Bioprocess 生物过程**, 2023, 13(1), 33-38**
Published Online March 2023 in Hans. https://www.hanspub.org/journal/bp
https://doi.org/10.12677/bp.2023.131005

植物中ABA和JA对盐胁迫的响应

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收稿日期：2023年2月17日；录用日期：2023年3月8日；发布日期：2023年3月15日

摘　要

土壤盐碱化是农业发展面临的重大难题，改良土壤难度大，花费多，很难解决大规模的农产品抗盐问题。研究植物的耐盐机制为研发耐盐植物提供理论依据，植物激素在植物对盐胁迫响应中起重要作用。本文通过查阅资料，总结了已经明确了的植物对盐胁迫响应途径及植物激素ABA和JA在抵抗盐胁迫方面的作用，为研制耐盐植物提供参考。

关键词

土壤盐碱化，盐胁迫，脱落酸，茉莉酸

Response of ABA and JA to Salt Stress in Plants

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Received: Feb. 17th, 2023; accepted: Mar. 8th, 2023; published: Mar. 15th, 2023

Abstract

Soil salinization is a major problem facing agricultural development. It is difficult to improve the soil and spend more, and it is difficult to solve the problem of large-scale agricultural products. Studying the salt resistance mechanism of plant provides theoretical basis for the development of salt-resistant plants, and plant hormones play an important role in plant's response to salt coercion. By consulting the information, this article summarizes the clear plants that have been clarified to salt coercion response pathway and vegetable hormone ABA and JA in resisting salt stress, and provides a reference for the development of salt-resistant plants.

文章引用: 王佳敏. 植物中 ABA 和 JA 对盐胁迫的响应[J]. 生物过程, 2023, 13(1): 33-38.
DOI: 10.12677/bp.2023.131005

Keywords

Soil Salinization, Salt Stress, Abscisic Acid, Jasmonates

1. 引言

土壤盐碱化是一个影响农业发展的全球性问题，因为土壤的盐碱化会导致农作物减产，甚至严重影响作物的生长发育。土壤中的盐对植物造成的不良胁迫包括渗透胁迫和盐毒性胁迫[1]。当外界离子浓度较高时，由于渗透作用植物的生长变得缓慢，侧芽的发育缓慢或保持静止。除了渗透胁迫，盐离子在植物体内大量累积造成的盐毒性胁迫，也会引起一系列不良的生理生化反应，进一步影响植物的正常生长发育[2]。植物面临盐胁迫时有着复杂的反应机制以应对损害。脱落酸(Abscisic Acid, ABA)和茉莉酸(Jasmonates, JA)是植物在响应盐胁迫调节机制中的重要组成部分，发挥了至关重要的作用。

2. 植物对盐胁迫的响应机制

应激信号被膜上的受体(离子通道、G 蛋白偶联受体、组氨酸激酶或受体类激酶)感知，从而产生许多次级信号分子，如：Ca^{2+}、肌醇磷酸盐、活性氧(Reactive Oxygen Species, ROS)和 ABA。胁迫信号随后在细胞核内转导，诱导许多胁迫响应基因，最终使植物能适应胁迫[3]。

Ca^{2+}通过质膜和细胞器膜流入细胞质，导致细胞质和某些细胞器(如细胞核)中的触发 Ca^{2+}峰值[4] [5]，在盐胁迫期间，拟南芥中的盐过度敏感(Salt Overly Sensitive, SOS)通路感知到特定的 Ca^{2+}信号，从而维持细胞内的稳定已经做出一系列的生理响应[6]；蛋白质磷酸化是植物响应各种非生物胁迫条件期间信号转导中常见且关键的生理反应，如 2C 型蛋白磷酸酶(PP2C)家族和 SnRK2 蛋白激酶亚家族的成员是多种应激信号通路的核心参与者。它们调节各种下游蛋白质，包括转录因子、控制气孔关闭的通道蛋白和产生过氧化氢(H_2O_2)的氧化酶 RbohF [7]；ABA 是气孔关闭和其他植物对盐、干旱和其他几种高渗胁迫诱导条件的反应的关键介质；植物响应非生物胁迫的另一个主要特征是产生 ROS，包括超氧阴离子、H_2O_2、羟基自由基和单态氧[8]。当 ROS 的水平超过细胞的解毒能力时，它们对生物分子有害，但它们也在应激信号中发挥重要作用[8]。尽管渗透压下的 ROS 积累可以独立于 ABA 而发生[9]，但 H_2O_2 的产生显然受 ABA 信号调节[10]。

3. ABA 的作用机制

ABA 属于倍半萜类物质，其前体是一种常见的 C5 化合物，是一种通常与植物应对胁迫有关的激素[11] [12]。ABA 通过产生渗透保护蛋白和代谢物的以及调节气孔导度的方式来保护植物免受非生物胁迫，特别是渗透胁迫和盐胁迫[13]。ABA 生物合成、转运、分解代谢等许多细节已经被阐明。然而，我们在 ABA 信号转导途径的揭示中仍然存在许多重大的空白[14] [15] [16] [17]。

ABA 早先被认为是生长抑制因子，后发现广泛参与植物的萌发和成长[18]，在应答非生物胁迫中发挥重要作用[19]，ABA 信号转导途径位于植物对盐胁迫响应途径网络中的核心[13]。在植物体内，ABA 可以与其受体家族 RCARs/PYR1/PYLs 结合[20]，在受体家族下游的是 ABA 信号转导通路的中心－蛋白磷酸酶 2C (PP2Cs) [21]。当没有 ABA 时，PP2C 可以与 SnRK2 激酶结合，抑制 SnRK2 激酶包括 ABI1、 ABI2 和 HAB1 的活性。当存在 ABA 时，ABA 和受体 RCARs/PYR1/PYLs 结合后又结合到 PP2C 的催化位点，以上的过程导致 PP2C 的酶活性被抑制，释放 SnRK2 激酶[22]，于是恢复活性的 SnRK2 激酶又参与了 bZIP 转录因子的磷酸化，又促进了 ABA 基因的表达。此外，与 PP2C 相互作用的蛋白质数量相对较多，这表明 PP2C 下游可能存在其他信息传递途径[23]。

在拟南芥中有多个 PYL 但功能并不完全相同。PYL8 的敲除导致在在胁迫抑制恢复侧根生长对 ABA 不敏感[24]，PYL6 与 MYC2 (JA 反应中的关键转录因子)相互作用，从而连接 ABA 途径和 JA 途径[25]。ABA 激活的 SnRK2s 也可以在质外体中产生 H_2O_2，这是一种信号分子，可以介导各种 ABA 反应以及调节钙信号[26]；钙信号对于 ABA 调节气孔关闭至关重要；除了上述外，ABA 还会促使一氧化氮(NO)和磷脂(如磷脂酸)的产生，NO 会亚硝基化 SnRK2s 催化位点附近的半胱氨酸残基，这会导致激酶失活[27]。NO 还会导致 PYL 的酪氨酸硝化和亚硝基化[28]；酪氨酸硝化会抑制 PYL 的活性，并且还会伴随 PYL 的泛素化和蛋白酶体介导的降解。

4. 茉莉酸的作用机制

JA 及其衍生物统称为 JAs，是脂质衍生的信号化合物，在植物发育和对生物及非生物胁迫反应过程中发挥重要的作用[29]。然而在植物激素的研究中，对茉莉酸及其衍生物的研究开展较晚。茉莉酸的生物合成和信号转导途径只存在于一些原核生物，一些低等植物和所有高等植物中，在动物，人类组织和酵母中不存在[30]，之后在陆地植物中发现茉莉酸普遍存在[29]。

JA 及其衍生物是植物的内源性生长调节激素[31]，也是响应盐胁迫的调控因子[32]。许多研究表明，JA 在非生物胁迫耐受中发挥着重要作用，由于 JA 能够诱导植物在胁迫下的保护作用。有研究表 JAs 是耐盐性的正向调节因子[32] [33] [34]。编码 AOC 的小麦基因 *TaAOC1* 在拟南芥中的异位表达可以提高 JA 水平并提高耐盐性，表明 JAs 正向调节植物的耐盐性。编码 OPR1 的小麦基因 *TaOPR1* 在拟南芥中过表达时也可以提高耐盐性[33]，JAs 增强了小麦抗氧化酶的活性以及耐盐性[32]。拟南芥中介体亚基 MEDIATOR25 (MED25)和 MYC2 通过螺旋–环–螺旋(helix-loop-helix)的方式相互作用从而调节 JA 信号。与此同时，MED25 还可以与转录因子 ABA-INSENSITIVE5 (ABI5)的启动子区域的亮氨酸拉链结合，负调控 ABI5 的转录功能。可以看出，MED25 与 MYC2 和 ABI5 的相互作用机制是不同的。这些说明拟南芥的 MED25 选择性地与特定转录因子相互作用来调节不同激素信号通路[35]。JA 途径在耐盐胁迫中的作用并不局限于拟南芥。在水稻中，RICE SALT SENSITIVE3 (RSS3)是一种在根尖表达的核蛋白，通过抑制根的 JA 反应来促进细胞伸长，这是在盐条件下根生长所必需的。因此，在盐胁迫下，丧失了 RSS3 功能的植物通过激活根尖的 JA 响应基因导致根的生长受到抑制[36]。综上所述，这些发现表明 JA 通路正向调控植物的耐盐性。

MYC2 被认为在激活 JA 的信号途径中是一个主要调节因子[37]。MYC2 包括 N 端的一个 JAZ 相互作用的结构域(JID) [38]，一个与 MED25 进行反式激活的转录激活结构域(TAD) [39] [40]，C 端一个可以聚集 JAZ 到细胞核的 NLS [41]，以及 C 端一个用于二聚化和结合 G-box (CACGTG)或类 G-box 的 bHLH 结构域[42]。MYC2 也是是不同激素信号途径的一个交叉点。JAZ 和赤霉素(GA)通路中的抑制因子 DELLA 均与 MYC2 相互作用，以抑制花中倍半萜的生物合成[43]，JA 和 GA 可以激活 MYC2 并诱导倍半萜的生物合成。脱落酸(ABA)可以促进 ABA 的受体 PYL6 与 MYC2 相互作用，并阻碍 MYC2 与靶启动子的结合能力[25]。

5. 结论和展望

最近的研究彻底改变了只有某些特定激素在植物生理调节中起主要作用的观点。相反，所有的植物

激素都与多种植物过程直接或间接相关，包括生物和非生物胁迫[36]。ABA 和 JA 在植物对盐胁迫响应中发挥了重要作用，是植物抵抗盐胁迫的重要途径，当前对 ABA 和 JA 两种植物激素的研究很多，在生产实践当中也取得了一定的成果，然而它们在盐胁迫下的作用机制还未被完全揭露，有待我们去发掘。在不同的发育阶段、组织类型中，ABA 和 JA 似乎协同或拮抗地发挥着作用，ABA 途径和 JA 途径之间存在着交联作用，但具体机制尚未明确，需要进一步研究来确认。

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