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一氧化氮信号在果树成花中的研究进展

李松刚[1],张 蕾[1],洪继旺[1],宋雯佩[2],杨子琴[1]

(1.中国热带农业科学院 热带作物品种资源研究所,农业部华南作物基因资源与种质创制重点实验室,国家热带果树品种改良中心,海南 儋州 571737;2.华南农业大学 园艺学院,广东 广州 510642)

摘 要:一氧化氮(NO)作为一种胁迫后的重要信号分子,在植物生长发育的许多过程中具有重要的调节作用。越来越多的研究证据表明,NO在植物花发育过程中具有重要作用,然而迄今尚鲜见关于NO调控果树成花发育方面的系统报道。该研究介绍了植物NO合成途径的最新研究进展,综述了NO在草本及木本植物中开花转变存在的差异,以期为植物内源NO对木本果树花芽分化的调节研究提供理论参考。

关键词:一氧化氮;生物合成;花芽分化;木本果树

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花芽分化是果树产量形成的第一步。探索成花信号物质也一直是果树学界最为引人入胜的课题之一。果树成花随季节有节律地呈现,这些活动受内源生物钟、C/N、激素、胁迫信号、成花基因调节[1-6]。

第一作者简介:李松刚(1976-),男,博士,副研究员,现主要从事热带果树栽培生理等研究工作。E-mail:397859405@qq.com.

责任作者:杨子琴(1981-),女,博士,副研究员,现主要从事热带果树栽培生理等研究工作。E-mail:yangziqin1@163.com.

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通常情况下,环境胁迫可打破自然规律,诱导果树成花,因此研究胁迫效应将是揭开成花信号物质的一个契机。任何环境的胁迫都会造成氧化胁迫,因此,氧化胁迫所产生的信号物质在果树成花过程中的作用显得日益重要,NO作为一种胁迫后信号分子,对其研究才刚刚起步。

以往的研究多聚焦在NO是动物细胞第二信使上,但越来越多的试验表明其同时也是植物细胞中一种重要的信号分子[7-8]。作为一个重要的活性基团,NO在叶片伸展、根系生长、花芽分化、枝条抽生、花粉管生长、组织衰老、抗旱性、气孔关闭、三重反应

Abstract:Xinjiang has colorful land, light and heat resources, varieties resources to meet advantage of apricot industry development conditions, this can be turned Xinjiang into an ideal production base of apricot. Therefore, to determine the apricot industry's future direction of all over the country, state, city in Xinjiang, and scale of the field to provide the scientific basis. In this study, literature material, statistical data and drawing methods were used to study around Xinjiang, apricot industrial advantages, development, size and yield variation and the problem, and the apricot industry, health, stability, standardization, large-scale development of countermeasures. The results showed that, all over the states and cities have the advantage of developing apricot industry, these natural resources and varieties resource advantages is just the basis and premise for developing apricot industry, it is not a sufficient condition. Only developed a resource characteristics and market competitiveness of products, to make natural resource advantages into economic advantages. All over the state, apricot acreage of different periods from 1999 to 2009 period increased, but the declining trend in period from 2009 to 2013, but has maintained a certain scale. Apricot industry have economic, ecological and social benefits, in addition pharmaceuticals, health care products and beverage development have a high value, therefore, it can be developed in the direction of development and the development of the field.

Keywords:apricot; development present situation; existing problems; countermeasures; Xinjiang

及生物/非生物胁迫适应性方面具有重要作用[9-17]，同时还与活性氧协同作用启动植物的应逆反应[18]。但 NO 在果树成花方面的研究还很薄弱，尚待进一步探索。

1 NO 与花芽分化

NO 是一个气态自由基分子，在它的轨道上有一个不成对的电子却不带电。因此，NO 可以得到或失去一个电子而存在 3 种可转换的形式，即 NO、NO^+、NO^-，所以既可以在细胞质中扩散，也可以穿透生物膜[19-20]。NO 一旦形成，可以从一个细胞扩散到另一个细胞，也可以在细胞内游移。作为一种胁迫后产生的信号分子，NO 也逐渐显露出在成花调控中的信号分子功能[21]。喷施硝普钠(SNP)可以促进龙眼树提前成花，NO 清除剂抑制龙眼成花[22]，这暗示了 NO 信号途径与成花有潜在的联系。在荔枝上，低温和干旱胁迫会引起 ABA 的积累[23]，而 ABA 在植物中充当了传递环境胁迫信号的第一信使[24-25]，而 NO 是参与 ABA 信号转导的主要物质[26]。外源 NO 促进剂可以诱导蝴蝶兰花器官中游离氧离子浓度增加，进而增加氧化损伤和脂质过氧化[27]。低温胁迫可诱导荔枝混合花芽中 NO 含量上升；NO 发生剂 SNP 处理同样增加荔枝混合花芽中 NO 的含量，促进抽生纯花芽；NO 合酶抑制剂 L-NNA 抑制荔枝成花，表明 NO 正调控荔枝成花[28]。ZAFRA 等[29]发现，油橄榄成花过程依赖于 NO 的参与。低温等环境胁迫及 NO 供体均可诱导 NO 产生，实际上，低温胁迫以及 NO 供体诱导还存在着另一共同的特征，都会导致植物顶端生长受到抑制[30]，是否因此而调控了果树营养生长向生殖生长的转变也未知。因此，研究 NO 途径与成花的关系将会成为一个揭示果树开花的新突破口。

草本植物中有相反的报道，认为 NO 供体 SNP 的应用导致拟南芥开花延迟，通过遗传筛选发现拟南芥突变体具有高或低的内源性 NO 水平，从而延迟或提早开花；高浓度的 NO 抑制花分生组织中 *LFY* 基因的表达和 *CO* 基因对成花的促进作用；此外，增加了成花限制基因 *FLC* 的表达[10]。

但是，NO 对龙眼成花的作用机理目前尚不明朗。尤其 NO 对成花的作用还存在争议，这些发现使课题组怀疑是否 NO 在木本与草本植物成花中存在不同效应？亦或高浓度的 NO 抑制成花，低浓度的 NO 促进成花？更甚至于 NO 在控制龙眼冬梢方面的作用更重于在成花促进方面的作用？这些问题都有待进一步的探索。

2 NO 合成途径

NO 由若干细胞反应所生成，可以通过酶及非酶系统在动植物体产生。在植物系统中，研究表明 NOs 类似物在过氧化物酶体、叶绿体及单个的线粒体有活性[31]；但是直至今天，NO 由精氨酸途径生成的论断还存在争议[32]。一部分研究支持 NO 由精氨酸利用途径产生，而非胍氨酸(一个重要的 NOs 特征产物)的协同产物[31]，并且已经从绿藻中获得与高等植物同源的 NOs[32-34]；另有研究表明，植物中的 NO 也可由硝酸/亚硝酸依赖途径产生，这涉及到细胞溶质硝酸还原酶(NR)，且该途径通过根系-特异质膜亚硝酸-NO 还原酶来实施[35]。在拟南芥的叶片中，内源 NO 显著的增加主要依赖于硝酸还原酶活性，且冷胁迫下还上调了 *NIA1* 基因的表达[36]；而非酶促途径也可生成 NO，亚硝酸在酸性条件下(pH<5)可歧化为 NO 和硝酸[37]。这种非酶促机制也是植物中 NO 产生的途径之一[38]。研究表明，在植物体内质外体空间等微环境中存在适合 NO 非酶促反应的 pH 条件[39]。亚硝酸根可以在 NADPH、还原性的谷胱甘肽、抗坏血酸等还原性物质作用下转化成 NO[40]，植物中的类胡萝卜素也可以通过光介导转化 NO_2 产生 NO[38,41]。

最常用的 NO 供体为 SNP(硝普钠)，其它的 NO 供体有 S-亚硝基硫醇类(RSNOs)，例如 GS-NO 和 SNAP[15,42]。RSNOs 非还原型降解依赖高温及 pH，并释放出二硫化物及 NO，而 NO 供体 DEA-NONOate 可自发地分解释放出 2 个 NO 分子和胺类，被广泛应用在动物试验中[43]。PTIO 和 cPTIO 常常被用来清除 NO，NOs 抑制剂(L-NNA)也被用来减少或抑制内源 NO 的产生[44-45]。钨酸钠也被广泛的用于降低 NR 所介导的硝酸/亚硝酸途径中产生的 NO，但是钨酸钠并非一个特异的 NR 抑制剂，且还可能影响其它的 NO 产生途径[46]。

最近的研究表明，NO 对拟南芥在低温下形成硝氨醇磷酸盐和神经酰胺磷酸盐的反应起负调控作用[47]；甚至在冷诱导的氧化损伤中，精氨酸途径生成的 NO 可充当一种抗氧化剂或者作为一个抗氧化信号，增强植物体对氧化损伤的耐受力[48]。越来越多的证据表明，NO 信号途径通过第二信使 cGMP 在多种生理及药理反应中有作用[49-50]。SALMI 等[51]报道，NO-cGMP 信号途径在百合花花粉萌发及花粉管伸长方面具有信号作用，主要起细胞极性重力定向作用。

3　NO-cGMP 信号途径

植物可感知 NO 并作出应答，而其完成应答的潜在机制还不清晰。NO 参与了众多的生物反应，且可能与众多的蛋白质有修饰或互作。这些分子活动大部分通过结合金属蛋白的过渡态金属和共价修饰半胱氨酸和酪氨酸残基来实现[52]。少部分的数据支持 NO 在成花调控方面具有潜在的功能，而可溶性鸟苷酸环化酶(sGC)作为 NO 的受体，参与 NO-cGMP 信号转导调节，其研究意义不可小觑。

NO 受体蛋白 sGC 的结构当中有一个血红素分子，NO 专一性与血红素簇可溶性鸟苷酸环化酶(sGC)结合，结合后血红素的构象改变，导致 sGC 活性升高，从而导致三磷酸鸟苷(GTP)转化为环鸟苷酸(cGMP)，进而激活下游通路[14,16]。cGMP 作为细胞内的第二信使，可被 PDE5 水解，从而终结第二信使所传导的生化作用。sGC 抑制剂包含 ODQ、ly85583；并且 PDE5 抑制剂(Sildenafil)的施用也造成了 cGMP 的累积，这些均说明 cGMP 在 NO 的下游。cGMP 的功能还通过研究 8-Br-cGMP (cGMP 类似物)在恢复 ODQ 的功能上得到进一步验证[26,53]。受体鸟苷酸环化酶(sGC)是一种一次跨膜的糖蛋白，其 N 端胞外域可结合配体，C 端胞内域有 2 个 GMP 环化酶催化结构。当受体与胞外信号分子 NO 结合时，胞内域表现出 sGC 活性，催化 GTP 生成 cGMP。cGMP 作为第二信使结合并激活 cGMP 依赖的蛋白激酶 G (PKG)，被激活的 PKG 将特定蛋白上的丝氨酸/苏氨酸残基磷酸化。近些年，人们已开始应用基因克隆技术研究 sGC，发现这是一个日益增大的基因家族[54]。在许多高等植物中，已经证实了 sGC 的活性，NO-cGMP 途径的研究也得到了极大的发展与进步，而在龙眼中关于成花与 NO-cGMP 途径关系的研究尚未见报道，因此，研究龙眼成花过程中 sGC 的特性及其在 NO-cGMP 途径中对成花的作用，对进一步了解 NO-cGMP 信号转导通路起到一定的帮助。

sGC 基因已经在草本植物番茄中获得(GenBank：EF017658.1)。然而，在许多案例中，依赖 NO 的生理及药理学反应往往受复杂信号网络所调控，依据现有的研究基础，绘制了 NO 合成及信号传导网络(图 1)，而 NO-cGMP 途径在成花中的生物化学和分子机制还有待深入研究。

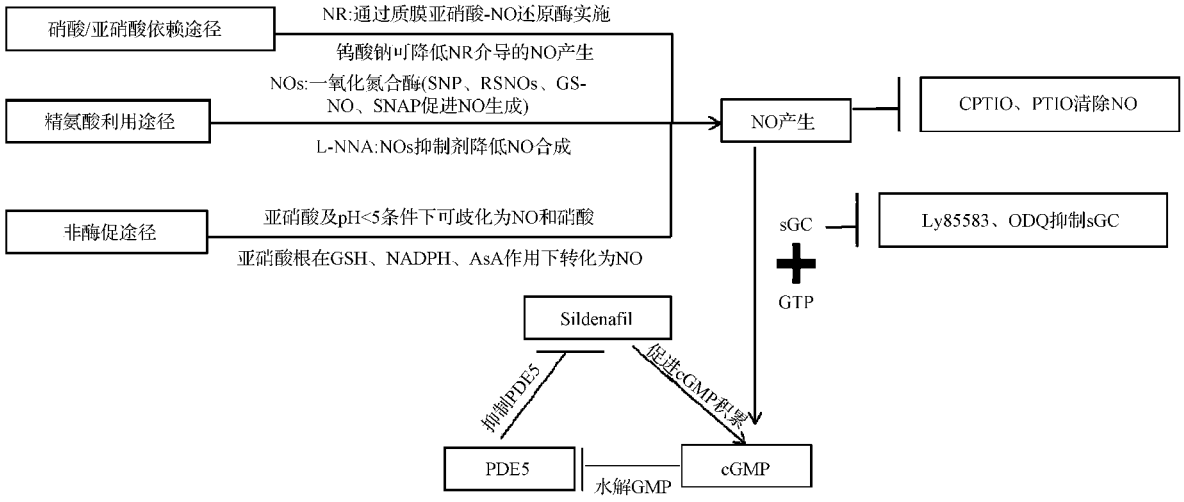

图 1　NO 合成及信号传导途径

Fig. 1　NO synthesis and signal transduction pathway

木本果树成花是一个复杂的过程，当植株营养生长达到一定积累后，光照、温度、水分等外界条件及植株营养状况等内部条件会刺激顶端分生组织启动成花。随着模式植物开花诱导过程的探明，木本果树的成花研究也有了很好的借鉴。研究木本果树成花调节机制，可为打破果树休眠、实现花芽分化调控、提高果实品质和产量提供依据。随着生理学、遗传与分子生物学技术的结合及不断发展，木本果树成花机制将逐步阐明，调控成花将成为可能。

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Research Progress of NO in Flowering of Fruit Trees

LI Songgang[1],ZHANG Lei[1],HONG Jiwang[1],SONG Wenpei[2],YANG Ziqin[1]
(1. Tropical Crops Genetic Resources Institute,Chinese Academy of Tropical Agricultural Sciences/Key Laboratory of Crop Gene Resources and Germplasm Enhancement in Southern China/The National Center for Tropical Fruit Tree Variety Imparovement,Danzhou,Hainan 571737;2. College of Horticulture,South China Agricultural University,Guangzhou,Guangdong 510642)

Abstract:Nitric oxide (NO),as an important signal molecule,plays an important role in many processes of plant growth and development. There was increasing evidence that NO plays a vital role in the process of flower development,which,however,had not been comprehensively reviewed for a long time. This study introduced the latest research progress of the plant NO synthesis pathway,and discussed the differences in flowering between herbaceous and woody plants by NO. In order to provide reference for the regulation of plant endogenous NO on the flower bud differentiation of woody fruit trees.

Keywords:nitric oxide;biosynthesis;flower bud differentiation;woody fruit trees