

植物激素ABA在水分胁迫下的功能及信号途径

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摘要: 植物根系感知外界水分胁迫刺激, 诱导ABA生物合成。ABA既可诱导气孔关闭或抑制气孔开放, 以降低植物的蒸腾失水, 又可影响植物根系发育, 以抵御水分胁迫。本文就植物激素ABA及其下游信号 H_2O_2 、NO以及 Ca^{2+} 等在植物生长调节方面的研究进展进行概述, 以构建水分胁迫下植物生长自我调控的可能模式。

关键词: 水分胁迫; 脱落酸; 过氧化氢; 一氧化氮

Function and Signaling of Plant Hormone ABA under Water Stress

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Abstract: Plant roots perceive water stress and induce the synthesis of abscisic acid (ABA). ABA not only could induce stomatal closure or inhibit stomatal opening to reduce transpiration, but also regulate the development of roots and increase drought tolerance. This paper focused on the functions of plant hormone ABA and its downstream signal intermediates (H_2O_2 , NO and Ca^{2+}) for establishing the basic model of its regulation of plant growth under water stress.

Key words: water stress; abscisic acid; hydrogen peroxide; nitric oxide

非充分灌溉条件下, 作物通过生长调节以保持较高产量(康绍忠等1997, 1999)。因此, 研究水分胁迫下植物的生长调节对于丰富非充分灌溉理论, 提高作物水分利用效率具有重要理论价值和现实意义。早期的研究认为, 植物根系在受到水分胁迫时, 根尖细胞膨压及体积发生变化, 脱落酸(abscisic acid, ABA)快速合成(Walton等1976; Comish和Zeevaart 1985; Zhang 1994), 伴随着木质部汁液ABA水平上升导致植物叶片气孔关闭(Davies和Zhang 1991; Sauter等2001), 即ABA可能作为长距离信号介导干旱条件下地下部与地上部的信息传递(Wilkinson和Davies 2002)。近年来这种观点受到质疑。Ikegami等(2009)通过分析离体叶片和根在干旱处理前后ABA水平的变化, 发现离体叶片中ABA含量增加的方式与完整植物的叶片类似; 而离体的根在干旱处理4 h后ABA含量却没有明显的变化, 同时当离体根遭受缺水处理时, 根中并未发现ABA的积累, 该研究表明ABA主要在植物叶片中合成。进一步的 ^{13}C ABA的同位素示踪实验证明叶片合成的ABA在干旱胁迫条件下向根部运输(Ikegami等2009)。即缺水条件可以激活植物叶

片合成ABA, 诱导气孔关闭, 减少蒸腾失水, 同时ABA向根部运输, 影响根系的发育, 提高植物对于旱条件的抗性。此外, Christmann等(2007)报道根部干旱产生的液压信号(hydraulic signal)可能作为长距离信号介导干旱条件下地下部分与地上部分的信息传递。本文基于前人的研究工作, 对逆境信号ABA调节水分胁迫下植物生长的作用机制进行综述。

1 水分胁迫下逆境信号ABA对植物适应性生长的调节

ABA作为一种植物激素, 几乎存在于所有高等植物中, 它不仅在诸如种子的成熟和休眠与萌发、气孔的运动、开花时间和果实成熟等植物生长发育的诸多生理过程中起重要的调节作用(Finkelstein等2002, 2006; Schroeder和Kuhn 1985), 而且还可调节植物对逆境胁迫如干旱、盐碱和病原侵袭等的反应(Versluis和Zhu 2005; Schroeder等2001)。已经证明, 水分胁迫下植物体内源ABA水平增加, ABA

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参与调节植物应对水分亏缺反应, 维持一定适应性生长速度, 增加植物逆境中存活的机会。干旱条件下, ABA能导致植物叶片伸展率(leaf expansion rate, LER)的明显下降, 使得叶面积减小进而降低水分丧失(Salah和Tardieu 1997)。Granier等(1999)的研究也表明水分胁迫或外施ABA均影响到植物叶片发育的空间模式(Granier和Tardieu 1997)。适当干旱时叶片伸展率受到植物细胞汁液pH的调控, 而这种调控依赖于ABA (Bacon等1997)。ABA与气孔导度也存在密切关系, 如外施ABA会引起柳树气孔导度下降, 除去ABA又可以逆转这种现象(王少先等2003)。同时, 气孔导度受到植物叶片中ABA浓度的调节(Heckenberger等1996; Fort等1998)。许多研究也都表明, 水分胁迫或ABA处理下会诱导植物产生许多与生理生化过程相关的特异保守性蛋白, 诸如具有运输水分功能的水孔蛋白(aquaporin, AQP)、对植物细胞进行渗透调节的渗透蛋白(osmotin)等(Han和Xue 2003; Christmann等2005; Raghothama等1997; Shao等2005)。Lea蛋白(late embryogenesis abundant protein)是胚胎发生后期种子中大量积累的一系列蛋白质, 随着种子的脱水成熟其含量也不断增加, 它们对提高植物脱水耐受力有很大作用。研究表明, 在植物个体发育的其它阶段, Lea蛋白也能因干旱胁迫或ABA诱导等在植物的营养器官中表达, 同时, Lea蛋白表达时序也和植物体中ABA变化相一致(Ingrtam和Bartels 2003; Christmann等2005; Martinez等2004; Xiao等2007)。另外, 水分充足的条件下, 植物细胞内ABA呈均匀分布, 水分亏缺时, 抗旱品系皮层和叶的细胞质中ABA含量较高, 而不抗旱品系液泡中的ABA含量较高, 这表明水分胁迫下, 植物细胞也通过调整ABA的分布影响其对干旱条件的适应性(Yamazaki等2003; Christmann等2005)。水分胁迫条件下, ABA除了上述生理上对植物适应性生长进行调节外, 其调节气孔运动及根的生长发育也为人们所熟知。在研究ABA参与植物对胁迫条件的反应及调节植物生长发育的过程中, 包括H₂O₂、NO、蛋白激酶、磷酸酶、Ca²⁺和质膜相关离子通道等许多重要的ABA信号转导元件也被陆续鉴定出来(Zhang等2001a, b, c; Bright等2006; Grabov等1997; Pei等2000)。

2 水分胁迫下ABA对植物气孔运动的调节

ABA通过与受体相结合, 进而引起植物体一系列生理反应。ABA受体的发现及鉴定, 对于研究植物激素ABA水分胁迫和植物生长发育的信号转导具有重要意义。近年来, 对于ABA受体的研究已有了突破性的进展。FCA、Mg离子螯合酶(Mg-chelatase) H亚基的CHLH以及G蛋白偶联受体分别被报道作为ABA受体(Fawzi等2006; Shen等2006; Liu等2007), 然而这些已被鉴定的ABA受体均因实验结果无法重复等原因存在争议(Johnston等2007; Jang等2007)。最近, 属于一个含有14名成员蛋白质家族的成员PYR/PYL/RCAR被鉴定为ABA受体, 它可以在体内外结合ABA, 之后会结合下游的蛋白磷酸酶PP2C并抑制其磷酸酶活性, 同时发现其中一个被命名为CL2的蛋白柔性区在介导ABA信号及抑制PP2C活性中起了至关重要的作用(Santiago等2009; Nishimura等2009; Hao等2010)。

ABA与受体结合后, 将胁迫信号通过第二信使进行传递并放大。Zhang等(2001c)首次证明了ABA可以诱导蚕豆气孔保卫细胞H₂O₂产生, NADPH氧化酶是调节H₂O₂产生的关键酶(苗雨晨等2000)。Kwak等(2003)分析拟南芥NADPH氧化酶的两个亚单位基因*AtrbohD*和*AtrbohF*发现, 破坏*AtrbohD*和*AtrbohF*可削弱ABA信号(Kwak等2003; Zhang等2009)。早期认为, ABA激活G蛋白, 活化磷脂酶C, 释放IP₃, IP₃通过激活液泡膜的Ca²⁺通道, 增加胞质Ca²⁺浓度([Ca²⁺]_{cyt}) (Armstrong等1995; Kühler等2003)。McAinsh等(1995)发现胞外Ca²⁺诱导胞内Ca²⁺升高不需要磷脂酶C, 涉及到胞外Ca²⁺内流(Mcainsh等1995), ABA和H₂O₂均可增加保卫细胞中游离Ca²⁺的浓度(Mcainsh等1996)。Pei等(2000)证实保卫细胞质膜上Ca²⁺通道可被H₂O₂激活, H₂O₂激活的Ca²⁺通道引起Ca²⁺内流及完整的保卫细胞中胞质[Ca²⁺]_{cyt}升高(Pei等2000)。[Ca²⁺]_{cyt}升高可有效模拟H₂O₂的行为, 激活质膜K⁺外流通道, 钝化K⁺内流通道, 阻挡了K⁺内流, 诱导气孔关闭(Armstrong等1995; Kühler等2003; Schroeder和Hagiwara 1989; Suh等2007)。在*AtrbohD*和*AtrbohF*的缺陷株中, ABA诱导胞质Ca²⁺增加和ABA激活保卫细胞质膜Ca²⁺通道等反应受到抑制(Kwak等2003; Zhang等2009)。但是外源H₂O₂可以弥补由于*AtrbohD*和

*AtrbohF*突变所造成的 Ca^{2+} 通道活性和气孔关闭的抑制, 暗示在ABA信号转导中, H_2O_2 通过激活保卫细胞质膜 Ca^{2+} 通道, 参与调节ABA诱导的气孔运动。此外, ABA引起气孔关闭, 也存在不依赖 Ca^{2+} 的信号转导途径(Gilroy等1990)。在不依赖 Ca^{2+} 的途径中, ABA引起保卫细胞 H_2O_2 积累, 胞质碱化, 有效抑制质膜内向 K^+ 通道, 活化了 K^+ 外向通道, 导致保卫细胞 K^+ 浓度下降, 细胞膨压下降, 气孔关闭(Zhang等2001b; Blatt等1999)。此外, ABA信号调节气孔运动的过程可以被蛋白磷酸酶2C (PP2C)、蛋白激酶OST1、离子通道等调节(Lee等2009)。PP2C (如ABI1和ABI2等)负调节ABA诱导的气孔关闭反应(Merlot等2001), 而蛋白激酶OST1/SRK2E/SnRK2-6则正调控这一过程(Yoshida等2006; Fujii等2007; Chae等2007; Belin等2007)。ABA与受体结合后, 阻止了type 2C蛋白磷酸酶调节的OST1去磷酸化, 以激活OST1, 进而实现OST1调节离子通道活性的功能(Lee等2009; Park等2009)。Lee等(2009)研究发现, PP2C家族成员PP2CA可以通过阻碍OST1激酶活性或直接使质膜阴离子通道SLAC1去磷酸化来调节SLAC1的活性, 进而参与调节ABA引起保卫细胞气孔关闭过程(Lee等2009; Geiger等2009)。

最近报道, NO清除剂cPTIO可以明显抑制ABA诱导的气孔关闭(Neill等2002; Garcia等2003; Desikan等2004)。比较分析不同的NO供体对蚕豆、拟南芥气孔运动的影响, 发现这些NO供体均可诱导气孔关闭(Neill等2002; Lozano和Leon 2010), 暗示NO参与ABA诱导的气孔关闭。研究表明, ABA诱导的NO产生依赖于 H_2O_2 的积累, 在ABA诱导气孔关闭过程中, H_2O_2 可能在NO的上游起作用并受NO的负反馈调节(吕东等2005; Wei等2009)。植物体内ABA诱导的NO合成主要来源于硝酸还原酶途径(Bright等2006; Lu等2009)。另外, NO和活性氧也包含在ABA抑制的气孔开放反应中(Garcia和Lamattina 2002; Neill等2008)。在检测和分析NO对保卫细胞质膜 K^+ 通道活性时发现, NO对蚕豆保卫细胞质膜内向及外向 K^+ 通道的调节, 存在不同机制(Neill等2002; Sokolovski和Blatt 2004)。如NO对气孔开放抑制, 主要通过激活质膜 Ca^{2+} 通道, 提高胞内 Ca^{2+} 浓度, 激活质膜外向 K^+ 通道促进

K^+ 外流, 同时, 可选择性抑制内向 K^+ 通道阻止 K^+ 内流(Zhang等2009)。此外, 在绿豆(*Phaseolus aureus*)保卫细胞中, Ca^{2+} 介导ABA诱导的NO产生(Pei等2000)。这一过程可被 Ca^{2+} 通道阻断剂异博定(verapamil)抑制(Hamilton等2000; Shi和Wu 2010)。Desikan等(2002)的研究表明, NO以cADPR依赖的方式促使胞内钙库释放 Ca^{2+} , 进而诱导气孔关闭。PLD、S1P等参与的G蛋白介导产生的IP3也是促使胞内钙库释放 Ca^{2+} 的重要途径(Coursol等2003; Zhang等2005)。这些结果说明 H_2O_2 、NO、蛋白激酶、磷酸酶、 Ca^{2+} 和质膜相关离子通道等参与ABA信号转导途径, 同时ABA信号转导途径各组分可能会相互牵制, 以调节气孔的合理开度, 应对复杂的胁迫环境。保卫细胞中ABA信号转导如图1所示(王忠和顾蕴洁主编《植物生理学》第2版基础上并参考宋纯鹏等译《植物生理学》第4版)。

3 水分胁迫下ABA对植物根生长发育的调节

植物根系的生长发育具有很强的可塑性, 容易受到环境条件的影 响, 植物激素ABA即使在不 受水分胁迫的条件下也能够影响到植物根系的形态建成(Deak和Malamy 2005)。水分胁迫下, 植物根系是最先感受干旱胁迫的敏感部位, 并使整个

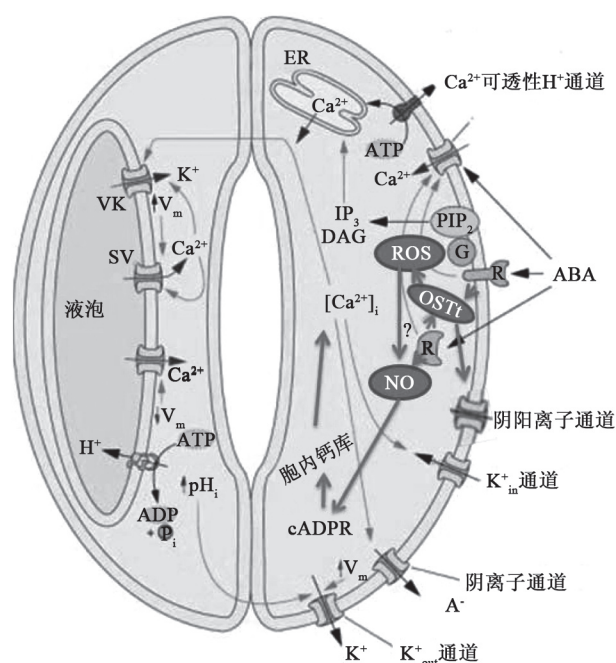


图1 保卫细胞中ABA信号转导

Fig.1 Signal transduction of ABA in guard cell

植株对其作出进一步的反应。所以,根生长发育状况和活力强弱对于植物的耐旱能力至关重要。已知,适度的干旱可诱导植物合成ABA,同时ABA又影响着植物根系的生长发育,而且由叶片合成并运输到根部的ABA对维持土壤干旱条件下根系的生长是必需的。水分胁迫下ABA可以调节根的生长发育,适度的干旱后复水可通过影响作物主根和侧根的生长发育,提高植物的抗旱性能(康绍忠等1997; Zhang等1995; Shanrp和Lenoble 2002)。干旱条件下ABA可通过限制乙烯的合成来维持玉米主根的延伸(Spollen等2000),ABA也可以调节水稻根的系统生长发育(Chen等2006)。Bai等(2009)在研究ABA抑制拟南芥根生长中发现,一个富含脯氨酸的伸展素类似的受体蛋白激酶AtPERK4参与了ABA的信号转导,通过调控相应基因的转录抑制了根细胞的生长(Bai等2009)。尽管如此,ABA对植物根系生长发育的调控机制还不甚清楚。

研究发现, H_2O_2 有效介导了赤霉素(GA)诱导的胡萝卜种子的萌发过程(Schopfer等2001)和根的向地性反应(Joo等2001)等。同时, H_2O_2 影响根毛的生长和发育,在拟南芥根毛的形成过程中,根中 H_2O_2 的积累是必需的(Foreman等2003)。在研究 H_2O_2 影响植物根发育的过程中发现, H_2O_2 调控植物根的生长是通过影响 K^+ 吸收相关基因的表达而实现的(Shin和Schachtman 2004)。然而,对NADPH氧化酶缺失的拟南芥双突变体 $atrbohD/F$ 幼苗根的生长却不受ABA的抑制(Kwak等2003),从而推测 H_2O_2 可能是ABA调控拟南芥根发育过程中的一个重要成分(Gapper和Doaln 2006)。水分胁迫下,ABA的合成受到促进,通过长距离运输至根部,ABA通过诱导根细胞内 H_2O_2 的产生,调控 *OXII*的表达促进根毛的形成和发育(Bai等2007),进而促进根对环境水分的吸收。

另外,在根器官发育方面,NO可替代生长素的作用,通过激活下游MAPK信号,介导了生长素诱导的侧根及不定根生长发育(Pagnussat等2002, 2004; Correa等2004; Fujii和Zhu 2009)。Pagnussat等(2002)报道,生长素能够诱导黄瓜根合成NO,进而调节黄瓜主根的生长和侧根形成。在对番茄、玉米和小麦的研究中发现,NO不仅能促进植物侧

根数目增加,还能促进主根生长(Pagnussat等2002; Correa等2004; Gouvea等1997; Zhao等2008)。比如Gouvea等(1997)的研究表明,NO能诱导玉米根尖延伸,Zhao等(2008)研究发现,NO的供体SNP可以影响小麦根系的生长,主要表现在增加小麦主根长度及主根上的侧根数目,进而增进小麦根系对周围水分的吸收。而进一步的研究发现,NO通过对根细胞质膜 K^+ 通道的调节及增强 K^+ 在植物胞质中的积累来提高小麦复水后补偿生长的原动力(闻玉等2008)。Desikan等(2004)报道,ABA可有效诱导NO在植物体内合成。因此我们推测,NO可能通过激活根细胞质膜相关离子通道,增强 K^+ 在植物体内的积累,从而介导ABA对植物根系细胞水势的调节,以改善植物渗透胁迫下的适应性生长。

Ca^{2+} 参与植物根系发育的调节,植物根细胞质膜 Ca^{2+} 通道的激活和胞质 Ca^{2+} 浓度的上升参与了植物对其主根伸长和根毛形成的调节(Schiefelbein等1992; Chen等2006)。植物根对 Ca^{2+} 的吸收主要通过根的伸长区完成,同时又受到质膜超极化激活阳离子通道的调节(Kiegle等2000; Very等2000)。Tang等(2007)针对拟南芥保卫细胞的研究结果表明,胞外 Ca^{2+} 作为一种信号,与质膜 Ca^{2+} 受体CAS结合,激活磷脂酶C (PLC),产生IP₃,诱导胞内钙库释放 Ca^{2+} ,以提升胞内 Ca^{2+} 浓度(Tang等2007)。ABA也可以激活磷脂酶C (PLC)信号通路,诱导胞内钙库释放 Ca^{2+} 。最近,在拟南芥和水稻的根细胞发现受ABA调节的质膜 Ca^{2+} 透性通道参与根生长的调节(Kurusu等2004; White等2002),进一步证实了 Ca^{2+} 介导ABA调节的根生长发育。

4 展望

经过几十年的研究,人们对植物激素ABA有了比较深入的了解。作为重要的植物激素,它在调节植物的生长发育的同时,广泛参与植物应对多种逆境胁迫的反应,其在植物针对干旱缺水胁迫中所扮演的角色尤其受到人们的青睐。适度的水分胁迫诱导植物叶片中合成ABA,ABA与相应受体结合通过 H_2O_2 、NO、蛋白激酶、磷酸酶、 Ca^{2+} 和质膜相关离子通道等传递逆境信号,诸如调节蛋白磷酸酶(ABI1和ABI2)、蛋白激酶OST1、相关转录因子等的表达以及保卫细胞质膜 Ca^{2+} 和 K^+ 通道活性,最终导致气孔关闭,以降低植株地上

部分水分过多散失。同时, 叶片中合成的ABA还可以被运输到植物的地下部分, 在 H_2O_2 、NO、 Ca^{2+} 等介导下调节植物主根延伸、侧根生长、根系活性等, 以使植物可在适度干旱条件下吸收尽可能多的水分以供地上部分的需要, 增强作物的抗旱性。在ABA调节植物生长发育参与植物对逆境胁迫反应的过程中, ABA信号转到途径、具体作用机制等尚不十分明确。其参与调节气孔运动等信号转导过程中, 对接受ABA信号的ABA受体及其作用方式等的研究仍是目前人们关注的重点。

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