陆生植物对淹水胁迫的适应机制

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摘要: 淹水是影响植物生长发育的一种重要的非生物逆境胁迫, 严重影响植物的形态结构、抗氧化系统、呼吸作用、光合作用和激素代谢, 从而降低产量和品质, 甚至造成绝产或大面积死亡。而植物遭受涝害后, 会积极调整自身形态结构、生理代谢和分子机制以缓解涝害产生的不良影响, 减少涝害损失。本文主要从形态学、生理学和分子生物学这三个层面, 综述了植物对淹水胁迫的响应机制, 旨在对植物抗涝性研究提供参考, 并为淹水胁迫的进一步研究提供新思路。

关键词: 淹水胁迫; 形态结构; 生理特性; 适应机制; 基因表达

Adaptive mechanism of terrestrial plants to waterlogging stress

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Abstract: Flooding is an important abiotic stress that affects the growth and development of plants, which can seriously affect the morphological structure, antioxidant system, respiration, photosynthesis and hormone metabolism of plants, resulting the reduction of the yield and quality, and even causing a large area death of plants. After waterlogging, adaptive response like morphological structure, physiological metabolism and molecular mechanism occurs to alleviate the adverse effects of waterlogging and reduce waterlogging losses. In this paper, the response mechanism of plants to waterlogging stress was summarized from the three aspects of morphology, physiology and molecular biology. The aim of this paper was to provide a reference for the study of waterlogging resistance of plants and to provide new ideas for the further study of waterlogging stress.
Key words: waterlogging stress; morphological structure; physiological characteristics; adaptive mechanism; gene expression

适宜的水分是植物进行一切正常生命活动的前提和基础, 水分过多或过少均会对陆生植物生长发育带来不良影响(张福锁1993)。水分过多对陆生植物造成的危害称为涝害, 主要是指土壤水分含量超过田间最大持水量后对植物造成的伤害。根据土壤水分含量的不同又将其分为湿害(waterlogging)和涝害(flooding)。湿害是由于土壤空隙充满水分, 根系生长因缺氧而遭受伤害; 涝害是指地面形成积水而导致植物部分或全部器官被水淹没(张瑞栋2020)。2种涝害对植物损伤的实质均在于水分过多而阻碍了植物与大气间的气体交换, 周围

收稿 2021-05-16 **修定** 2021-08-14
资助 贵州省科技成果转化项目(黔科合成果[2021一般009])、国家自然科学基金(31460371)、贵州省生物学一流学科开放基金(GNYL[2017]009FX4KT37)和大学生"SRT计划"项目[贵大SRT字(2019)311号]。

O_2浓度过低形成低氧或无氧状态, 导致植物受淹组织缺氧, 而CO_2和乙烯等积累增加(Patel等2019; Sairam等2009), 致使植物生长受阻, 作物产量降低(Boyer 1982)。植物为适应淹水胁迫, 在胁迫来临后会调整自身的形态结构、生理分子代谢过程以降低损伤。其适应机制可概括为三个方面: (1)低氧静止适应机制: 涝害后植物生长减缓, 能量和物质消耗降低, 延长涝害后的存活时间; (2)低氧逃避机制: 涝害后植物加速生长, 新生组织尽快接触空气, 摆脱缺氧胁迫; (3)自我调节补偿机制: 涝害后植物地上部的氧气向根尖的运输加速, 缓解根系缺氧的胁迫(Patel等2019; 张瑞栋2020; 张艳军和董合忠2015)。

随着气候变化, 洪涝灾害已成为导致全球作物产量和质量下降的主要逆境因子之一。从2000年到2011年间, 美国因涝害受灾损失近2.17亿美元(Tanoue等2016); 2010年夏天, 巴基斯坦、印度、哥伦比亚和澳大利亚等地区均遭受严重洪灾(Kundzewicz等2014)。我国也是世界上受洪涝灾害较严重的国家之一, 在过去54年中, 我国中东区域极端洪涝事件频率平均值为每年2.783 3次, 并以每年0.011 8次的速度不断上升(Zhang等2015)。因此, 研究作物耐涝响应机制, 提高其抗涝性, 减少涝害损失意义重大。本文对植物淹水胁迫下形态结构适应变化、呼吸作用、光合作用和植物激素等生理学响应过程进行了综述, 并探讨了相关生理过程的转录调控情况, 以期为植物耐涝机理研究及培育耐涝品种提供参考。

1 形态结构的适应性变化及转录调控

淹水胁迫下, 根系是第一个面临低氧胁迫的器官, 存在显著的生长损伤和表型变化(Eysholdt-Derzso和Sauter 2019; Panozzo等2019)。植物受淹后会根系处于极度缺氧状态, 细胞的有氧呼吸转变为无氧呼吸, 导致乙醇、乙醛、乳酸等呼吸产物大量积累, 致使根系细胞死亡, 引起黑根数量增加, 根系活力降低, 影响矿质营养元素的吸收, 破坏叶绿素的合成, 进而导致地上部光合作用降低(Sun等2018)。淹水胁迫抑制新叶形成, 加速老叶脱落, 致使植株总叶面积减少(Tang和Kozlowski 1982)或引起叶片变色、萎蔫(吴麟等2012)。

受淹后植株的轴根和侧根停止生长, 植株的茎基部形成大量不定根(adventitious roots, ARs), 以此取代因缺氧而窒息死亡的初生根, 从而提高植物的耐淹能力(Lin等2004)。不定根的根尖细胞具有较高的细胞分裂能力和生理活性, 伸长区内形成发达的通气组织(aerenchyma), 根内部组织孔隙度大幅提高, O_2摄取和运输能力明显改善(孔妤等2008; 潘澜和薛立2011; 尹冬梅等2012)。根系通气组织中的O_2不仅纵向扩散至根尖, 根细胞吸收O_2也会径向运输至根际。为减少O_2的径向泄漏, 根基部栓质化加重, 形成屏障, 减少O_2的径向损失, 促进O_2沿通气组织向根尖扩散, 以缓解根尖缺氧胁迫(Colmer 2003; Yamauchi等2018)

众多研究表明, 淹水后通气组织及不定根的形成与乙烯的积累有关(Wany等2017; Rasmussen等2017; 谭淑端等2009)。淹水条件下, 植物受淹器官内乙烯生物合成酶1-氨基环丙烷-1-羧酸合酶(1-aminocyclopropane-1-carboxylic acid synthase, ACS)和ACC氧化酶(1-aminocyclopropane-1-carboxylic acid oxidase, ACO)的基因转录丰度增加(Rauf等2013), 促进了乙烯(ethylene, ETH)的大量合成, 增强了纤维素酶活性, 加速了细胞分裂和部分细胞的程序化死亡(programmed cell death, PCD), 细胞排列变疏松, 组织间隙增大, 形成了通气组织(尹冬梅2011)。木葡聚糖内转糖苷酶/水解酶(xyloglucan endoglycosidase/hydrolase, XTH)是一种细胞壁松弛因子, 可改变细胞的形状和大小, 影响细胞的再生分化, 由*XTHs*基因编码, 受乙烯的诱导调节, 参与细胞壁的扩展和降解。淹水胁迫下, *XTH13*、*XTH32*、*XTH8*、*XTH9*和*XTH23*均参与了玉米细胞通气组织的形成(Thirunavukkarasu等2013)。淹水条件下, 乙烯响应元件(ethylene response factors, ERFs)诱导相关基因的表达, 调控不定根的形成。在番茄中, 调控乙烯合成关键基因*ACS*的表达促进乙烯积累, 从而刺激了生长素的运输, 并导致生长素在茎中的积累, 以此触发额外的乙烯合成, 进一步刺激生长素向植株淹水部分流动, 诱导不定根的形成(Vidoz等2010)。在拟南芥中, ERF-VII (the group VII ethylene response factors)成员*HRE2* (*HY-*

POXIA RESPONSIVE ERF1)也参与调控了不定根的形成, *HRE2*的过表达可以显著提高不定根的密度(Eysholdt-Derzso和Sauter 2019)。也有研究表明, 叶源性化学物质的长距离运输影响下胚轴或茎基部ARs的形成(Verstraeten等2014; Wu等2020), 叶片中血红素可通过*AU*-HO-1-血红素-CO传输通路运输至茎部发挥作用。光敏色素合酶基因(phytochromobilin synthase gene *AUREA*, *AU*)可以维持叶片中血红素稳态, 导致叶片褪绿, 启动不定根的发生。*AU*功能的丧失可导致叶片中大量积累血红素, 然后长距离运输到茎部, 而茎中高血红素水平提高了血红素氧合酶(HO-1)的活性, 进一步分解茎中过量的血红素, 其分解的下游副产物CO的释放诱导了茎中ARs的发生。

2 呼吸作用的适应性变化及厌氧多肽的调控作用

淹水胁迫下, 植物根际氧浓度降低, 极大限制了植物与外界的氧气交换, 从而抑制了线粒体呼吸和氧化磷酸化(Zhou等2020), 使其由有氧呼吸转变为无氧呼吸, 导致能量供给减少(魏和平和利容千2000; Schmidt等2018)。植物为维持体内能量供给, 发生了系列代谢变化, 以增加能量供给, 减少能量耗散, 抵抗淹水伤害(Setter等2009)。淹水胁迫初期会诱导蔗糖合成酶(sucrose synthase, SS)、醛缩酶、丙酮酸脱羧酶(pyruvate decarboxylase, PDC)、乙醇脱氢酶(alcohol dehydrogenase, ADH)和乳酸脱氢酶(lactic dehydrogenase, LDH)等酶活性, 促进了糖酵解和发酵作用, 加速可溶性和再生性碳水化合物的分解代谢, 生成ATP以及NAD^+, 增加体内的能量供应(Panda和Barik 2021)。但随着糖酵解速度的加快, 糖的降解和消耗加速(Zhou等2020), 乙醛、乙醇、乳酸以及丙氨酸等发酵产物大量积累(Sokolov等2015), 细胞质酸化(Portner 1987; Peng等2020), 植物此时会减缓代谢速度和生长速率, 减轻淹水伤害(向镜等2016)。在缺氧条件下, 植物也会启动脱氢酶系统分解乳酸、乙醇及苹果酸等毒性物质, 缓解淹水胁迫(陈鹭真等2006)。ADH是植物组织对酒精发酵自我适应代谢过程的一个关键酶, 可催化乙醇脱氢分解, 降低乙醇的毒害作用, 维持了能量平衡, 延长缺氧条件下植株的存活时间(潘澜和薛立2012), 是陆生植物应答低氧胁迫的生存策略之一(Crawford 1992)。随着胁迫时间的延长, 耐淹植物的形态结构发生适应性变化, 皮孔、不定根和通气组织的形成促进O_2的运输, 使无氧呼吸又转变为有氧呼吸(Vidoz等2016), 从而增强了耐淹性。

植物的耐淹能力与植物的耐缺氧能力密切相关。在低氧条件下, 植物可通过氧浓度依赖型转录因子的稳定作用调节低氧耐受性基因的表达, 从而激活下游信号适应和恢复低氧环境(Patel等2019)。在常氧条件下, ERF-VIIs家族的成员*RAP2.12*处于失活状态, 与酰基辅酶A结合蛋白1/2 (ACBP1/2)结合在质膜上(Patel等2019)。当植物处于低氧条件下, *RAP2.12*被输出到细胞核, 刺激低氧基因*PDC*和*ADH*的表达(Licausi等2011; Zhou等2020)。当植物体重新获得O_2, *RAP2.12*就会通过26S蛋白酶体系统(26S-proteasome system)迅速降解(Licausi等2011; Zhou等2020)。

在低氧/缺氧条件下, 正常蛋白质的生物合成受到抑制, 厌氧多肽(anaerobic polypeptides, ANPs)被诱导合成(李绪行1993; Sachs等1980)。Li等(2013)应用双向荧光差异凝胶电泳技术对黄瓜差异蛋白质分析发现, 低氧胁迫诱导合成了碳代谢、抗氧化系统、防御胁迫及氮代谢的蛋白质或多肽, 以缓解低氧胁迫, 促进黄瓜生长。目前所报道的ANPs主要包括PDC、LDH、ADH、葡萄糖-6-磷酸异构酶、甘油醛3-磷酸脱氢酶、SS、醛缩酶、甲酸脱氢酶、丙酮酸磷酸双激酶、丙酮酸激酶及木葡聚糖转葡糖苷酶等, 均为糖代谢和发酵相关酶(Voesenek和Bailey-serres 2013; Evans和Gladish 2017)。PDC是*Pdcs*基因的厌氧诱导产物, 为乙醇发酵途径的关键调节酶(丁君辉等2010), 拟南芥中有4个*Pdc*基因, *Pdc1*是主要的厌氧诱导基因, 最初在根内表达; *Pdc2*在根和叶中都有持续的微量表达; 而*Pdc3*和*Pdc4*很少表达(Kürsteiner等2003), 且*Pdc1*和*Pdc2*的高表达有助于提高拟南芥的耐涝性(Ismond等2003)。另外*Pdcs*基因在水稻(Hossain等1996)、拟南芥(Dolferus等1997)及玉米(Thelen等1999)等植物中均有报道。ADH是植物体内发酵过程中主要

末端酶, 与厌氧状态下NAD^+的再循环有关。*Adh*是最早被分离出来的厌氧基因, 在植物细胞中有厌氧诱导表达型*Adh1*和组成型*Adh2*两种类型(Sachs等1976), 在玉米(Gerlach等1982)、拟南芥(Dolferus等1997)、水稻(Mujer等1993)、大麦(Hart等1980)和小麦(Mitchell等1989)等植物中已获得*Adh1*基因序列全长。淹水胁迫下玉米幼苗中ADH活性不断增加, *Ahd1*和*Adh2*表达量均显著提高, 耐淹性增强(Freeling 1973; Scandalios 1969)。LDH可将乙醛氧化为乙酸, 同时将NAD^+还原成NADH, 降低无氧呼吸途径中乙醛的毒性, 目前已经从拟南芥、玉米、水稻及烟草中分离出LDH相关基因*Adh2a*和*Adh2b* (郑俊骞等2013)。

3 光合作用的适应性变化

气孔是绿色植物进行蒸腾、光合和呼吸作用时水分、CO_2及O_2的重要通道。植物各生育期遭受淹水胁迫, 均可导致叶绿素含量、光合参数(P_n、G_s、C_i和T_r)、叶绿素荧光参数(F_m、F_m'、ETR、q_P、q_N、NPQ)以及光合酶活性(白丹凤等2019; Wu等2018)下降, 降低其光合作用; 且生育前期的危害大于生育后期(Shao等2013; Zheng等2016; Ren等2017)。淹水胁迫初期, 为维持体内水平平衡, 叶片气孔关闭, 水分蒸发减少, 植物耐涝性增强; 但叶片气孔关闭会影响气体扩散, 降低光合作用(朱敏等2015); 同时会造成胞间CO_2的亏缺和O_2的冗余(Ashraf和Arfan 2005), 导致活性氧积累, 破坏光合反应中心和叶绿体结构(Ladygin 2004)。研究表明耐淹植物在淹水初期, 由于气孔限制会导致光合速率降低(李芳兰和包维楷2005), 但随着不定根及通气组织的形成, O_2摄取和运输能力明显改善(魏和平和利容千2000), 气孔导度不断增大, 光合作用得以恢复(罗芳丽等2007)。当植物地上部(部分或全部)淹没时, 会在叶片表面形成一层疏水气膜(50~100 μm厚), 减小气体交换的阻力(Verboven等2014), 增加叶片表面气体交换速度, 维持植物在水中生存(Winkel等2016)。叶片表面结构, 如角质层的空间结构(如沟和槽)、乳突、毛状体和蜡层, 都可促进叶片的疏水性, 保证了叶片气膜的形成(Barthlott等2010)。因此, 气膜的形成增强了完全淹没植物的水下光合作用、暗呼吸和内部通气(Winkel等2013), 提高了陆生植物的耐淹性。

4 抗氧化保护系统的变化及其调控作用

正常生长条件下, 植物体内存在一套维持体内活性氧(reactive oxygen species, ROS)动态平衡的保护机制。淹水胁迫下, ROS动态平衡被打破, 植物体内代谢紊乱及电子渗漏, 导致超氧阴离子(O_2^-)、羟基自由基(OH^-)、过氧化氢(H_2O_2)和单线态氧($^1O_2$)等ROS的积累(汤玉喜等2008; Rachana等2016)。为抵御淹水胁迫条件下ROS的毒害作用, 陆生植物可启动抗氧化酶和非酶抗氧化保护机制来维持ROS代谢平衡(喻娟娟2018)。抗氧化酶主要包括超氧化物歧化酶(superoxide dismutase, SOD)、过氧化物酶(peroxisome, POD)、过氧化氢酶(catalase, CAT)及抗坏血酸过氧化物酶(ascorbate peroxidase, APX)等(Bansal和Srivastava 2012)。SOD主要清除O_2^-, 使其形成H_2O_2和O_2, 而POD和CAT则主要催化H_2O_2形成H_2O和O_2。这三种酶组成一个完整的防氧化链, 可有效地保护植物免受伤害(王芳等2019)。非酶抗氧化保护物质主要包括可溶性蛋白、可溶性糖、抗坏血酸(ascorbic acid, AsA)、脯氨酸(proline, Pro)、α-生育酚(vitamin E, VE)、类胡萝卜素和谷胱甘肽(glutathione, GSH)等(Wang等2019; 刘超颖等2019; 吴麟等2012; 王国骄等2012), 这些抗氧化物质不仅可以清除O_2^-、OH·和$^1O_2$等活性氧, 有的还能协同提高相关酶的活性(宋纯鹏等1993), 或作为相关酶的底物(Shao等2007), 从而提高植物对逆境胁迫的耐受能力(王国骄等2012)。如VE可直接与$^1O_2$反应, 抑制脂类过氧化, 另一方面也可提高SOD的活性, 减少O_2^-的积累, 从而抑制叶绿素和蛋白质的降解, 维持PSII的活性, 延缓叶片的衰老。但随着淹水胁迫的持续加重, 抗氧化保护系统破坏加剧, 致使ROS积累, 细胞膜脂过氧化产物丙二醛含量增加, 细胞膜的功能遭受破坏, 因而引发和加剧膜脂过氧化作用, 导致植物细胞受到伤害, 甚至植株死亡(Salah等2019)。

逆境胁迫条件下, ROS也作为一种信号分子发挥着重要的调控作用, 其在细胞内的积累浓度不同, 调控作用存在差异(Lindermayr和Durner 2015)。

ROS在低浓度时, 作为信号分子调节植物的生长发育及对逆境的应答, ROS/NO信号可提高植物在低氧胁迫下的耐受性(Pucciariello和Perata 2017); 在高浓度时, 可以通过与NO互作参与PCD等通路的激活(Patel等2019), 维持体内的氧化还原稳态(Lindermayr和Durner 2015)。植物NADPH氧化酶是ROS产生的关键酶, 在ROS介导的信号转导中起着重要作用(Pan等2021)。淹水胁迫可诱导NADPH氧化酶相关基因*Atrboh D*的表达, 正向调控H_2O_2的产生和*ADH1*基因表达, 增强乙醇发酵能力, 提高植物在淹水条件下的存活率(Sun等2018)。*Atrboh D*参与初级缺氧信号通路, 调控ETH合成基因*ACS7/8*的转录以及缺氧诱导基因*ERF73*/*HRE1*和*ADH1*等下游基因的表达(Yang和Hong 2015)。Liu等(2017)的研究发现, *Atrboh D*和*Atrboh F*均可通过产生ROS, 提高Ca^{2+}含量, 介导*ADH1*、*PDC1*、*ERF73*、*MYB2*、*LDH*、*SUS1*和*SUS4*等缺氧下游基因的表达, 提高拟南芥对低氧胁迫的耐受性。

5 内源激素的变化及其调控作用

淹水胁迫对植物内源激素的含量、合成及运输均有影响(Pan等2008)。乙烯的快速积累是植物对淹水作出反应的重要途径(Hartman等2019)。根系在淹水条件下会诱导乙烯合成前体物质氨基环丙烷羧酸(1-aminocyclopropane 1-carboxylic acid, ACC)基因的表达, 促进植物根系中ACC合成, 运输至地上部, 氧化生成乙烯(Luan等2018; Sasidharan等2018; 刘光亚等2019)。乙烯是受淹植物最主要的信号分子(陈发棣等2018), 与乙烯响应因子(MYB、bZIP、bHLH和ERT)结合发挥调控作用(Bailey-Serres等2012)。乙烯可诱导VII ERF家族中的*SK1*/*SK2* (*SNORKEL1*/*SNORKEL2*)调控赤霉素(gibberellin acid, GA)合成基因的表达, 增加植物体内GA含量, 加速植株节间伸长, 使植物逃离缺氧环境(Hattori等2009)。乙烯也可通过诱导VII ERF家族中*Sub1A*调控水稻GA合成抑制因子*SLR1* (*Slender rice-1*)基因的表达, 减少植株生长点GA含量, 抑制其茎尖生长, 减少能量消耗, 增加耐涝性(Xu等2006; Fukao和Bailey-Serres 2008)。乙烯可诱导细胞的PCD的级联反应或激发ROS的产生, 进而介导溶生型的通气组织(Ni等2019)或不定根的形成(Qi等2019)。由此可见, 乙烯在植物的耐涝形态适应机制中发挥着重要的信号转导作用。

生长素(auxin)在植物顶端分生组织合成, 极性运输到各组织器官发挥功能, 极性运输载体蛋白PIN (PIN-FORMED)介导了吲哚-3-乙酸(indole-3-acetic acid, IAA)在植物体中的动态运输。研究表明, 淹水条件下ARs的形成发育与IAA的浓度及其极性运输密切相关(Yamamoto等2007; Yavas等2012)。淹水可诱导IAA极性转运蛋白基因*PIN2*的表达(Dawood等2016), 进而促进IAA向植株淹水部位运输, 从而启动细胞分裂诱导ARs的形成(Jia等2021)。拟南芥IAA响应因子(auxin response factor, ARF)家族基因参与了ARs形成的调控, 其中*ARF6*和*ARF8*为正调控因子, *ARF17*为负调控因子, 三者协调调控IAA, 诱导*GH3* (*Gretchen-Hagen3*)基因(*GH3.3*、*GH3.5*和*GH3.6*)参与下胚轴的ARs启动(Gutierrez等2009)。当*PIN2*沉默后, IAA转运受阻, ARs原基的启动生根受到抑制(Dawood等2016)。淹水条件下, 外源施用IAA转运抑制剂1-萘酞酸(1-naphthylphthalamic acid, NPA), 会阻碍番茄(Vidoz等2010)、黄瓜(Qi等2019)和烟草(McDonald和Visser 2003)的ARs的诱导及生长。淹水水稻经NPA处理后, 其*OsPIN1*的表达量降低, ARs的发育受阻(Xu等2005)。

脱落酸(abscisic acid, ABA)是植物逆境响应中重要的信号物质, 可通过细胞质Ca^{2+}、ROS和NO等信号分子调控气孔的开闭(Trapet等2015)。植物遭受涝害后, ABA含量显著增加, 气孔关闭, 可有效减少植株水分散失, 提高水分利用效率, 从而增强植物的耐涝性(Kim等2015)。在拟南芥中, 过表达*AP2/ERF*家族基因*RAP2.6L*可促进ABA生物合成, 提高ABA的浓度, 从而关闭气孔, 启动抗氧化防御系统, 降低氧化损伤, 延缓衰老, 显著提高耐涝性(Liu等2012), 类似的研究结果在棉花(Zhang等2016)、小麦(Nan等2002)和其他作物中也有报道。但也有研究表明, ABA在植物耐淹机制中可作为负调控因子, 起负调控作用(Pan等2021)。如在淹水胁迫下, 欧白英(*Solanum dulcamara*)茎中ETH的积累, 伴随着ABA浓度的急剧下降, 促进了ARs的

形成。外源施用1 mmol·L^{-1} ABA可显著抑制ARs的形成; 用100 mmol·L^{-1} ABA抑制剂——氟啶草酮(fluridone)处理则诱导了ARs的产生(Dawood等2016); 淹水深水稻内源ABA含量降低, GA浓度增加, 促进了节间伸长(Yang和Choi 2006)。

淹水胁迫可诱导水稻节间GA合成基因的表达, 提高节间GA含量, 促使其快速生长, 脱离缺氧环境(Hattori等2009)。在淹水条件下, 乙烯响应因子*OsEIL1a*与*SD1* (*SEMIDWARF1*)启动子结合催化GA生物合成, 增加GA的敏感性, 刺激节间生长(Kuroha等2018); *OsEIL1a*也可与*SK1*和*SK2*启动子直接结合, 促进*SK1*和*SK2*的转录, 以此介导下游基因的表达, 促进受淹植物节间伸长(Kuroha等2018)。在淹水胁迫下, *SUB1A*可增加GA信号抑制因子DELLA蛋白*SLR1* (*slender rice1*)和*SLRL1* (*slender rice1 like 1*)的积累, 抑制受GA诱导的淀粉代谢相关基因的表达, 调控植株节间生长和呼吸作用(Perata 2018)。另外, Nagai等(2020)报道了2个基因, 即促进节间伸长的*ACE1* (*ACCELERATOR OF INTERNODE ELONGATION 1*)和抑制节间伸长的*DEC1* (*DECELERATOR OF INTERNOD ELONGATION 1*), 且这两个基因功能的发挥均受GA的影响。GA可以诱导*ACE1*促进分生组织区域细胞分裂, 从而促进水稻节间伸长。而*DEC1*则抑制植株的节间伸长, 在禾本科植物中其表达是保守的。在*dec1*突变植株中, 与细胞分裂相关的基因*HISTONE H4*和*CDKA1*在节间组成性表达, 促使*dec1*突变体节间细胞分裂增强, 节间伸长, 而GA处理可进一步提高节间分生组织的活性。

油菜素类固醇(brassinosteroids, BRs)是一种天然甾体化合物, 可诱导植物对多种生物和非生物胁迫的抗性, 促进植物生长发育(Ahammed等2020)。Kang等(2009)研究发现, 24-表油菜素内酯(exogenous 24-epi-brassinolide, EBR)可促进低氧胁迫下黄瓜幼苗叶片碳水化合物向根系的转移, 提高根系糖酵解酶活性, 触发抗氧化酶活性, 减少ROS的产生, 从而提高幼苗对低氧胁迫的抵抗力。EBR还通过促进黄瓜幼苗乙烯的产生, 提高与细胞壁降解相关酶的活性, 促进黄瓜下胚轴的膨大、疏松和ARs的形成, 从而改善植株的供氧状况, 增强植株对低氧胁迫的耐受性(Ma和Guo 2014)。另外, BR可以在*Sub1A*基因的调控下与GA互作, 以限制水稻地上部伸长。淹水时, *Sub1A*基因型水稻的BR生物合成基因表达量较高, 从而触发了内源BR水平增加, 导致GA分解代谢基因*GA2ox7*的转录, 使GA含量降低。同时, GA介导的反应在淹水条件下可被DELLA家族成员GA信号抑制因子*SLR1*蛋白负调控, 从而抑制水稻植株的伸长(Schmitz等2013)。

茉莉酸(jasmonic acid, JA)是茉莉科植物中最具特征的一种独特的植物激素, 可调节植物生殖生长、养分储存和同化物运输(Alisofi等2020), 并参与非生物胁迫产生的防御反应(Ou等2017; Balfagón等2019; Ghaffari等2020)。Xu等(2016)发现, 涝渍敏感黄瓜品系Pepino的下胚轴中JA含量在淹水2 d后约为对照组的2倍。而耐涝品种‘Zaoer-N’的下胚轴JA含量在淹水过程中显著降低, 说明JA与植物耐涝性可能呈负相关。但其他研究表明, JA处理抑制了淹水胁迫下根系的生长和SA的作用。与对照相比, JA处理的淹水大豆中含有649种不同的蛋白质, 主要与胁迫响应代谢途径、糖酵解、乙醇发酵、细胞壁和细胞组织代谢有关。施用JA显著降低了淹水对大豆植株的伤害, 并通过改变蛋白质组学特征促进了植物生长(Kamal和Komatsu 2016)。淹水条件下, 同一植物不同组织中JA含量存在显著差异。如柑桔叶片JA含量在淹水条件下显著高于对照, 但根系JA含量急剧下降。这可能是由于在缺氧条件下抑制JA合成途径的关键脂氧合酶引起的(Arbona和Gómez-Cadenas 2008)。

水杨酸(salicylic acid, SA)是一种内源植物生长调节剂, 可作为一种信号分子调节植物的代谢和生理反应, 影响植物的生长发育过程, 并在植物体内介导多种环境胁迫诱导的生理反应(Sayyari和Ghanbari 2013; Yang等2016)。一些研究表明, SA能减轻洪涝灾害, 增强对植物对淹水胁迫的耐受性, 并提高抗氧化能力(Janda等2012; Shen等2014)。Bai等(2009)研究发现, 外施SA可显著减轻低氧对八棱海棠(*Malus robusta*)生长的抑制作用, 并显著降低O_2^-、电解质渗漏和脂质过氧化水平, 提高SOD、POD和APX活性。Ying等(2013)以杨梅(*Myric rubra*)为试材, 研究了外源SA对淹水胁迫下杨梅幼

苗的生理生化变化, 发现经SA处理的幼苗较未处理幼苗表现出较高的叶绿素含量、光合速率、气孔导度、SOD、CAT活性和脯氨酸含量, 以及较低的相对电解质电导率和丙二醛含量。这些结果说明, SA在减轻淹水带来的负面效应方面具有重要作用, 可以作为一种潜在的生长调节剂, 促进淹水胁迫下的植物生长。另外, SA被报道参与通气组织和ARs的形成。植物根细胞内SA的增加会触发PCD反应, 导致根细胞壁脂质过氧化增加, 进而导致根内通气组织细胞的发育, 通气组织细胞能增加O_2向根组织的转移, 减轻水分胁迫。此外, SA的积累还可以刺激ARs原基的形成, 并通过诱导大量ARs的发育进一步增强耐涝性(Kim等2015)。

褪黑素(melatonin, MT)是一种具有强抗氧化能力的植物激素, 可在多种胁迫过程中促进植物生长(Sharif等2018)。Zheng等(2017)对遭受淹水胁迫的苹果幼苗进行MT处理, 发现MT处理的幼苗可通过提高抗氧化酶活性、改善有氧呼吸和光合机制来增强苹果幼苗对淹水胁迫的耐受性。另外, MT生物合成基因(如*MbT5H1*、*MbAANAT3*和*Mb-ASMT9*)的表达增加了经MT处理幼苗中内源性MT的产生, 从而维持其他生理生化过程的稳定(Zheng等2017)。因此, 可以认为MT在调节植物对淹水胁迫的反应中起着关键作用。

多胺(polyamines, PAs)是一类具有脂肪氮结构的植物激素类脂肪胺天然化合物, 亚精胺(spermidine, Spd)是其中一种, 具有抗酸中和、抗氧化、稳定细胞膜和细胞壁的能力, 在调节植物对各种环境胁迫的防御响应中起着重要作用(Gill和Tuteja 2010)。前人在研究外源Spd对黄瓜幼苗根系在低氧水培时的生长状况以及内源PAs的变化时, 发现外源Spd对低氧胁迫下黄瓜幼苗根系的生长有促进作用, 并增加了根系中的PAs含量, 从而降低了根系中H_2O_2含量, 减缓了低氧伤害(汪天等2010)。γ-氨基丁酸(γ-aminobutyric acid, GABA)也参与了植物的淹水响应机制(Gilliham和Tyerman 2016)。目前的研究表明, 外源施用GABA能促进玉米叶片中GABA含量, 提高光合作用, 抗氧化能力, 叶绿素含量及叶绿体数量, 并改善叶肉细胞叶绿体超微结构和线粒体结构(Salah等2019)。

6 展望

植物淹水响应的研究是目前逆境胁迫研究的热点之一, 其中以普通野生稻和拟南芥为模式植物的研究已取得了突破性进展, 使我们对淹水胁迫响应机制的了解更加深入。然而, 在这一研究领域中, 我们还有许多问题亟待解决。

首先, 植物在淹水条件下会遭受到低氧胁迫, 这会影响植物正常的生理代谢。在进化过程中, 植物已经开发出低氧感应机制, 主要是通过O_2浓度依赖型转录因子的稳定作用来调节涉及低氧耐受性基因的表达。一些植物细胞器如线粒体、叶绿体、过氧化物酶体和质外体等都会产生ROS和NO来响应低氧胁迫, 但ROS和NO是如何互作低氧胁迫的? 转录因子是如何调控结构基因调控植物应对淹水胁迫的? 以及识别更多与低氧胁迫耐受性相关的基因, 将有助于预防因洪涝和其他非生物胁迫对植物的伤害。

其次, 与空气中的光合作用相比, 对水生和沉水湿地植物光合作用的研究较少, 因为水下的环境比空气中的环境更复杂, 所以水下的光与CO_2利用率往往很低。而水生植物之所以能在水下生长良好, 可推测水生植物可能具有特殊的光合作用机制, 从而使其克服水下低光和低CO_2的环境。我们可以通过了解一些水生植物的水下光合作用机制, 以此为基础设计陆生植物耐淹性能力的研究, 对陆生植物的叶片进行驯化, 以促进陆生植物在完全淹没条件下叶片的气体交换、内部通气和光能利用能力。这对于水生植物的生理生态、陆生植物的耐淹能力以及一些洪涝易发地区的生产是至关重要的。

再者, 植物激素在逆境胁迫中的作用是不可替代的。其中, 乙烯的生成是植物响应淹水胁迫的早期信号, 它能够通过调控多种转录因子来调节不定根、通气组织的形成, 还可以感应低氧胁迫相关信号以激活下游信号来适应低氧环境, 在淹水胁迫适应性中起着十分重要的作用。GA也是响应淹水胁迫的关键激素之一, 特别是在低氧静止和低氧逃避机制中, GA发挥着重要的作用。然而, 这些植物激素是通过怎样复杂的网络来发挥其生物

学功能的？不同激素之间的互作网络是如何运作的？淹水条件下植物激素间的相互作用是否受遗传因素的影响？ERF-VII家族中, 有哪些重要的基因参与了低氧和淹水胁迫的响应与调控过程？对这些科学问题的深入研究将对全面了解植物洪涝响应和作物生产具有重要的价值。

最后, 淹水胁迫严重影响植物的生长发育, 使植物品质降低, 作物产量下降。因此, 研究各植物对淹水胁迫的响应规律, 开发增强植物耐淹性的方法应是我们所关注的焦点。最直观快速的方法是进行耐淹品种筛选和耐淹性评价。通过人为控制淹水条件进行淹水致死试验, 根据淹水处理过程中植物各品种的表型变化, 便可建立一个简单直观, 并能基本上客观反映植物真实受害状况的耐淹性评价方法, 以此筛选出抗淹品种。使用外源物质也可有效地缓解淹水胁迫对植物造成的伤害, 提高植物耐淹性。前人研究表明, 外源施用SA、JA、GABA、BR、Spd、褪黑素和烯效唑等植物生长调节剂, 可清除植物体内的活性氧, 维持胞浆pH值、调节渗透压、提高涝害后植物的光合特性, 降低膜脂过氧化程度, 减轻涝害对植物的胁迫(Liu等2007; Ahammed等2013; 张洪鹏等2016; Marta等2016; Kim等2018; Salah等2019; 向镜等2016)。除此之外, 也可以运用一些分子生物学技术, 将目前已发现的编码ANPs的基因分离出来, 转到抗性较弱的优良品种中以增强品种耐淹性。

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