

植物干旱胁迫响应机制研究进展

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摘要:干旱是限制植物生长的重要因素,会诱导植物产生渗透失衡、膜系统损伤、呼吸与光合速率降低等不良反应,不仅妨碍植物各阶段的生长代谢,还影响农作物的高质高产。在与外部环境的互作过程中,植物会产生干旱响应,如通过根系和叶片结构、代谢物质成分的改变以及抗旱基因的表达来抵御干旱胁迫。从表型水平、生理水平和分子水平阐述了植物干旱胁迫响应的研究进展。其中,植物表型水平的干旱胁迫响应主要体现在根系和叶片的结构改变,而植物生理水平的干旱胁迫响应主要体现在光合作用、渗透调节代谢、抗氧化代谢和激素物质等方面,详细阐述了植物干旱胁迫响应的分子机制及参与其中的调节基因和功能基因,对研究中存在的问题进行了讨论,展望了植物干旱胁迫响应的研究前景。

关键词:干旱;表型;生理;分子;基因工程

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Research Advance on Drought Stress Response Mechanism in Plants

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Abstract: Drought stress is one of the major limitations to plant growth and development. Drought can lead to osmotic imbalance, damage of membrane system, decrease of respiration rate and photosynthesis rate, etc. adverse reaction. It not only hinders plant growth and metabolism at different stages, but also affects crops to achieve good quality and high yield. In the interaction between plants and external environment, plants will build drought response, such as changing the structure of plant root system and leaf blades, composition of metabolites and expression of drought-resistant genes to resist drought stress. The paper reviewed the research progress in the mechanism of plant response to drought stress from phenotypic level, physiological level and molecular level. The response of drought stress in phenotypic mainly included the structure change of root system and leaf. The response of drought stress to physiological was mainly reflected in photosynthesis, osmotic regulation, antioxidant metabolism and hormone, etc.. The paper elaborated in detail the molecular mechanism of plant drought stress response and regulatory and functional genes involved in drought stress, discussed the existing problems and look forward the research prospect.

Key words: drought; phenotype; physiology; molecule; genetic engineering

近年来,环境与可持续农业之间的矛盾日益突显,其中,水资源匮乏使我国粮食种植面临严峻的干旱问题。干旱作为植物生长过程中的主要制约因素之一,会阻碍植物的呼吸作用、光合作用和气孔运动等,进而影响植物的生长发育和生理代

谢。而植物为应对缺水逆境会启动自身的干旱响应机制,如通过形态结构的改变、抗旱基因的表达、激素与渗透调节物质的合成等来缓解干旱逆境。目前关于植物干旱响应机制的研究热度呈上升趋势,本文详细剖析了植物表型水平、生理水平

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和分子水平的干旱胁迫响应方面所取得的研究进展,关注植物抗旱基因工程的应用,对研究中可能存在的问题进行了探讨,以期为现代农业生产中的作物高产稳产、抗旱育种与种质创新等提供参考。

1 植物表型水平的干旱胁迫响应

1.1 植物根系的干旱胁迫响应

根系结构(解剖结构和根系构型)的改变能协助植物缓解干旱胁迫,其中,导管和皮层组织等根系解剖结构在植物干旱胁迫响应的过程中起重要作用。例如,水稻(*Oryza sativa*)根系导管数量的增多促进水分运输效率提高,帮助植株抵御干旱^[1]。Chimungu 等^[2]研究发现,玉米(*Zea mays*)根系皮层细胞减少利于降低代谢消耗,以此提高水分利用率。根毛和根系密度等根系构型也影响植物的缺水适应。如缺失根毛的拟南芥(*Arabidopsis thaliana*)突变体的根系吸水强度显著减弱,对缺水逆境胁迫的反应更加敏锐^[3]。另外,根系分支与密度增加也可促进水稻根系吸水,提高植株抗旱性^[4]。

1.2 植物叶片的干旱胁迫响应

叶片可通过气孔、腺毛、叶肉组织和角质膜等形态变化来响应缺水逆境。Hughes 等^[5]研究表明,大麦(*Hordeum vulgare*)叶片气孔密度减小可增强其对缺水胁迫的耐受性;苏适等^[6]试验发现,耐旱性芝麻(*Sesamum indicum*)品种冀 9014 的腺毛分泌能力强于不耐旱品种;Wang 等^[7]研究发现,叶肉组织越紧密的葡萄品种抗旱性越好。此外,还有研究表明,旱生环境下针叶植物的叶角质膜较厚,叶片的萎蔫卷曲运动可抵御太阳直射以提高植株的保水性^[8,9]。

2 植物生理水平的干旱胁迫响应

2.1 植物光合作用的干旱胁迫响应

光合作用是植物生长的基本代谢过程,植物受到干旱胁迫时,其叶片光合生理会发生明显变化,主要通过叶绿素含量、净光合速率和蒸腾速率等来反映。例如,范志霞等^[10]将叶片的叶绿素含量作为主要抗旱指标来比较紫穗槐(*Amorpha fruticosa*)的抗旱性,发现施用 150 mg/L 的多效唑

可通过显著提高叶绿素含量来改善植株抗旱性。而在缺水逆境中,褪黑激素处理的玉米由于净光合速率、气孔导度和蒸腾速率均上升,其水分状况得到改善^[11]。Deeba 等^[12]研究证实,随着干旱强度的增加,棉花的净光合速率、蒸腾速率和气孔导度等会降低。

2.2 植物渗透调节代谢的干旱胁迫响应

干旱胁迫条件下,植物合成的渗透调节相关物质可提高植物渗透调节能力,渗透调节相关物质包括脯氨酸、甜菜碱和多胺类等。其中,脯氨酸的偶极性可以维持膜蛋白形态完好,而降低植物水分散失^[13]。Gomes 等^[14]试验发现,干旱胁迫会诱导椰子(*Cocos nucifera*)叶片脯氨酸的积累,降低其细胞渗透势;Gou 等^[15]探究证实,玉米叶片甜菜碱含量增多可提高植株抗旱性。另外,干旱胁迫可促进腐胺、亚精胺和精胺等多胺类的生物合成,从而提高植物抗旱性^[16]。

2.3 植物抗氧化代谢的干旱胁迫响应

植物过氧化氢酶(catalase, CAT)和超氧化物歧化酶(superoxide dismutase, SOD)等可以减轻植物活性氧伤害,帮助植物抵御干旱。郑清岭等^[17]研究发现,随着干旱胁迫的加剧,沙芥(*Pugionium cornutum*)幼苗的 CAT、POD 活性先升高后降低,且 CAT 可通过减少 H₂O₂ 的含量来调节氧化还原信号传导途径,提高植株的抗氧化能力;Wang 等^[18]对萌芽期的紫花苜蓿(*Medicago sativa*)进行干旱处理,发现 Xinmu 1 比 Northstar 幼苗生长速度快且芽尖和根部的 SOD 含量高,进而说明 Xinmu 1 是相对耐旱的品种。

2.4 植物激素的干旱胁迫响应

植物激素主要包括脱落酸(abscisic acid, ABA)、赤霉素(gibberellin, GA)和生长素(auxin, IAA)。其中,ABA 与植物的抗旱关系最为密切。拟南芥 ABA 的大量合成可促进叶片气孔关闭,进而增强其抗旱性^[19]。Akhkha 等^[20]试验表明,ABA 能增强谷氨酰基磷酸酶的活性,加快脯氨酸累积,提高小麦的缺水耐受性。另外,匍匐剪股颖(*Agrostis stolonifera*)叶片中 GA 减少会提高植株抗氧化性,缓解干旱胁迫^[21];Xing 等^[22]研究发现,IAA 含量提高可增强大豆幼苗的干旱耐受性。

3 植物分子水平的干旱胁迫响应

缺水条件下,植物会表达抗旱调控基因和功能基因,进而编码功能性蛋白和有机分子合成酶,调节干旱信号转导并参与激素、渗透物质等的合

成与积累,来帮助植物响应缺水逆境。随着分子生物学技术的发展,已得到一些抗旱调控基因和功能基因,主要包括转录因子、信号因子、渗透调节基因、抗氧化代谢基因、逆境诱导蛋白基因等(表 1)。

表 1 植物主要抗旱调控基因和功能基因
Table 1 Main drought tolerant regulatory genes and functional genes in plants.

基因类型 Gene type	类别 Category	基因 Gene
调控基因 Regulatory gene	MYB/MYC	<i>AtMYB2</i> ^[23] 、 <i>PbrMYB21</i> ^[24]
	DREB/CBF	<i>AtDREB2A</i> ^[25] 、 <i>ZmDREB2A</i> ^[26] 、
	WRKY	<i>TaWRKY33</i> ^[27] 、 <i>GhWRKY11</i> ^[28] 、 <i>SpWRKY6</i> ^[29]
	AREB/ABF	<i>PtrABF1</i> ^[30]
	bZIP	<i>OsbZIP46</i> ^[31] 、 <i>OsbZIP66</i> ^[32] 、 <i>BhbZIP60</i> ^[33]
功能基因 Functional gene	NAC	<i>SlNAC11</i> ^[34] 、 <i>GhNAC79</i> ^[35]
	信号因子 Signaling factor	<i>HvCPK2a</i> ^[36]
	渗透调节基因 Osmotic regulator gene	<i>AtP5CS</i> ^[37] 、 <i>SbmtlD</i> ^[38] 、 <i>LcP5CS1</i> ^[39]
	抗氧化代谢基因 Antioxidant metabolic gene	<i>AtMPK12</i> ^[40] 、 <i>TaMPK4</i> ^[41]
	逆境诱导蛋白基因 Stress induced protein gene	<i>LeHARDY</i> ^[42] 、 <i>PePP2C</i> ^[43] 、 <i>GmPP2C</i> ^[44]

3.1 抗旱调控基因

3.1.1 转录因子 转录因子可特异性结合下游基因的核苷酸序列,产生相关调控蛋白来响应干旱胁迫,主要包括 DREB、MYB/MYC、NAC、WRKY 和 bZIP 类。例如,转录因子 DREB2 和 DREB3 能减轻干旱对小麦的伤害,增强植株的干旱耐受性^[45]。*MYB1R-1* 可调节 ABA 信号途径而参与植株的干旱胁迫响应^[46]。*NAC2* 可促进马铃薯根、茎、叶中抗氧化酶的合成,*TaWRKY82*、*TaWRKY19-C* 和 *TaWRKY16* 能调节气孔的开闭,提高气孔密度,进而改善植株抗旱性^[47,48]。玉米 *bZIP72* 基因的表达促进植株积累脯氨酸,维持渗透平衡,进而减少水分散失,增加植物在干旱条件下的存活率^[49]。

3.1.2 信号因子 信号因子可通过蛋白磷酸化和去磷酸化和 Ca²⁺ 感知来实现植物对缺水逆境的感应。CPK 和 SnRK 类信号因子正调控植物的抗旱途径。大麦 *CPK2a* 基因在缺水环境下会上调表达,促进钙依赖蛋白激酶合成,调节植株的干旱感知和信号传递^[50]。Shen 等^[51] 研究表明,樱桃

(*Cerasus pseudocerasus*) 的 *SnRK2.4*、*SnRK2.5* 基因均能被脱水胁迫诱导表达,从而调节 ABA 信号转导。信号因子还可负调控植物抗旱途径。拟南芥的法呢基转移酶 *ERA1* 会抑制脱落酸信号转导,降低拟南芥对缺水逆境的耐受性^[52]。此外,信号因子可调控多个干旱信号转导途径,例如,拟南芥 *MPK6* 不仅参与 *MKK2-MPK6* 信号途径,还可参与 *MKK4-MKK5-MPK6* 信号途径的缺水胁迫应答^[53]。

3.2 抗旱功能基因

3.2.1 渗透调节基因 干旱逆境可诱导植物渗透调节基因的表达,从而合成和积累脯氨酸、糖类、甜菜碱、多醇类和多胺类等渗透调节物质,*P5CS*、*hcf1*、*BADH* 和 *mtlD* 等均属于渗透调节相关基因。例如,Su 等^[54] 研究发现,*P5CS* 基因表达量的提高,促进高粱(*Sorghum bicolor*)的脯氨酸浓度提高。Zhang 等^[55] 研究证明,水稻 *hcf1* 基因的表达,使植株游离脯氨酸和可溶性糖含量均提高,保水能力也显著增强。苜蓿(*Medicago sativa*)

BADH 基因的表达会促进植株合成更多甜菜碱,使植株的渗透平衡力明显优于对照,抗旱性也显著提高^[56]。过表达 *mtlD* 基因的高粱合成和积累较多甘露醇,叶片含水量明显上升,植株对水分亏缺的耐受性增强^[57]。

3.2.2 抗氧化代谢基因 *ABP9*、*GbMPK3* 和 *ZFP245* 等基因的表达均可促进植株活性氧的清除,增强植物对干旱的忍受能力。Zhang 等^[58] 研究表明,拟南芥 *ABP9* 基因的表达可减轻植株氧化损伤,进而在植物干旱耐受中发挥重要作用。干旱条件下, *GbMPK3* 基因的表达能够显著提高烟草的抗氧化酶活性,并通过增强植株活性氧清除能力来应对干旱^[59]。Huang 等^[60] 试验发现, *ZFP245* 基因的表达可促进水稻抗氧化酶的合成以抑制活性氧的积累,增强植株的干旱耐受性。

3.2.3 逆境诱导蛋白基因 在水分亏缺环境下植物会表达逆境相关基因,从而合成胚胎发育晚期丰富蛋白(late embryogenesis abundant proteins, LEA)和水通道蛋白(aquaporin, AQP)等来维持细胞渗透压,而 *HVA1*、*OLP* 等基因均参与植株逆境诱导蛋白的合成。例如,水稻可通过 *HVA1* 基因的表达来合成 LEA,提高植株的缺水耐受性^[61]。油菜(*Brassica napus*)质膜上的水通道蛋白 AQP,可通过磷酸化和去磷酸化来维持细胞水势,调节植株对干旱胁迫的响应^[62]。还有研究发现,芝麻渗透调蛋白 *OLP* 基因参与叶绿素和脯氨酸的合成,其表达有助于植株抗氧化能力和抗旱性的增强^[63]。

3.3 植物干旱胁迫响应的分子机制

植物分子水平的干旱胁迫响应是一个复杂的生物学过程,需要多种信号因子、转录因子和功能基因等参与。首先,由 Ca^{2+} 、激酶和磷酸酶等感知干旱信号。其次,主要经过 ABA 依赖途径和 ABA 不依赖途径。在 ABA 依赖途径中,拟南芥 NCED3 是 ABA 生物合成的关键酶并受干旱胁迫诱导,产生的 ABA 由受体复合物 PYR/PYL/RCAR 感知,使 PP2C 释放 SnRK2,进而磷酸化激活 SnRK2 下游的 AREB/ABF 等转录因子,这个过程受 OsMYB48-1、GsWRKY20、AhNAC2、OsDBRE1F、TaMYB33 和 OsNAP 正调控;在 ABA 不依赖途径中, DREB/CBF、OsDERF1、LcWRKY5 和 SINAC 等调节下游干旱胁迫相应基因的表达,在这个过程中,生长因子 GRF7 会抑制 *DREB* 启

动子区的转录。最后, *OsCAS*、*OsLEA3-1*、*P5CS* 和 *TPS1* 等功能基因被诱导表达,使植物产生生理生化反应并做出干旱应答^[64]。

从分子水平调控植物生理代谢将会为植物抗旱基因工程的探究提供技术支撑。例如, Oh 等^[65] 构建启动子 *OsCc1* 驱动 *AP37*、*AP59* 基因并导入水稻,轻度干旱后,植株的水分利用效率大幅提高,耐旱性增强。Bhatnagar-Mathur 等^[66] 研究发现,设置 *Atrd29A* 启动 *At-DREB1A/CBF* 基因的表达,转基因花生可合成和积累较多脯氨酸,具备更强的脱水耐受性。这些研究均运用植物抗旱的分子机制来改善植物耐旱性,并证明了通过基因工程提高植株抗旱能力的重要性。

4 展望

综上所述,植物表观水平、生理水平、分子水平的干旱胁迫响应研究虽已取得很大进展,但以下问题还需进一步研究:①植物的干旱响应机制仍不完全清楚。参与其中的酶和基因种类较多,信号感知、传导途径以及抗旱物质的合成与转运等一系列过程尚未完全明了;②新的抗旱相关基因有待发掘。植物抗旱是由多基因控制的数量性状,仍需进一步挖掘新的耐旱相关基因;③缺乏系统的植物抗旱评价体系。不同物种或同一物种不同时期,植物的干旱响应均存在较大差异,目前还缺少完整统一、精准化的抗旱鉴定指标和评价体系;④传统抗旱育种手段存在缺陷。常规抗旱育种技术面临不可预测、选择效率低等制约因素;⑤研究者大多是在模拟条件下探究植物的干旱胁迫响应。如何成功应用基因工程增强植物对多种胁迫的抗性需要在本质上有突破;⑥植物干旱相关的应用研究相对薄弱。大部分植物抗旱研究是在理论水平得出相关结论。

针对植物干旱胁迫响应研究中存在的问题,对其未来的研究提出如下建议:①可利用免疫共沉淀、酵母双杂交和 DNA 分子标记等技术,探究植物抗旱相关的转录因子调节和信号转导途径,从更深层次研究植物的干旱胁迫响应机制;②通过转录组技术构建差减文库来探寻新的植物抗旱基因,并运用串联质谱与蛋白组学等手段研究其表达特性;③有效地、综合地分析干旱胁迫下植物的响应过程,筛选合适的指标,建立科学的耐旱评

价体系;④分子育种技术可弥补传统育种的欠缺,缩短育种时间并提高育种水平;⑤实验室试验、田间试验和野外试验并重,优化试验设计和数据分析方法,使植物抗旱研究的环境更接近自然状态,并提高所测数据的精准度和说服力;⑥运用转基因技术并关注微生物与植物的互作,选育抗旱、高产和稳产的作物新品种,进而将植物抗旱研究应用到现代农业生产实际中。

此外,植物的干旱胁迫响应机制一直是国内外的研究热点。已有研究大多集中于干旱前后植物的表型和生理测定,即对生理生化的响应机制研究较为常见,而对其分子响应机制探究尚浅,包括抗旱基因表达调控、蛋白互作机理和信号转导途径等。需借助基因芯片、基因沉默和酵母双杂交等分子生物学技术等鉴定更多抗旱基因,探究其表达模式并筛选其上下游蛋白。全面开展植物表型、生理和抗旱分子机制研究将是未来相关研究的发展方向,这些都将是探明植物干旱响应分子机制、分子遗传育种和农业可持续发展等工作提供理论参考。

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