

The Role of Nitric Oxide in Plant Immune Response

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Abstract

Reactive oxygen species (ROS) is an important component of the signalling network that plants use for responding to environmental challenges. NO has an important function as a key signalling molecule in plant growth, development, and senescence, and reactive nitrogen species (RNS), like reactive oxygen species (ROS), also play an important role as signalling molecules in the response to biotic stress. Similarly, NO is a key mediator, in co-operation with ROS, in the defence response to pathogen attacks in plants. NO regulates diverse cellular signaling through S-nitrosylation of specific Cys residues of target proteins. The intracellular level of S-nitrosoglutathione (GSNO), a major bioactive NO species, is regulated by GSNO reductase 1 (GSNOR1), a key enzyme that regulates cellular homeostasis of S-nitrosylation across kingdoms. GSNOR1 also plays an important role in plant immune defense response. Here we review the research progress of the role of NO in plant defense responses.

Keywords

Nitric Oxide, S-Nitrosoglutathione Reductase, Programmed Cell Death, Disease Resistance

一氧化氮在植物免疫反应中的作用

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摘要

活性氧(Reactive Oxygen Species, ROS)是植物响应外界胁迫信号通路中的重要组分。一氧化氮(Nitric Oxide, NO)是植物生长、发育和衰老中的关键信号分子。与ROS一样, 活性氮(Reactive Nitrogen Species,

RNS)在植物应对生物胁迫中发挥着重要的作用。此外, NO可以和ROS协同应对病原菌的侵袭。NO通过调控特定靶蛋白半胱氨酸残基的S-亚硝基化来进行信号转导, 而亚硝基谷胱甘肽(S-nitrosoglutathione, GSNO)是生物体内具有生物活性的NO形式。亚硝基谷胱甘肽还原酶1 (S-nitrosoglutathione reductase 1, GSNOR1)可以特异性还原GSNO以达到植物体内亚硝基化水平稳态平衡。GSNOR1在植物免疫防御反应中同样具有重要的作用。在这里我们就NO在植物防御反应中的作用的研究进展进行了综述。

关键词

一氧化氮, 亚硝基谷胱甘肽还原酶, 细胞程序性死亡, 免疫反应

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1. 引言

一氧化氮(Nitric oxide, NO)是参与动物和植物各种发育过程和胁迫响应的关键信号分子[1]。通过对催化NO合成的酶以及NO调控靶蛋白的不断研究, NO信号转导机制越来越明了[2] [3]。动物中NO不仅来自亚硝酸盐, 还来自L-精氨酸(L-Arg), L-Arg是动物NO合成的主要底物[4]。而在植物中NO不仅可以在体内产生还可以从周围的环境或土壤中获得[4]。

NO通过调控特定靶蛋白半胱氨酸残基的S-亚硝基化来进行信号转导[5] [6]。近年来, 植物中大量蛋白质被鉴定为S-亚硝基化的靶标, 蛋白质亚硝基化可以直接或间接的影响植物细胞程序性死亡(Programmed cell death, PCD) [7]。在植物应对生物和非生物胁迫响应中, ROS和NO的爆发及其相互调节对于早期信号转导至关重要。GSNO是植物体内主要的具有生物活性的NO形式[6]。GSNO可以被保守的亚硝基谷胱甘肽还原酶1 (GSNOR1)特异性降解, 从而使植物体内亚硝基化水平可以保持稳态平衡[8]。NO及其信号网络组分的改变都会对植物免疫产生重要影响。

2. 植物一氧化氮产生及ROS信号转导

NO是活性氮(Reactive nitrogen species, RNS)种类之一[9], 它在植物生长、发育、应对生物和非生物胁迫以及细胞程序性细胞死亡(PCD)中具有重要作用[10] [11]。动物中NO主要由一氧化氮合成酶(Nitric oxide synthase, NOS)产生[1]。植物中产生NO有两种不同的酶途径: 硝酸盐/亚硝酸盐依赖途径和L-精氨酸依赖的合成途径。第一个途径涉及硝酸还原酶(Nitrate reductase, NR)和根特异性膜亚硝酸盐还原酶(Nitrite-NO reductase, Ni-NOR) [1] [12]。在植物体内的研究多认为NR可能调控多种植物叶和根中NO产生[13] [14] [15]。在拟南芥中研究发现, NR是NO产生的关键酶, NR介导的NO的产生是ABA信号转导途径中的关键组分[16] [17]。除了NR外, Ni-NOR也可以催化亚硝酸盐形成NO, 但是只限在根中合成, NR可以将硝酸盐还原成亚硝酸盐, Ni-NOR可以与NR相协调共同调控NO的合成[18]。另外Ni-NOR还参与一系列根的生理过程[19], 但是除此之外我们对于Ni-NOR知之甚少。

在植物发育过程中不同酶或细胞器中可以产生一些过氧化物[10] [20], 尤其是羟基自由基(Hydroxyl radical)和单线态氧(Singlet oxygen), 都是非常强的氧化剂[21] [22]。因此, 为了防止氧化应激的产生, 植物细胞产生了一系列的酶和非酶抗氧化剂来清除过量的氧化物。以上是植物生物学中之前关于氧化胁迫的普遍观点, 而现在这一观点慢慢向氧化信号转导转变。这意味着, 原本被认为有害的ROS其实是植物用来发育和应对外界胁迫的重要信号分子。植物体内高效的抗氧化系统很可能是植物细胞为避免氧化胁迫

迫, 并利用这些活性物质作为信号转导媒介所产生的[23]。在不利环境条件下的细胞响应过程其实是由 ROS 的持续产生和不同的抗氧化系统之间的平衡来实现的[24]。因此, 除了 ROS 单独增加外, 抗氧化酶的下调也可能参与了植物胁迫过程中的信号转导。

3. ROS 与 RNS 协同参与植物免疫

在植物免疫反应过程中, ROS 和 RNS 都会迅速过量产生, 两者协同在植物防御反应中起着重要的作用[23] [25]。NO 和 ROS 可以调控植物应对病原菌侵袭产生的超敏反应(Hypersensitive reaction, HR), 但是这一过程更依赖于 NO 和 ROS 之间的紧密平衡, 而不是仅仅依赖于单一分子的调控。例如, 用双芳基甲烷酮激发子(NUBS-4190)可以使本生烟草单独产生一氧化氮从而增强植物免疫, 但是却观察不到 ROS 依赖的 HR 的发生[26]。

NPR1 是系统获得性抗性(System acquired resistance, SAR)必须的, 防御反应中 NO 和 ROS 信号之间的交互可以从对 NPR1 的影响上体现出来。NPR1 的寡聚化是植物防御相关基因表达所必需的, 然而这一过程需要 S-亚硝基化的调控[6]。另一方面 NPR1 转移到细胞核的过程也受到胞浆内过氧化氢浓度的影响[27]。由此可以看出, NO 和 ROS 均会影响 NPR1 的功能, 从而展现了两者之间复杂的调控机制。NO 和 ROS 的相互影响还体现在 NO 可以调控 ROS 的产生。AtRBOHD 可以在病原菌侵染植物后产生 ROS, 但是其活性却可以被 S-亚硝基化所抑制[28] [29]。不过与此相反的是, 糖醛酸(Hyaluronic Acid, HA)要想完全诱导拟南芥 ROS 的产生还需要 NO 的参与[30]。这些结果的发现同样也说明了 NO 和 ROS 信号转导之间的复杂关系。S-亚硝基谷胱甘肽是生物体内重要的 NO 流动库[31], 在 O₂ 存在的条件下, NO 可以通过 S-亚硝基化反应与还原型谷胱甘肽(GSH)反应形成 S-亚硝基谷胱甘肽(GSNO)。过氧亚硝酸盐(ONOO⁻)是由 NO 和 O₂⁻之间的快速反应形成的一种强氧化剂/硝化物质[32]。由于植物组织中存在 NO 和 GSNO, 再加上 ONOO⁻的产生, 使得 S-亚硝基化和蛋白质硝化这些重要的共价翻译后修饰(PTM)可以在自然或胁迫条件下发生[33]。尽管目前已经公认 ROS 和 RNS 在细胞间和细胞内分子通讯中起着关键作用, 但是关于 ROS 信号的启动、传感和响应机制以及生产与清除之间的微妙平衡是如何实现的, 仍有许多问题需要我们去解决。

4. NO 可以介导植物免疫过程中的 PCD

病原菌诱导的 HR、植物衰老、及非生物胁迫等都可以诱导细胞程序性死亡(PCD) [34], NO 和 ROS 是 PCD 信号中的关键调节因子[35]。抗坏血酸过氧化物酶(APX)可以调节细胞中过氧化氢(H₂O₂)的水平[36]。当用 NO 处理烟草悬浮细胞的时候能够明显抑制 APX 的活性, 说明 NO 可能通过抑制 APX 的活性来参与防御反应[37]。另有报道指出 APX 重组蛋白的亚硝基化可以增强其酶活性[38]。抛去这两者结果的矛盾不管, S-亚硝基化确实可以通过影响 APX 酶的活性来调控 H₂O₂ 介导的防御反应。抗氧化蛋白(Peroxiredoxins, Prxs)具有巯基催化活性, 几乎存在于所有生物体内, 根据它们的结构不同可以将 Prxs 分为 6 类。Prx5 是植物中最具多样性和分布最广的 Prx 亚族, 包括 PrxII-E 和 PrxII-F [39]。在植物防御反应期间, PrxII-E 的亚硝基化不仅抑制了其对过氧化物的解毒能力, 同时也降低了该酶对过氧亚硝酸盐(ONOO⁻)的解毒能力, 从而促进了 PCD 的发生[40]。PrxII-F 的 S-亚硝基化可以促进柠檬酸合酶(Citrate (Si)-synthase, CS)和 PrxII-F 之间的相互作用, 从而使植物免受氧化和亚硝化胁迫的影响[41]。由此可以看出 PrxII-E 和 PrxII-F 的 S-亚硝基化对于植物 PCD 过程以及在植物应对外界胁迫的各种响应中都具有重要作用。

水杨酸(Salicylic acid, SA)是植物应对病原菌侵袭的一类重要激素, SA 可以和植物体内免疫防御相关的多种蛋白质结合, 从而调节它们的活动诱导 HR 的产生[42] [43]。水杨酸结合蛋白 3 (SABP3)表现出和 SA 很高的亲和性, 并且在线粒体中表现出碳酸酐酶(Carbonic Anhydrase, CA)的活性[44]。AtSABP3 在

Cys²⁸⁰ 处的 *S*-亚硝基化可以抑制 AtSABP3 的 SA 亲和能力和 CA 活性,从而负调控植物免疫反应[45]。NPR1 是另外一种与 SA 相关的蛋白,它可以和 SA 结合并且在免疫应答中激活 SA 信号途径中相关防御基因的表达[46]。植物可以通过 *S*-亚硝基化调控 NPR1 的稳态从而与其与 TGACG 基序结合因子 1 (TGA1)相互作用参与调控植物免疫[47]。

5. GSNOR1 在植物 NO 免疫信号通路中具有重要作用

GSNO 是植物体内 NO 主要的运输形式,尽管 NO 和 GSNO 并不总是与相同的靶蛋白相互作用[48]。但作为一氧化氮的缓冲剂,GSNO 可以维持蛋白质的 *S*-亚硝基化稳态平衡[8]。GSNOR1 作为 GSNO 的特异性还原酶在 RNS 的代谢中起着关键作用,它可以维持细胞内 NO 的稳态变化和控制 *S*-亚硝基化蛋白与 GSNO 之间的反式亚硝化平衡[48] [49]。GSNOR1 是 NO 介导的植物免疫信号分子中的重要调控者,这已经在拟南芥 GSNOR1 功能丧失的突变体(AtGSNOR1-3)中得到了证实,该突变体体内 *S*-NOs 水平增加,SA 积累减少,并伴随着基础和/或非宿主抗性受损[49]。拟南芥 GSNOR1 等位基因突变体 hot5 也显示出相似的表型特征,说明 *S*-NOs 稳态在调节生物、非生物胁迫反应中具有重要作用[50]。除上述作用外,由 GSNOR1/HOT5 调节的细胞内 NO 水平变化是否参与其他细胞活动很大一部分仍然是未知的。

系统获得性抗性(SAR)在 GSNOR1 反义沉默植株中增强,在超表达植株中降低,与系统获得性抗性一致,植株中的 *S*-NOs 的水平也发生了相应的变化[51]。另有报道指出 GSNO 和 SA 可以在 SAR 中起到协同作用[49]。但是报道中也有与此相反的结果,即 GSNOR1 在病原菌侵染植物早期具有正向调控植物免疫的作用。当敲除 AtGSNOR1 之后,植物的基础抗性减弱,并且伴随着 SA 依赖的抗病基因表达量的减少[49],之后在向日葵[52],以及黄瓜中也发现了类似的结果[53]。抛去以上矛盾之处,这些证据也进一步证实了 GSNOR1 在植物免疫防御中的重要作用。

植物免疫反应过程中,GSNOR1 在 NO/GSNO 介导的化学修饰中也具有重要的作用。GSH 可以促进烟草 BY-2 细胞 GSNOR1 及水杨酸依赖基因 NPR1 显著上调[54]。GSNO 还可以诱导拟南芥 NPR1 的表达和 SA 的积累从而增强拟南芥对 Pst DC3000 的抗性[6]。研究表明 NO 可以诱导 GSH 的产生,而 GSH 是 SA 积累和 NPR1 诱导所必需的,但是在拟南芥 NO 过表达突变体(nox1)中 SA 的生物合成以及依赖 SA 表达的基因都有所降低[55]。之后通过不同的双突变体 nox1/AtGSNOR1-1 (植物过表达 GSNOR1)或 nox1/AtGSNOR1-3 (GSNOR1 敲除的植物)发现 NO 或 GSNO 可以通过调控独立的或者重叠的靶标来对细胞进行调控。这就说明了 GSNOR1 调控的 GSNO/NO 信号通路在植物免疫过程中具有高度的复杂性[56]。

GSNOR1 还可以参与植物免疫反应过程中的 PCD。当用 Pst DC3000 侵染 AtGSNOR1-3 时,突变体叶片较野生型中出现了更严重的细胞死亡;但是在 AtGSNOR1-3/sid2 (水杨酸缺乏突变体),AtGSNOR1-3/AtRBOHD 或 AtGSNOR1-3/rbohF (缺乏活性氧中间体)双突变体植株中却没有观察到死亡减轻的现象,说明在没有 SA 和活性氧中间体合成的情况下植物体内升高的 *S*-NOs 就可以促进 HR 的发生[28]。前面我们讲到 NO 可以和 ROS 协同调控植物死亡,但需要注意的是,当 *S*-NOs 浓度升高时,一氧化氮介导的 AtRBOHD 的 *S*-亚硝基化形成一个反馈回路抑制了超敏反应的发生[28]。百草枯(Paraquat, PQ)是一种研究 PCD 的重要试剂,它可以诱导绿色植物产生大量活性氧,从而促使植物死亡。但是当用 PQ 处理拟南芥 GSNOR1 等位基因突变体 par2-1 时,该突变体却表现出对百草枯诱导死亡增强的抗性[57]。以上可以看出 GSNOR1 在不同条件下可以起到正负调控细胞死亡的功能。

6. 结语

S-亚硝基化是植物 NO 信号通路中的重要组成部分。GSNOR1 作为调控蛋白质亚硝基化、去亚硝基化以及 GSNO 稳态的关键酶,在植物免疫反应中扮演着重要的角色,但是关于 GSNOR1 的体内调控机制

还有很大一部分是未知的。虽然有大量的证据表明 NO 和 ROS 在植物免疫信号转导之间存在着串扰，但是 S-亚硝基化如何参与其中还需要我们去进一步探索。此外 NO 来源的鉴定，以及植物中不同亚细胞区间中 NO 介导 S-亚硝基化的产生依然是研究的重点。最后我们期望能够通过模式植物对 NO 调控免疫信号通路中的相关基因进行研究，从而将已有知识扩展到经济作物，增强作物抗逆性和提高作物产量。

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