expressed in distinct flower organs and vascular bundles. The Plant Journal, 2000, 24(1): 113-126.

[22] Hause B, Hause G, Kutter C, Miersch O, Wasternack C. Enzymes of jasmonate biosynthesis occur in tomato sieve elements. Plant and Cell Physiology, 2003, 44(6): 643-648.

[23] Koo A J K, Gao X, Jones A D, Howe G A. A rapid wound signal activates systemic synthesis of bioactive jasmonates in Arabidopsis. The Plant Journal, 2009, 59(6): 974-986.

[24] Wang L, Allmann S, Wu J, Baldwin I T. Comparisons of LOX3- and JAR4/6-silenced plants reveal that JA and JA-AA conjugates play different roles in herbivore resistance of *Nicotiana attenuata*. Plant Physiology, 2007, 146(3): 904-915.

[25] Nelson C E, Walker-simmons M, Makus D, Zuroske G, Graham J, Ryan C A. Regulation of synthesis and accumulation of proteinase-inhibitors in leaves of wounded tomato plants. ACS Symposium Series, 1983, 208(6): 103-122.

[26] Malone M. Rapid, long-distance signal transmission in higher plants // Callow J A, ed. Advances in Botanical Research. 1996, 22: 163-228.

[27] Farmer E E, Ryan C A. Interplant communication: airborne methyl jasmonate induces synthesis of proteinase inhibitors in plant leaves. Proceedings of the National Academy of Sciences of the United States of America, 1990, 87(19): 7713-7716.

[28] Park S W, Kaimoyo E, Kumar D, Mosher S, Klessig D F. Methyl salicylate is a critical mobile signal for plant systemic acquired resistance. Science, 2007, 318(5847): 113-116.

[29] Kost C, Heil M. The defensive role of volatile emission and extrafloral nectar secretion for lima bean in nature. Journal of Chemical Ecology, 2008, 34(1): 2-13.

[30] Karban R, Baldwin I T, Baxter K J, Laue G, Felton G W. Communication between plants: induced resistance in wild tobacco plants following clipping of neighboring sagebrush. Oecologia, 2000, 125(1): 66-71.

[31] Feys B, Benedetti C E, Penford C N, Turner J G. Arabidopsis mutants selected for resistance to the phytotoxin coronatine are male sterile, insensitive to methyl jasmonate, and resistant to a bacterial pathogen. The Plant Cell, 1994, 6(5): 751-759.

[32] Xie D X, Feys B F, James S, Nieto-Rostro M, Turner J G. *COI1*: an Arabidopsis gene required for jasmonate-regulated defense and fertility. Science, 1998, 280(5366): 1091-1094.

[33] Devoto A, Nieto-Rostro M, Xie D, Ellis C, Harmston R, Patrick E, Davis J, Sherratt L, Coleman M, Turner J G. COI1 links jasmonate signalling and fertility to the SCF ubiquitin-ligase complex in *Arabidopsis*. The Plant Journal, 2002, 32(4): 457-466.

[34] Thines B, Katsir L, Melotto M, Niu Y, Mandaokar A, Liu G, Nomura K, He S Y, Howe G A, Browse J. JAZ repressor proteins are targets of the SCF^{COI1} complex during jasmonate signalling. Nature, 2007, 448(7154): 661-665.

[35] Staswick P E. JAZing up jasmonate signaling. Trends in Plant Science, 2008, 13(2): 66-71.

[36] Chini A, Fonseca S, Chico J M, Fernάndez-Calvo P, Solano R. The ZIM domain mediates homo- and heteromeric interactions between Arabidopsis JAZ proteins. The Plant Journal, 2009, 59(1): 77-87.

[37] Sheard L B, Tan X, Mao H, Withers J, Ben-Nissan G, Hinds T R, Kobayashi Y, Hsu F F, Sharon M, Browse J, He S Y, Rizo J, Howe G A, Zheng N. Jasmonate perception by inositol-phosphate-potentiated COI1-JAZ co-receptor. Nature, 2010, 468(7322): 400-405.

[38] Takahashia F, Yoshida R, Ichimurac K, Mizoguchi T, Seo S, Yonezawa M, Maruyama K, Yamaguchi-Shinozaki K, Shimozaki K. The mitogen-activated protein kinase cascade MKK$_3$-MPK$_6$ is an important part of the jasmonate signal transduction pathway in *Arabidopsis*. The Plant Cell, 2007, 19(3): 805-818.

[39] Kenton P, Mur L A J, Draper J. A requirement for calcium and protein phosphatase in the jasmonate-induced increase in tobacco leaf acid phosphatase specific activity. Journal of Experimental Botany, 1999, 50(337): 1331-1341.

[40] Santner A, Estelle M. Recent advances and emerging trends in plant hormone signaling. Nature, 2009, 459(7250): 1071-1078.

[41] Dombrecht B, Xue G P, Sprague S J, Kirkegaard J A, Ross J J, Reid J B, Fitt G P, Sewelam N, Schenk P M, Manners J M, Kazan K. MYC2 differentially modulates diverse jasmonate-dependent functions in *Arabidopsis*. The Plant Cell, 2007, 19(7): 2225-2245.

[42] Fernάndez-Calvo P, Chini A, Fernάndez-Barbero G, Chico J M, Gimenez-Ibanez S, Geerinck J, Eeckhout D, Schweizerd F, Godoy M, Franco-Zorrillae J M, Pauwels L, Witters E, Puga M I, Paz-Aresa J, Goossens A, Reymond P, De Jaeger G, Solano R. The *Arabidopsis* bHLH transcription factors MYC$_3$ and MYC$_4$ are targets of JAZ repressors and act additively with MYC$_2$ in the activation of jasmonate responses. The Plant Cell, 2011, 23(2): 701-715.

[43] Song S, Qi T, Huang H, Ren Q, Wu D, Chang C, Peng W, Liu Y, Peng J, Xie D. The jasmonate-ZIM domain proteins interact with the R2R3-MYB transcription factors MYB21 and MYB24 to affect jasmonate-regulated stamen development in *Arabidopsis*. The Plant Cell, 2011, 23(3): 1000-1013.

[44] Qi T, Song S, Ren Q, Wn D, Huang H, Chen Y, Fan M, Peng W, Ren C, Xie D. The jasmonate-ZIM-domain proteins interact with the WD-Repeat/bHLH/MYB complexes to regulate jasmonate-mediated anthocyanin accumulation and trichome initiation in *Arabidopsis thaliana*. The Plant Cell, 2011, 23(5): 1795-1814.

[45] Delessert C, Kazan K, Wilson I W, van der Straeten D, Manners J, Dennis E S, Dolferus R. The transcription factor ATAF2 represses the expression of pathogenesis-relatedgenes in *Arabidopsis*. The Plant Journal, 2005, 43(5): 745-757.

[46] Lu P L, Chen N Z, An R, Su Z, Qi B S, Ren F, Chen J, Wang X C. A novel drought-inducible gene, *ATAF1*, encodes a NAC family protein that negatively regulates the expression of stress-responsive genes in *Arabidopsis*. Plant Molecular Biology, 2007, 63(2): 289-305.

[47] Bu Q, Jiang H, Li C B, Zhai J, Wu X, Sun J, Xie Q, Li C. Role of the *Arabidopsis thaliana* NAC transcription factors ANAC019 and ANAC055 in regulating jasmonic acid-signaled defense responses. Cell Reasearch, 2008, 18(7): 756-767.

[48] Nakano T, Suzuki K, Fujimura T, Shinshi H. Genome-wide analysis of the ERF gene family in Arabidopsis and Rice. Plant Physiology, 2006, 140(2): 411-432.

[49] McGrath K C, Dombrecht B, Manners J M, Schenk P M, Edgar C I, Maclean D J, Scheible W R, Udvardi M K, Kazzan K. Repressor-and activator-type ethylene response factors functioning in jasmonate signaling and disease resistance identified via a genome-wide screen of *Arabidopsis* transcription factor gene

expression. Plant Physiology, 2005, 139(2): 949-959.

[50] Lorenzo O, Piqueras R, Sánchez-Serrano J J, Solano R. ETHYLENE RESPONSE FACTOR1 integrates signals from ethylene and jasmonate pathways in plant defense. The Plant Cell, 2003, 15(1): 165-178.

[51] Pré M, Atallah M, Champion A, de Vos M, Pieterse C M J, Memelink J. The AP2/ERF domain transcription factor ORA59 integrates jasmonic acid and ethylene signals in plant defense. Plant Physiology, 2008, 147(3): 1347-1357.

[52] Gu Y Q, Yang C, Thara V K, Zhou J, Martin G B. *Pti*4 is induced by ethylene and salicylic acid, and its product is phosphorylated by the Pto kinase. The Plant Cell, 2000, 12(5): 771-785.

[53] Eulgem T, Somssich I E. Networks of WRKY transcription factors in defense signalling. Current Opinion in Plant Biology, 2007, 10(4): 366-371.

[54] Li J, Brader G, Palva E T. The WRKY70 transcription factor: a node of convergence for jasmonate-mediated and salicylate-mediated signals in plant defense. The Plant Cell, 2004, 16(2): 319-331.

[55] Xu X P, Chen C H, Fan B F, Chen Z X. Physical and functional interactions between pathogen-induced *Arabidopsis* WRKY18, WRKY40, and WRKY60 transcription factors. The Plant Cell, 2006, 18(5): 1310-1326.

[56] Zheng Z, Qamar S A, Chen Z, Mengsite T. Arabidopsis WRKY33 transcription factor is required for resistance to necrotrophic fungal pathogens. The Plant Journal, 2006, 48(4): 592-605.

[57] Miao Y, Laun T, Zimmermann P, Zentgraf U. Targets of the WRKY53 transcription factor and its role during leaf senescence in *Arabidopsis*. Plant Molecular Biology, 2004, 55(6): 853-867.

[58] Mao P, Duan M, Wei C, Li Y. WRKY62 transcription factor acts downstream of cytosolic NPR1 and negatively regulates jasmonate-responsive gene expression. Plant and Cell Physiology, 2007, 48(6): 833-842.

[59] Skibbe M, Qu N, Galis I, Balawin I T. Induced plant defenses in the natural environment: *Nieotiana attenuala* WRKY3 and WRKY6 coordinate responses to herbivory. The Plant Cell, 2008, 20(7): 1984-2000.

[60] Cerrudo I, Keller M M, Cargnel M D, Demkura P V, Wit M, Patitucci M S, Pierik R, Pieterse C M J, Ballaré C L. Low Red/Far-Red ratios reduce *Arabidopsis* resistance to *Botrytis cinerea* and jasmonate responses via a COI1-JAZ10-dependent, salicylic acid-independent mechanism. Plant Physiology, 2012, 158(4): 2042-2052.

[61] Moreno J E, Tao Y, Chory J, Ballaré C L. Ecological modulation of plant defense via phytochrome control of jasmonate sensitivity. Proceedings of the National Academy of Sciences of the United States of America, 2009, 106(12): 4935-4940.

[62] Svyatyna K, Riemann M. Light-dependent regulation of the jasmonate pathway. Protoplasma, 2012, 249(12): 137-145.

[63] Izaguirre M M, Mazza C A, Svatoš A, Baldwin I T, Ballaré C L. Solar ultraviolet-B radiation and insect herbivory trigger partially overlapping phenolic responses in *Nicotiana attenuata* and *Nicotiana longiflora*. Annals of Botany, 2007, 99(1): 103-109.

[64] Zhao M L, Wang J N, Shan W, Fan J G, Kuang J F, Wu K Q, Li X P, Chen W X, He F Y, Chen J Y, Lu W J. Induction of jasmonate signalling regulators MaMYC2s and their physical interactions with MaICE1 in methyl jasmonate-induced chilling tolerance in banana fruit. Plant, Cell and Environment, 2012, 36(1): 30-51.

[65] Siripatrawan U, Assatarakul K. Methyl jasmonate coupled with modified atmosphere packaging to extend shelf life of tomato (*Lycopersicon esculentum* Mill.) during cold storage. International Journal of Food Science and Technology, 2009, 44(5): 1065-1071.

[66] Sayyari M, Babalar M, Kalantari S, Martínez-Romero D, Guillén F, Serrano M, Valero D. Vapour treatments with methyl salicylate or methyl jasmonate alleviated chilling injury and enhanced antioxidant potential during postharvest storage of pomegranates. Food Chemistry, 2011, 124(3): 964-970.

[67] Cao S F, Zheng Y H, Wang K T, Jin P, Rui H J. Methyl jasmonate reduces chilling injury and enhances antioxidant enzyme activity in postharvest loquat fruit. Food Chemistry, 2009, 115(4): 1458-1463.

[68] González-Aguilar G A, Fortiz J, Cruz R, Baez R, Wang C Y. Methyl jasmonate reduces chilling injury and maintains postharvest quality of mango fruit. Journal of Agricultural and Food Chemistry, 2000, 48(2): 515-519.

[69] González-Aguilar G A, Tiznado-Hernández M E, Zavaleta-Gatica R, Martínez-Téllez M A. Methyl jasmonate treatments reduce chilling injury and activate the defense response of guava fruits. Biochemical and Biophysical Research Communications, 2003, 313(3): 694-701.

[70] Yang H G, Yan S L, Chen H J, Yang Z F, Yang F S, Liu Z F. Effect of exogenous methyl jasmonate, calcium and salicylic acid on the heat tolerance in phalaenopsis seedlings under high temperature stress. Chinese Agricultural Science Bulletin, 2011, 27(28): 150-157.

[71] Arbona V, Argamasilla R, Gómez-Cadenas A. Common and divergent physiological, hormonal and metabolic responses of *Arabidopsis thaliana* and *Thellungiella halophila* to water and salt stress. Journal of Plant Physiology, 2010, 167(16): 1342-1350.

[72] Ollas C, Hernando B, Arbona V, Gómez-Cadenas A. Jasmonic acid transient accumulation is needed for abscisic acid increase in citrus roots under drought stress conditions. Physiologia Plantarun, 2013, 147(3): 296-306.

[73] Pan R C, Gu H Q. Effect of methyl jasmonate on the growth and drought resistance in peanut seedlings. Acta Phytophysiologica Sinica, 1995, 21(3): 215-220.

[74] Dong T X, Cai K Z, Zang J X, Rong H, Xie G Z, Zeng R S. The physiological roles of methyl jasmonate (MeJA) in drought resistance of rice seedlings. Ecology and Environment, 2007, 16(4): 1261-1265.

[75] Anjum S A, Xie X Y, Farooq M, Wang L C, Xue L L, Shahbaz

M, Salhab J. Effect of exogenous methyl jasmonate on growth, gas exchange and chlorophyll contents of soybean subjected to drought. African Journal of Biotechnology, 2011, 10(47): 9640-9646.

[76] Wu H L, Wu X L, Li Z H, Duan L S, Zhang M C. Physiological evaluation of drought stress tolerance and recovery in cauliflower (*Brassica oleracea* L.) seedlings treated with methyl jasmonate and coronatine. Journal of Plant Growth Regulation, 2012, 31(1): 113-123.

[77] Evans N H. Modulation of guard cell plasma membrane potassium currents by methyl jasmonate. Plant Physiology, 2003, 131(1): 8-11.

[78] Horton R F. Methyl jasmonate and transpiration in barley. Plant Physiology, 1991, 96(4): 1376-1378.

[79] Asensi-Fabado M A, Munné-Bosch S. The *aba*3-1 mutant of *Arabidopsis thaliana* withstands moderate doses of salt stress by modulating leaf growth and salicylic acid levels. Journal of Plant Growth Regulation, 2011, 30(4): 456-466.

[80] Pedranzani H, Racagni G, Alemano S, Miersch O, Ramírez I, Peña-Cortés H, Taleisnik E, Machado-Domenech E, Abdala G. Salt tolerant tomato plants show increased levels of jasmonic acid. Plant Growth Regulations, 2003, 41(2): 149-158.

[81] Kramell R, Miersch O, Atzorn R, Parthier B, Wasternack C. Octadecanoid-derived alteration of gene expression and the 'oxylipin signature' in stressed barley leaves. Implications for different signaling pathways. Plant Physiology, 2000, 123(1): 177-188.

[82] Yoon J Y, Hamayun M, Lee S K, Lee I J. Methyl jasmonate alleviated salinity stress in soybean. Journal of Crop Science and Biotechnology, 2009, 12(2): 63-68.

[83] An S H, Choi H W, Hwang I S, Hong J K, Hwang B K. A novel pepper membrane-located receptor-like protein gene *CaMRP*1 is required for disease susceptibility, methyl jasmonate insensitivity and salt tolerance. Plant Molecular Biology, 2008, 67(5): 519-533.

[84] Ismail A, Riemann M, Nick P. The jasmonate pathway mediates salt tolerance in grapevines. Journal of Experimental Botany, 2012, 63(5): 2127-2139.

[85] Ballhorn D J, Reisdorff C, Pfanz H. Quantitative effects of enhanced CO_2 on jasmonic acid induced plant volatiles of lima bean (*Phaseolus lunatus* L.). Journal of Applied Botany and Food Quality, 2011, 84(1): 65-71.

[86] Overmyer K, Tuominen H, Kettunen R, Betz C, Langebartels C, Sandermann H J, Kangasjārvi J. Ozone-sensitive *Arabidopsis rcd*1 mutant reveals opposite roles for ethylene and jasmonate signaling pathways in regulating superoxide-dependent cell death. The Plant Cell, 2000, 12(10): 1849-1862.

[87] Kanna M, Tamaoki M, Kubo A, Nakajima N, Rakwal R, Agrawal G K, Tamogami S, Ioki M, Ogawa D, Saji H, Aono M. Isolation of an ozone-sensitive and jasmonate-semi-insensitive *Arabidopsis* mutant (*oji*1). Plant Cell Physiology, 2003, 44(12): 1301-1310.

[88] Rao M V, Lee H, Creelman R A, Mullet J E, Davis K R. Jasmonic acid signaling modulates ozone-induced hypersensitive cell death. The Plant Cell, 2000, 12(9): 1633-1646.

[89] Koch J R, Creelman R A, Eshita S M, Seskar M, Mullet J E, Davis K R. Ozone sensitivity in hybrid poplar correlates with insensitivity to both salicylic acid and jasmonic acid. The role of programmed cell death in lesion formation. Plant Physiology, 2000, 123(2): 487-496.

[90] Grantz D A, Vu H B. Root and shoot gas exchange respond additively to moderate ozone and methyl jasmonate without induction of ethylene: ethylene is induced at higher O_3 concentrations. Journal of Experimental Botany, 2012, 63(11): 4303-4313.

[91] Devoto A, Ellis C, Magusin A, Chang H S, Chilcott C, Zhu T, Turnter J G. Expression profiling reveals *COI*1 to be a key regulator of genes involved in wound- and methyl jasmonate-induced secondary metabolism, defence, and hormone interactions. Plant Molecular Biology, 2005, 58(4): 497-513.

[92] Chen Y Z, Pang Q Y, Dai S J, Wang Y, Chen S X, Yan X F. Proteomic identification of differentially expressed proteins in *Arabidopsis* in response to methyl jasmonate. Journal of Plant Physiology, 2011, 168(10): 995-1008.

参考文献：

[14] 蒋科技，皮妍，候嵘，唐克轩. 植物内源茉莉酸类物质的生物合成途径及其生物学意义. 植物学报，2010，45(2)：137-148.

[70] 杨华庚，颜速亮，陈慧娟，洋重法，杨福孙，刘子凡. 高温胁迫下外源茉莉酸甲酯、钙和水杨酸对蝴蝶兰幼苗耐热性的影响. 中国农学通报，2011，27(28)：150-157.

[73] 潘瑞炽，古焕庆. 茉莉酸甲酯对花生幼苗生长和抗旱性的影响. 植物生理学报，1995，21(3)：215-220.

[74] 董桃杏，蔡昆争，张景欣，荣辉，谢国政，曾任森. 茉莉酸甲酯(MeJA)对水稻幼苗的抗旱生理效应. 生态环境，2007，16(4)：1261-1265.