植物抗旱节水: 从实验室到田间

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摘要 干旱是植物在生长发育过程中可能面临的最重要的环境胁迫之一, 严重影响着世界范围内的农业生产格局和生产力. 随着全球气候的变化, 这种影响越来越明显. 因此, 研究植物的抗旱机理, 挖掘优良的抗旱基因, 培育抗旱节水的农作物尤为迫切. 植物在长期进化过程中形成了很多不同的抗旱策略以适应环境. 本文将从植物的御旱性和耐旱性这两大策略, 结合国际上最新的研究进展和本研究组多年来应用抗旱基因来提高作物抗旱性的实践来阐述植物抗旱的分子机制, 并发掘这些抗旱基因在抗旱节水作物培育中的潜在应用, 同时分析抗旱研究中仍然存在的问题, 展望抗旱研究的广阔前景.

关键词 抗旱节水, 御旱性, 耐旱性, *AtHDG11/AtEDT1*, 水分利用率, 气孔, 根系构型

植物在生长发育过程中常遭遇各种不同程度的生物和非生物胁迫, 这些胁迫严重影响植物的生长发育和农作物的产量. 在非生物胁迫中, 干旱是制约农业生产力的主要因素, 影响全球超过50%农作物的产量^[1]. 据统计, 干旱和半干旱地区约占地球陆地面积的40%, 占我国国土面积的1/2以上^[2]; 我国每年约有 4.7×10^7 hm²农田遭受旱灾威胁, 受旱面积约 2.2×10^7 hm², 成灾面积约 8.9×10^6 hm². 随着全球气候变化, 干旱威胁将变得越来越严重. 同时我国农业用水占全国总用水量的比例高达73%. 由于灌溉管理不当等原因, 农作物水分利用效率比较低, 我国面临着严重的水资源危机^[3,4].

在水资源匮乏, 气候变化加剧, 耕地面积不断减少的背景下, 如何保证粮食生产的安全是我们面临的

重要问题之一. 针对这一问题, 需要开展一场“蓝色革命”——让每一滴水生产出更多的粮食^[5], 深入开展植物的抗旱节水机理研究, 寻找优良的抗旱基因, 通过常规育种或基因工程的方法改良农作物, 在保证产量的前提下增强其抗旱性和水分利用效率(water use efficiency, WUE). 本文将结合本研究组多年来在植物抗旱节水领域的研究成果, 综述植物抗旱节水的最新研究进展, 探讨目前存在的问题和解决策略.

1 植物抗旱性

抗旱性是植物在水分缺乏环境下生存并形成产量的能力. 植物适应干旱的机制可分为3类: 避旱(drought

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escape)、御旱(drought avoidance)和耐旱(drought tolerance), 其中御旱性和耐旱性又统称为抗旱性(drought resistance)^[6].

1.1 植物的御旱性

御旱性是指植物在干旱条件下保持体内充足水分的能力. 植物在长期的进化过程中形成了一套有效的机制, 并以此实现对水分的“开源节流”: 发达的根系可以最大限度地获取土壤中的水分(开源), 调节气孔的运动和角质层蜡质可以减少水分的流失(节流).

(1) 根系. 发达的根系是植物应对干旱胁迫最显著, 也是最重要的特征. 某些沙漠植物根系干重可达总干重的90%, 根长可达数10米. 根系的构型, 包括根体积、根长、根粗细、根冠比等, 可以决定植物对水分和营养的吸收, 从而影响植物地上部分的生长和抗旱性^[7]. 在干旱条件下, 深根系可以吸收深层土壤中的水分, 帮助植物抵抗干旱胁迫. 发达的根系对于维持植物在干旱条件下的产量也十分重要^[8]. 在胁迫环境中, 根系发达的水稻(*Oryza sativa*)品种其产量也具有明显的优势^[9,10]. 将深根性状引入到浅根系品种中是一种有效的改善水稻抗旱性的育种策略^[11]. 正因为如此, 国际水稻研究所的水稻抗旱项目聚焦根系研究长达50多年^[12]. 截止目前, 尽管许多水稻数量性状座位(quantitative trait loci, QTL)已经被定位, 但是很少克隆到控制深根系的QTL^[13]. 第一个水稻根系QTL是2013年克隆到的控制旱稻深根系的QTL基因*DROI*(deeper rooting 1), 该基因受生长素负调控, 影响根的向地性和根尖细胞的伸长. 过表达*DROI*可以改变水稻根系的生长角, 从而使根系向下扎得更深, 增强水稻的抗旱性和干旱条件下的产量^[14]. 通过转基因的方法, 在水稻中过表达*OsNAC9*和*TaMOR*可以改良水稻的根系构型, 提高水稻的抗旱性和干旱条件下的产量^[15,16]. 玉米(*Zea mays*)中也发现了许多控制根系构型的QTL^[17], QTL(root-ABA1)和QTL(root-yield-1.06)是两个控制干旱条件下根系构型的主效QTL^[18,19]. 在拟南芥(*Arabidopsis thaliana*)和烟草(*Nicotiana tabacum* L.)根系中特异表达细胞分裂素氧化酶/脱氢酶可以使得植物具有更为发达的根系和显著增强的抗旱性^[20].

根系能够感知土壤水分含量, 并产生信号经木质部长距离传递到地上部分, 调控气孔的关闭和植物的生长^[21,22]. 干旱初期, 根系产生的化学信号占主导, 这

些化学信号主要有脱落酸(abscisic acid, ABA)、pH、细胞分裂素(cytokinin, CK)、乙烯前体和苹果酸等^[22]. 其中, ABA受到的关注最多. 当根系感受到干旱胁迫时, 根中合成的ABA增加, 以结合态ABA(conjugated forms of ABA)的形式通过木质部运输到地上部分, 促进气孔的关闭以降低蒸腾速率. 干旱胁迫时, 木质部的pH会升高, 从而引起叶片气孔的关闭, pH变化的这种效果可能是和ABA协同作用的结果^[23,24]. 随着干旱的发展, 当叶片水势下降出现萎蔫时, 根系水压信号(hydraulic signals)起主导作用, 驱动叶片合成更多的ABA^[25]. 农业生产中非充分灌溉、干湿交替灌溉、根区交替灌溉和部分根干燥等节水灌溉方式正是利用根源信号提高作物WUE的方法. 这几种方法都可以降低蒸腾速率和叶片的生长, 提高WUE^[26-28].

(2) 气孔. 气孔是叶片水分散失和CO₂吸收的主要通道, 每年植物通过气孔散失的水分高达35×10¹⁸ g, 相当于大气中水量的2倍^[29]. 植物灌溉获得水分的13%~18%通过叶片气孔的蒸腾作用散失^[30], 因而植物对气孔蒸腾作用的调控是决定植物抗旱性的关键因素之一. 植物通过生理和发育机制来调节气孔运动、气孔密度和气孔指数, 从而控制植物在不同环境, 尤其是干旱环境下的WUE^[29,31]. 影响光合作用和叶片水分状况的各种体内体外因素都会影响气孔的运动: 强光、蓝光、低CO₂浓度以及高湿度促进气孔的开放; 而干旱、脱落酸、高CO₂、H₂O₂、黑暗和病原菌侵染等则诱导气孔的关闭^[32,33]. ABA是植物应对干旱胁迫最重要的激素, 在干旱条件下植物合成更多的ABA, 诱导保卫细胞中活性氧自由基(reactive oxygen species, ROS)和一氧化氮(NO)的产生, 调节胞内第二信使(Ca²⁺, 1,4,5-三磷酸肌醇等)和多种离子通道, 从而促进气孔的关闭^[34,35]. 同时, NO和ABA可以在相互促进的情况下独立诱导气孔关闭^[36]. 通过调控ABA的生物合成和信号转导, 可以减小气孔的开度, 优化植物水分利用效率, 增强植物的耐旱性, 有些研究还显示作物生物量和产量也同时得到了提高^[37]. 例如, 过表达ABA受体*PYL1*(pyrabactin resistance 1 like 1), *PYL5*, *PYL8*和*PYL9*, 以及ABA合成通路基因*ZEP*(zeaxanthin epoxidase)和*NCED*(9-*cis*-epoxycarotenoid dioxygenase)等都可以提高拟南芥或水稻的抗旱性^[38-40]. 此外, 利用合成生物学方法开发ABA受体的新版本, 使其能够被农药双炔酰菌胺(mandipropamid)激活, 或者合成

ABA受体激动剂AM1(ABA mimic 1), 都能够有效地诱导气孔的关闭, 提高植物的抗旱性^[41,42].

除了气孔的运动外, 气孔的发育和分布也对植物的抗旱性至关重要. 气孔的大小和密度成负相关, 气孔密度低的植物比气孔密度高的植物更适合在干旱的环境下生存^[43]. 气孔的发育受到严格的遗传调控^[44]. 多种植物激素, 包括油菜素内酯(brassinosteroid, BR)^[45]、赤霉素(gibberellin, GA)^[46]、生长素(auxin)^[47]、独角金内酯(strigolactone, SL)^[48]等都参与对气孔发育的调控. 通过遗传操作和转基因技术等手段, 利用非ABA依赖型抗旱机制来减小气孔的开度和气孔的密度都可以达到抗旱节水的目的. 例如, 在拟南芥和烟草中遗传修饰*ERECTA*, *GTL1*(GT-2 like 1), *EDT1/HDG11*(enhanced drought tolerance 1/homeodomain glabrous 1), *GPA1*(G protein alpha subunit 1), *IRX3*(irregular xylem 3), *EPF1*(epidermal patterning factor 1), *EPF2*和*EPF9*等基因导致叶表气孔密度和气孔指数改变, 影响植株的蒸腾效率, 使植物抗旱能力增强, 光合效率提高, 生物量增加, 从而提高水分利用效率^[43,49-53].

(3) 角质层. 角质层是覆于陆生植物地上器官表面的一层脂肪性物质, 是植物与外界环境接触的重要保护性屏障, 它包括蜡质和角质. 植物角质层在抵抗各种非生物和生物胁迫中起着非常重要的作用^[54-56]. 干旱胁迫可以诱导蜡质含量增加, 导致叶片水分流失的敏感性降低, 增强植物的抗旱能力^[57]. 近几年来, 在拟南芥中已经克隆了很多调控角质层蜡质合成的基因^[58]. 据报道, 干旱诱导ABA的产生, ABA又可以进一步诱导很多蜡质和角质合成通路基因的表达^[59]. MYB类转录因子*MYB16*, *MYB96*, *MYB94*, *MYB106*的表达受ABA诱导, 参与调控干旱诱导的蜡质合成通路^[60,61]. 过表达*WXP1*, *WXP2*, *DWAI*(drought-induced wax accumulation 1), *CER1*(eceriferum 1)和*OsGL1-6*(rice glabrous1-6)可以增加表皮层蜡质的含量, 降低叶表皮的渗透性和水分的流失, 增强植物的抗旱能力^[62,63]. 过表达*WIN1/SHN1*(wax induced 1/shine 1)不仅促进表皮层蜡质的积累, 还能降低气孔密度, 从而提高植物的抗旱性^[64]. 乙烯响应基因*OsWRI*(rice wax synthesis regulatory gene 1)和*OsWR2*在干旱条件下可以转录激活蜡质合成相关基因的表达, 提高蜡质产量和植物的抗旱性^[65]. *CER9*是拟南芥中发现的第一个突变后可以增加角质层厚度, 提高抗旱性和WUE的角质合成基因^[66].

1.2 植物的耐旱性

耐旱性指植物在体内水势较低的情况下维持代谢的能力, 一方面是在干旱条件下, 植物通过渗透调节以维持较高的膨压; 另一方面, 通过解毒作用, 清除体内所积累的有害物质, 维持细胞膜稳定性, 减轻细胞受到的损伤.

(1) 渗透调节(osmotic adjustment). 干旱胁迫条件下, 细胞内外的水势会发生变化, 理论上细胞膜上存在一个蛋白可以感知细胞外的渗透势改变^[67]. 酵母渗透压感知蛋白SLN1(synthetic lethal of N-end rule 1)的植物同源蛋白ATHK1(*Arabidopsis thaliana* histidine kinase 1)起初被认为可能是这类渗透感知蛋白^[68,69], 但是最近的研究发现, ATHK1可能并不是主要的渗透压感受器(osmosensor), 因为ATHK1突变后并不影响植物在低水势条件下体内ABA和一些渗透调节物的积累^[70]. 一个新的钙离子通道蛋白OSCA1(reduced hyperosmolality-induced $[Ca^{2+}]_i$ increase 1)可能作为渗透压感受器参与植物对渗透胁迫的感知^[71].

渗透胁迫被感知后, 可以经过依赖于ABA和不依赖于ABA的信号通路进行信号传导, 引起一系列生理水平的渗透调节以维持细胞的渗透势和膨压. 首先, 干旱胁迫会增加细胞内渗透压调节物的含量, 如甜菜碱^[72]、可溶性糖、脯氨酸^[73]等有机物和 K^+ , Na^+ , Ca^{2+} 等无机离子^[74], 前者可以调节细胞的渗透势, 保护生物膜和蛋白质的活性, 后者主要调节液泡的渗透势, 维持细胞膨压. 除此之外, 干旱还可以诱导合成一些干旱诱导蛋白. 这类蛋白主要可分为两类, (i) 起间接保护作用的调节蛋白, 主要包括G蛋白、钙调素、蛋白激酶、磷脂酶、转录因子蛋白等; (ii) 功能蛋白, 包括离子通道蛋白、LEA蛋白(late embryogenesis abundant protein)、热激蛋白、水通道蛋白、渗透调节蛋白、代谢酶等. 在干旱耐受过程中, 这些蛋白可以直接在细胞内发挥重要的保护作用, 提高植物对干旱的耐受性^[75].

(2) 抗氧化(antioxidant defense). 干旱胁迫会导致细胞内的活性氧自由基ROS的积累, 对细胞的膜结构、生物大分子和DNA等造成不可逆的损伤. 植物拥有两套抗氧化系统: (i) 依赖于超氧化物歧化酶(superoxide dismutase, SOD)、过氧化物酶(peroxidase, POD)、过氧化氢酶(catalase, CAT)、谷胱甘肽

还原酶(glutathione reductase, GR)等抗氧化酶来清除活性氧自由基, 这些酶的活性和含量与植物的抗旱性呈正相关^[76]; (ii) 不依赖于酶, 主要通过半胱氨酸(cysteine)、脯氨酸、还原性谷胱甘肽(reduced glutathione)、维生素C、维生素E、维生素B6、黄酮类物质、花青素、类胡萝卜素等抗氧化剂来平衡体内的氧化还原状态^[77-79]. 抗氧化酶的活性和抗氧化物的含量对于植物有效清除体内的活性氧, 抵抗各种环境胁迫至关重要. 大量报道表明, 提高抗氧化系统相关基因的表达可以有效增强植物的耐逆性^[77].

(3) 植物激素. 除上述机制外, 植物激素也是一类调控植物耐旱性的重要物质, 多种植物激素相互作用, 共同调控植物对干旱的响应^[80]. ABA是最为熟知的植物抗逆激素, 受干旱、高盐等多种胁迫诱导. ABA与其受体结合后激活下游AREB/ABFs, MYB2, MYC2, NAC等一系列转录因子, 进而启动下游*RD29A*, *RD29B*, *RD22*等众多胁迫诱导基因的表达, 从而提高植物对逆境的耐受性^[75,81].

除ABA外, 其他植物激素也参与对耐旱性的调控. 干旱降低植物体内源赤霉素GA的含量^[82]. 内源GA含量降低的突变体表现出对干旱的耐受性^[83]. GA信号通路最重要的调节蛋白DELLA可以抑制细胞内的ROS积累, 从而增强植物对逆境的耐受性^[83]. 细胞分裂素CK含量高的植物对干旱具有耐受性^[84], 外源施加CK可以增强草坪草(turf grass)的耐旱性^[85,86], 改变水稻中的CK含量也影响其抗旱能力^[87]. 在烟草中用衰老相关基因*SAG12*启动子驱动CK合成的异戊烯基转移酶基因*IPT(isopentenyltransferase)*可以抑制干旱诱导的叶片衰老, 提高植物的耐旱性^[88]. 外源施加油菜素内酯BR(brassinosteroids)也可以提高植物在干旱环境中的存活率^[89], 提高大豆(*Glycine max* (Linn.) Merr.)在正常和干旱条件下的生物量和产量^[90]. BR可以诱导内源ABA含量的增加并提高抗氧化酶的活性, 这可能是它增强植物耐旱性的原因^[91]. 调控BR信号通路也可以影响植物的耐旱性, 例如, 敲除*BIN2*(BR-insensitive 2)的水稻同源基因*OsGSK1*(rice glycogen synthase kinase3-like gene 1), 可以提高水稻对寒冷、高温、盐和干旱的耐受性^[92], 下调BR受体*BR11*(BR-insensitive 1)同源基因*BdBR11*在二穗短柄草(*Brachypodium distachyon*)中的表达量可以增强植物的耐旱性^[93]. 最近有研究显示, 叶片中的IAA(indole-3-acetic acid)含量与干旱耐受

性呈正相关, 外源施用吲哚丁酸(indole-3-butyric acid, IBA)可以增加内源的IAA含量, 增强高羊茅(*Festuca arundinacea*)的抗旱性^[94,95]. 内源IAA含量提高的*iaaM*过表达和*YUC6*过表达转基因植物都表现出耐旱性增强的表型, 而生长素合成基因的三突变体*yuc1yuc2yuc6*则表现出对干旱更为敏感的表型, 可能原因是生长素可以影响根系构型基因和ABA响应基因的表达, 影响ROS的代谢^[96,97]. 在水稻中过表达生长素的转运蛋白基因*OsPIN3t*同样可以显著提高水稻的耐旱性^[98].

2 应用*AtHDG11/EDT1*提高植物的抗旱性, 从实验室到田间

随着对植物抗旱性机理的深入研究, 大量抗旱基因被发现, 并用于基因工程改良作物的抗旱性^[99], 但是这些研究主要集中在实验室中, 经过严格田间实验验证的比较少, 真正进入商业开发的则更少^[100]. 目前, 只有两种转基因抗旱作物被批准商业化种植. 2013年, 孟山都公司转细菌*cspB*基因的抗旱玉米DroughtGard首次被批准在美国种植, 截止2015年, 其种植面积已达到 8.1×10^5 hm², 并被获批在南非商业化种植^[101]. 阿根廷政府也于2015年批准了一种转向向日葵(*Helianthus annuus*) *HAHB-4*基因的转基因大豆上市, 该转基因大豆能抗旱并能适应盐碱地, 在干旱环境中能增产14%. 由此可见, 抗旱转基因作物从实验室走进田间应用需要历经极其艰难和漫长的过程.

优良抗旱基因的挖掘对于培育能够进行田间生产应用的抗旱农作物至关重要. 本研究组通过激活突变体库的筛选, 得到了一个抗旱性增强的突变体*edt1*(enhanced drought tolerance 1), 该突变体的抗旱表型是由于一个编码HD-START转录因子的基因*AtHDG11/EDT1*超表达所致^[53]. *edt1*突变体具有发达的根系, 主根显著增长, 侧根数量显著增多. 后续研究发现, *AtHDG11*可以直接结合在许多细胞壁松弛蛋白基因, 如*EXPA5*(expansin A), *XTH*(xyloglucan endotransglucosylase/hydrolase), *CEL*(cellulase), *PMEI*(pectin methylesterase inhibitor)等启动子区的HD顺式结合元件(HD-binding cis-element)上, 调控这些基因的表达, 从而促进主根的生长^[102]. Cai等人^[103]的研究则发现, *AtHDG11*可以直接调控JA合成通路关键基因*AOS*(allene oxide synthase), *OPR3*(OPDA reductase

3), *OPCL1* (OPC-8:0 CoA ligase 1), *AOC3* (allene oxide cyclase 3) 的表达, 促进根系中JA的合成, JA含量的增加又诱导根系中*ERF109* (ethylene response factor 109) 转录因子基因的表达, *ERF109*通过直接调控生长素合成基因*YUC2*和*ASA1* (anthranilate synthase alpha subunit 1) 增强根系中生长素的合成, 从而促进侧根的发生^[104]. 基于这些机制, *AtHDG11*过表达可以促进根系的发育, 从而有利于植物在干旱条件下从土壤中获得更多的水分. 另一方面, *AtHDG11*过表达可以通过上调植物中*ERECTA*的表达来调控气孔的大小和密度, 同时通过调控ABA合成关键基因*NCED3*的表达来增加体内ABA的含量, 进而调控气孔的运动, 最终降低地上部分的水分流失, 使得*AtHDG11*过表达植物具有较高的水分利用效率. *AtHDG11*还可以调控一些光合相关基因的表达, 提高植物的光合效率. *AtHDG11*过表达植物还具有较高表达水平的干旱胁迫相关基因, 更高的渗透调节物和ABA的含量, 因而可以在干旱条件下更好地进行渗透调节. 除此之外, 在干旱条件下, *AtHDG11*过表达植物体内的SOD和CAT等抗氧化酶的活性更高, 能够更好地清除体内的活性氧自由基, 提高植物的抗氧化防卫水平, 减轻植物的氧化胁迫损伤(图1).

尤为重要的是, 过表达*AtHDG11*不仅不影响植物的正常发育, 反而可以提高植物的生物量^[53]. 目前为止, 已经在烟草^[53]、水稻^[105]、高羊茅^[106]、甘薯(*Dioscorea esculenta* (Lour.) Burkill)^[107]、棉花(*Gossypium* spp)和杨树(*Populus* L.)^[33]、辣椒(*Capsicum annuum* L.)^[108]、

芥蓝(*Brassica alboglabra*)^[109]、小麦(*Triticum aestivum*)、玉米等10个不同的物种中进行了功能重演, 过表达*AtHDG11*都可以重演*edt1*突变体的表型, 显著增强植物的抗旱性. 经过多年多地田间评估验证, 过表达*AtHDG11*可以提高植物的光合效率和生物量, 提高水稻和棉花的产量^[33,105]. 因此, *AtHDG11*是一个培育抗旱高产农作物新品种的优良候选基因. 通过遗传杂交, 本研究组与合作者已经将*AtHDG11*导入到了水稻两系和三系不育系中, 以期产业化提供既抗旱又高产的杂交组合亲本.

3 问题与展望

尽管传统遗传育种在改良作物抗逆性方面取得了不少进展, 但是这种方法比较依赖于抗逆性强的种质资源, 并且费时费力^[110,111]. 基因工程为快速高效改良作物耐逆性提供了很好的工具, 但仍有许多问题需要解决. 时至今日, 大量基因被用于基因工程以改良植物的抗逆性, 但是这些研究主要基于在温室中对拟南芥的研究^[1,112]. 然而, 温室环境和大田环境存在较大差别, 温室中得到的研究结果在实际农业生产中并不一定能重复, 因此, 实验室成果和田间应用之间仍存在差距^[113]. 另一方面, 高产是作物育种的最终目标, 任何对作物的改良都不应以牺牲作物的生长和产量为代价. 但是由于基因工程改良中普遍使用组成型启动子驱动抗逆基因的表达, 往往会引起植物的生长发育异常, 导致产量的下降^[114~116]. 同时, 大量研究是通过单基因调控某一条信号通路来改良作物的单一性状, 这一策略在田间复杂环境中可能很难达到预期效果. 由于这些问题的出现, 实验室成果要走进田间, 成功用于作物的改良往往有很长的路要走.

为了更好地通过基因工程的方法来改良作物的抗旱性, 让实验室的研究成果真正走向田间, 今后的研究中可以进行以下方面的改进: (i) 寻找合适的启动子, 如器官特异性的或干旱诱导的启动子, 来驱动目标基因的表达; (ii) 构建多基因载体, 协调改良作物的抗旱性和其他农艺性状; (iii) 将实验室抗旱性评估的基因进行田间评估, 寻找优良的能够应用于改良作物田间抗旱性的候选基因; (iv) 综合运用转录组学和代谢组学等先进分析方法寻找优良的抗旱候选基因, 将传统育种方法和现代基因工程方法有效结合起来进行作物遗传育种.

图1 *AtHDG11*调控植物抗旱节水的分子机制 (网络版彩图)

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Drought-resistant and water-saving plants: from laboratory to field

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Drought is one of the most severe environmental stresses affecting plant growth and development. It has profound impacts on agriculture worldwide, causing enormous yield reduction and increasing production cost every year. Global climate change will likely worsen this situation in the future. Therefore, it is imperative for us to study the mechanisms of drought resistance and identify candidate genes that are useful for breeding drought-resistant and water-saving crops. Plants have evolved an array of different mechanisms to cope with drought stress and adapt to the changing environment. Here, in the context of our progress in drought-resistant crop improvement within the past decade, we briefly review the latest advances in plant drought resistance and potential applications in drought-resistant crop breeding in terms of drought avoidance and drought tolerance and discuss issues in drought resistance.

drought resistance and water-saving, drought avoidance, drought tolerance, *AtHDG11/AtEDT1*, water use efficiency, stomata, root architecture

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