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评 述
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# 干旱胁迫下植物体内ROS的作用机制

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**摘要** 环境胁迫是农业生产中面临的主要问题之一, 其中干旱胁迫对植物的生长发育、农作物减产及环境恶化具有重要影响. 面对自然环境危害, 植物在形态学、生理学、生物化学、细胞和分子水平等方面已进化形成了一系列的适应性, 如植物的避逆性、耐逆性及抗逆性等. 因此, 了解干旱胁迫对植物的影响以及植物对干旱信号的感知、传递和应答对解决和提高作物产量具有重要的意义. ROS作为植物有氧代谢的副产物, 在植物的生长发育过程中发挥着双重的调节作用. 正常环境条件下, 植物细胞中ROS的产生和清除处于动态平衡, 当植物遭遇干旱胁迫刺激后这种平衡被破坏, 导致植物体内ROS的产生和代谢发生紊乱, ROS介导的氧化应激能够引起生物膜过氧化、细胞核受损、光合作用受阻、呼吸作用异常等多种有害的细胞学效应. 另外, ROS作为重要的信号分子, 与其他信号分子, 如CaM, G蛋白, MAKP, miRNA及NO之间相互作用共同构成植物体庞大而复杂的信号网络, 在植物的生长发育、生理生化反应、细胞程序性死亡(PCD)、激素代谢以及生物胁迫和非生物胁迫应答等方面起着重要的调控作用. 此外, 植物为防止ROS的过度积累导致的氧化应激对细胞造成氧化损伤, 植物细胞已经进化出多种抗氧化机制, 如酶促系统和非酶促系统, 以清除ROS过度积累所带来的毒害. 本文综述了干旱胁迫对植物生长发育、形态结构和生理生化等方面的影响以及植物对干旱胁迫应答之间的相互关系, 系统地介绍了干旱胁迫下ROS的类型、产生部位及作用机制, 讨论了ROS作为第二信使与其他信号分子之间可能存在的信号网络, 旨在进一步为植物体内ROS的作用机制以及如何提高植物抗逆性研究提供理论依据.

**关键词** 干旱胁迫, 活性氧(ROS), NADPH氧化酶(NOX), 氧化应激, 第二信使

外界胁迫(生物胁迫和非生物胁迫)是农业生产中面临的主要问题之一, 了解其作用机制是解决和提高作物产量的一种行之有效的方法. 干旱引起的胁迫对植物的生长发育、农作物减产及环境恶化都具有重要影响. 干旱胁迫可造成植物体ROS的产生和积累. ROS的产生可能是植物细胞在非生物胁迫和衰老条件下最早的反应之一[1,2]. 在正常条件下, 植物细胞中产生的ROS可通过体内抗氧化酶系统(如酶促抗氧化系统和非

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酶促抗氧化系统)维持在相对稳定的水平, 这种平衡可能也会因抗氧化酶的消耗或ROS的过量积累而被中断导致氧化应激, 从而对细胞大分子和生物膜造成损害以及增加脂质过氧化[3]. 最初ROS被认为是破坏细胞成分的有毒代谢产物, 但最近许多研究证明, ROS可作为许多生物合成和代谢途径的重要调节剂在信号转导过程中发挥着重要作用[4~6]. 据报道, ROS可调节某些关键信号化合物, 如丝裂原活化蛋白激酶(mitogen-activated protein kinase, MAPK)激酶的活性[7], 又可增强植物对非生物胁迫的耐受性[8]. 此外, 植物细胞可以通过特定的酶产生一些ROS以满足植物体生理生化调节的需要, 如正常细胞遭遇病原体攻击时, 需要通过氧化应激来激活复杂的信号传导网络和蛋白质网络, 从而对病原菌的入侵起防御作用[9~11]. 总之, ROS作为第二信使能与植物体多种信号分子相互作用, 直接或间接地参与植物的各种代谢过程[12~16].

## 1 干旱胁迫与植物应答的相互关系

### 1.1 干旱胁迫对植物的影响

干旱胁迫对植物的影响涉及诸多方面, 如影响植物的生长发育、改变其形态结构以及打破内源激素平衡等, 最终导致植物生长缓慢、矮化、分蘖数减少、落花落果及产量的大幅度降低等. 缺水条件下, 植物叶片的生长、叶面积、气孔指数、气孔的开闭及叶绿素含量均发生变化. 同时, 植物的根(根的生长、总根长、根表面积、侧根数、根冠比)也发生显著的变化, 根的活力下降, 呼吸作用减弱, 根系对水分和矿质元素的获取及转运受阻. 为了增加缺水条件下根系的吸水率, 植物根系将会被扩大, 干物质在根和树冠之间的分配比例发生改变, 胁迫越重, 根冠比越大[17,18].

光合作用和呼吸作用作为所有生命有机体的基本生理功能, 往往易受外界胁迫的影响. 干旱、高温及高光条件下, 植物叶片温度升高、水分蒸腾速率加快、气孔开度减小、叶绿体对光能的吸收和传递受抑制、$CO_2$固定受阻, 导致光合作用降低和/或抑制. 随着干旱胁迫的加重, 叶绿体的希尔反应减弱, 光系统I(photosystem Ⅰ, PSI)和光系统II(photosystem Ⅱ, PSII)活力下降, 核酮糖-1,5-二磷酸羧化酶/加氧酶(Ribulose-1,5-bisphosphate carboxylase/oxygenase, RuBisCO)、磷酸烯醇丙酮酸羧化酶(Phosphoenolpyruvate carboxykinase, PEPCK)活力降低, 及1,5-二磷酸核酮糖(Ribulose-1,5-disphosphate, RuBP)再生受阻, 同时植物光合器官和光合系统遭遇破坏; 另外, 由于电子传递速率的降低和类囊体膜通透性的改变, 造成膜内外质子浓度梯度的减小, 最终使光合磷酸化能力下降及ATP的合成受阻. 干旱胁迫初期, 植物的呼吸速率先升高, 随着干旱胁迫的进一步增大, 其呼吸速率又下降. 随着干旱胁迫的变化, 植物叶片线粒体结合酶(如$Mg^{2+}$-ATPase, $Ca^{2+}$-ATPase等)活性增加, 乙醇酸氧化酶下降, 造成膜的透性改变、结构受损. 此外, 干旱胁迫下, 植物内源激素, 如脱落酸(abscisic acid, ABA)、生长素(auxin, IAA)、细胞分裂素(cytokinin, CTK)、赤霉素(gibberellin, GA)、乙烯(ethylene, ETH)、多胺(polyamine, PA)、水杨酸(salicyli cacid, SA)等的合成、分配和运输均发生变化.

### 1.2 植物对干旱胁迫的应答机制

植物对干旱胁迫的响应是各种机制相互作用的共同结果, 主要涉及植物生长发育、形态结构、生理生化、水分运输、营养物质的合成与转运、干旱信号转导、氧化还原稳态、渗透调节、植物内源激素变化、基因表达调控及干旱诱导蛋白等. 面对各种环境胁迫, 植物可通过调整其生长周期或改变其形态结构以形成不同的适应性, 如植物的避逆性、耐逆性及抗逆性等[19~23]. 同时, 各种相关性状, 包括根性状、叶性状、渗透调节能力、水势、ABA含量和细胞膜的稳定性等均可用作评价植物抗旱性的指标. 干旱胁迫下, 植物可通过渗透调节的改变来维持植物正常的生长发育、形态结构变化、生理生化反应、光合作用和呼吸作用及物质代谢运输等过程或尽量降低其对植物的伤害[24]. 另外, 在干旱压力下植物的叶片也会发生一系列变化, 如叶片萎蔫、方位改变和叶角度发生改变等[25]. 研究表明, 植物叶片也可通过增大叶肉栅栏组织、减小海绵组织、增加细胞层数、减少细胞体积、缩短细胞间隙等显微结构变化来适应干旱逆境[26]. 生长在干旱季节或干旱地区的一些植被, 还可以通过增粗叶脉、缩小叶表皮细胞、增多叶毛、增加角质层及蜡质层的厚度等方式来减少水分的散失[27]. 此外, 有研究表明, 在土壤水分亏缺情况下不同物种的植物可通过不同方式改变其根系生长或根系结构来适应水分的动态变化[28~30].

在分子水平方面, 植物对干旱胁迫的应答涉及许多基因的转录调控和信号转导过程. 干旱胁迫条件下, 外部干旱刺激首先被膜上的传感器感知和捕获, 然后

干旱信号通过多个信号转导途径向下传递并不断级联放大, 以引起干旱相关基因的转录调控应答[31]. 这些干旱响应基因的表达产物主要主要有三方面的作用: (1) 参与信号转导和转录调控, 如蛋白激酶、蛋白磷酸酶和转录因子等; (2) 对细胞膜和其他蛋白质起保护作用, 如晚期胚胎发育丰富蛋白、抗氧化剂和渗透调节蛋白; (3) 参与水分的吸收和运输以及离子的摄取和转运, 如水通道蛋白、离子转运蛋白和糖转运蛋白等[32~34]. 在干旱信号传导和级联放大过程中, 各种第二信使(如$Ca^{2+}$, ROS, MAPK, 磷酸甘油, ABA等)和转录调节因子在各种信号传递途径中发挥关键作用. 许多研究表明, 干旱胁迫可诱导植物体发生蛋白质的磷酸化和去磷酸化, 许多激酶, 如钙依赖蛋白激酶(CDPKs)、类钙调磷酸酶(CBL)和促分裂原活化蛋白激酶(MAPK)均与植物的耐旱性相关[35~39]. 转录因子作为一类重要的调节因子可通过调控基因表达来响应干旱胁迫. 据报道, 来自不同转录因子家族的许多成员, 如APETALA-2转录因子、EREBP转录因子、bZIP转录因子、MYB转录因子及NAC转录因子等都与干旱胁迫应答相关[40~42]. 干旱胁迫也影响到植物内源激素的合成、转运及代谢. 如干旱胁迫下, 调控植物生长的激素(CTK, GA等)合成减少, 而调控植物衰老或脱落的激素(ABA, ETH等)含量增加. ABA作为与干旱胁迫最密切相关的植物激素在调节气孔开闭及信号转导中发挥重要作用. 有研究表明, 在过表达*AtNCED3*和*PvNCED1*基因的转基因植物中其内源ABA含量显著增加, 抗旱性显著增强[43,44]. 在逆境胁迫条件下, 细胞分裂素可通过延迟植物衰老来改善植物对干旱胁迫的适应性[45], 油菜素类固醇的积累可增强植物对水分的摄取和维持细胞膜的稳定性, 并且还可以减少膜的离子泄漏[46]; 而PA与膜结构的稳定、活性氧的清除、信号转导及生物大分子的功能有关[47]; 最近研究表明, 独脚金内酯(strigolactone, SL)在植物对干旱胁迫响应中起正向调节作用[48]. 与此同时, 越来越多的研究证明, ROS的产生和清除会影响植物的抗旱性[49]. 例如, 在水稻叶绿体中过表达豌豆锰超氧化物歧化酶基因(*MnSOD*)能够增强转基因水稻植株的耐旱性[50], 编码拟南芥谷胱甘肽过氧化物酶的基因(*ATGPX3*)在ABA、干旱胁迫信号传导及$H_2O_2$稳态中发挥着独特作用[51]. 另外, 其他一些基因, 如*OsSKIPa*和*OsSRO1c*可通过控制ROS代谢和调节植物中ROS的稳态来调节植株的抗旱性[52,53]. 胚胎发育晚期丰富蛋白(late embryogenesis abundant proteins, LEA)在晚期胚胎发育的特定阶段表达, 其亲水性溶质可通过增强水分吸收、稳定和保护蛋白质及膜的结构和功能以及作为分子伴侣等来保护细胞减轻/免受干旱胁迫的损害[54].

此外, 不同植物或同种植物在不同的生长发育阶段对干旱胁迫的应答也不相同. 不同基因型的植物对干旱胁迫的耐逆性和适应性也有很大的差异, 因此, 利用分子生物学方法对干旱基因以及调节干旱相关基因的挖掘和研究就显得十分重要. 目前, 已从水稻中克隆到多个与耐旱相关的基因和转录因子(表1), 这些基因在转录、转录调控、翻译、蛋白质修饰以及激素代谢方面直接或间接地参与植物对干旱胁迫的应答.

## 2 植物体内活性氧的作用机制

### 2.1 植物体内ROS的类型及产生部位

活性氧(ROS)是大气中部分氧的还原或激发形式, 也是植物细胞内氧化还原反应或$O_2$活化衍生的代谢产物[83~86]. 植物体内的活性氧主要以自由基和非自由基形式存在, 主要包括过氧化氢($H_2O_2$)、超氧阴离子自由基($O_2^-$)、羟基自由基(·OH)、单线态氧($^1O_2$)、有机氧自由基(RO·和ROO·)等, 这些不同种类的活性氧之间存在着相互代谢关系(图1), 且在植物的生长发育、信号转导以及生物胁迫与非生物胁迫应答中起着重要的作用. ROS介导的氧化应激可对植物细胞造成氧化胁迫, 使生物膜过氧化、细胞核受损、氨基酸氧化、蛋白质变性、DNA链断裂、色素破坏、光合作用受阻、呼吸作用异常、酶的失活及植物生长素IAA分解等多种有害的细胞学效应. 另外, ROS作为信号分子又参与植物细胞的增殖和分化、细胞程序性死亡、种子萌发、根的向地性、根毛生长和花粉管发育及植物衰老等过程[87].

在植物正常生长和发育期间, ROS在活细胞中的不同细胞区室中均可产生(图2), 如质膜、线粒体、叶绿体、过氧化物酶体、内质网及质外体等, 在外界胁迫下其浓度增加. 质外体ROS的产生主要来源于质膜NADPH氧化酶、细胞壁过氧化物酶和胺氧化酶等[92], 而细胞内ROS的产生主要来自叶绿体、线粒体和过氧化物酶体/乙醛酸, 水平较低[93].

在光合组织(叶片)中, 叶绿体是植物中ROS的主要来源[94,95]. 干旱胁迫条件下植物的气孔开度发生改变, 叶绿体和光合器官遭到破坏, 植物对光能的吸收、传

**表 1** 水稻中已克隆的耐旱相关基因及其功能

**Table 1** The cloned genes and their functions of drought tolerance in rice

| 基因 | 基因号 | 相关功能 | 文献 |
|---|---|---|---|
| *OsNAP* | Os03g0327800 | NAC转录激活因子 | [55,56] |
| *OsNAC2* | Os04g0460600 | NAC转录因子 | [57,58] |
| *OsNAC6* | Os01g0884300 | NAC转录因子 | [59] |
| *OsMYB48* | Os01g0975300 | MYB转录因子 | [40] |
| *OsbZIP71* | Os09g0306400 | bZIP转录因子 | [41] |
| *OsbZIP2* | Os02g0766700 | bZIP转录因子 | [60,61] |
| *OsAP37* | Os04g0448500 | AP2/ERF转录因子 | [62] |
| *OsEREBP1* | Os02g0782700 | EREBP转录因子 | [63] |
| *OsMsr9* | Os07g0561300 | 多逆境响应基因 | [64] |
| *OsDi19-1* | Os05g0562200 | 干旱诱导基因 | [65] |
| *AP37* | Os01g0797600 | 耐旱性转录因子基因 | [66] |
| *SNAC1* | Os03g0815100 | 胁迫响应的NAC转录因子基因 | [67] |
| *DSM2* | Os03g0125100 | β胡萝卜素羟化酶基因 | [68] |
| *OsSRO1c* | Os03g0230300 | SRO蛋白,SNAC1靶基因(ROS相关) | [52] |
| *OsPOX1* | Os01g0263300 | 过氧化物酶基因(ROS相关) | [69] |
| *OsAPX1* | Os03g0285700 | 抗坏血酸过氧化物酶基因(ROS相关) | [70] |
| *OsAPx8* | Os02g0553200 | 抗坏血酸过氧化物酶基因(ROS相关) | [71] |
| OsCATB | Os06g0727200 | 过氧化氢酶(ROS相关) | [72] |
| OsCATC | Os03g0131200 | 过氧化氢酶(ROS相关) | [72] |
| OsCATA | Os02g0115700 | 过氧化氢酶(ROS相关) | [72] |
| OsDHAR1 | Os05g0116100 | 脱氢抗坏血酸还原酶(ROS相关) | [73] |
| OsGPX1 | Os04g0556300 | 线粒体谷胱甘肽过氧化物酶(ROS相关) | [74] |
| *OsAlba1* | Os03g0179400 | 干旱应答的核蛋白 | [75] |
| *OsSIDP366* | Os06g0693700 | 胁迫诱导的DUF1644蛋白 | [76] |
| *OsAREB1* | Os06g0211200 | ABRE结合蛋白 | [77] |
| *OsABA8ox3* | Os09g0457100 | 脱落酸代谢基因 | [78] |
| *OsPYL5* | Os05g0213500 | ABA受体 | [79,80] |
| *GUDK* | Os03g0179400 | 干旱诱导的受体类胞质激酶 | [81] |
| *OsSAPK6* | Os02g0551100 | 应激活化蛋白激酶 | [82] |

递、利用效率降低, 同时光合$CO_2$固定受阻, 导致烟酰胺腺嘌呤二核苷酸磷酸(nicotinamide adenine dinucleotide phosphate, $NADP^+$)供应减少, $O_2$等被迫作为电子受体, 在内囊体膜PSI的还原侧形成$O_2^-$, 产生的$O_2^-$既可进入类囊体膜外基质通过酶促或非酶促歧化反应生成$H_2O_2$, 又可经PSII捕光叶绿素复合蛋白将来自PSI的$O_2^-$转化为$H_2O_2$, 而$O_2^-$和$H_2O_2$又可经不同的反应(芬顿反应或哈伯-韦斯反应)生成·OH[96](图1). 在植物的非光合组织(根、分生组织、种子及花器官)中线粒体是ROS产生的关键来源(图2). 植物线粒体电子传递链(electron transport chain, ETC)包括4种复合物: NADP脱氢酶(Complex I)、琥铂酸脱氢酶(Complex II)、辅酶Q-细胞色素bc1还原酶(Complex III)、细胞色素C氧化酶(Complex IV), 这些复合体均有电子传递的功能特性(图2). 干旱胁迫条件下, 由于呼吸作用相关酶的活性受到抑制或植物线粒体ETC与ATP的偶联受到破坏, 导致呼吸链电子传递中部分电子泄露, 从而产生ROS, 其产生部位主要包括NADH-黄素蛋白和UbQ-Cytb[97,98]. 其中, NADH脱氢酶组分(复合物I)上黄素蛋白区域能直接还原氧产生$O_2^-$, 而还原态的泛醌可进一步失去电子

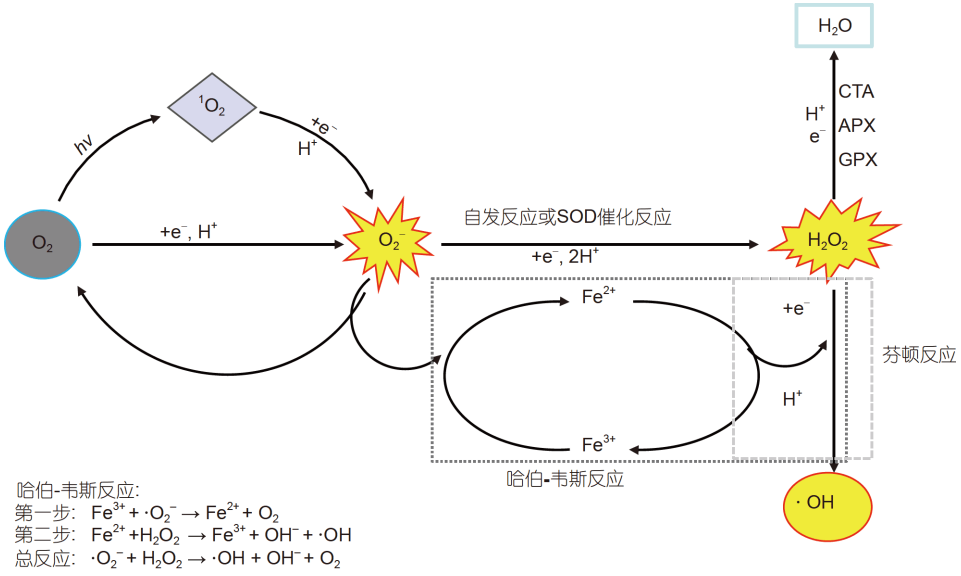



**图 1** 植物ROS产生示意图[87,88]
**Figure 1** Diagram of ROS generation in plants[87,88]

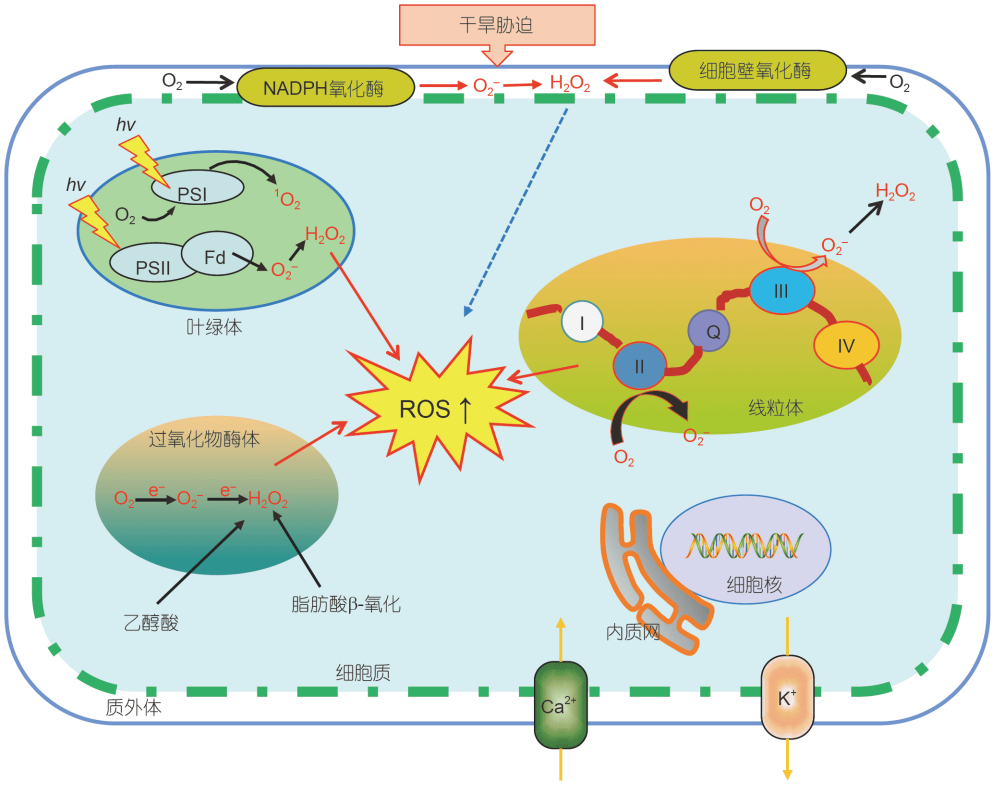



**图 2** 干旱胁迫下植物细胞中ROS的产生部位[89~91]
**Figure 2** Production sites of ROS in plant cells under drought stress[89–91]

成为具有高还原活性的半醌，半醌很容易将电子泄漏给氧而生成$O_2^{-}$[99]. 其他ROS主要来源于细胞内过氧化物酶体和乙醛酸体以及质外体NADPH氧化酶和细胞壁过氧化物酶等. 在过氧化物体的基质和膜上都可进行氧的相关代谢, 通过乙醇酸氧化酶(GOX) 脂肪酸β-氧化酶、黄素氧化酶(FOX)、黄嘌呤氧化酶(XOX)等

氧化产生$H_2O_2$及$O_2^-$等活性氧分子[100~102]. 其中, 大部分的$H_2O_2$均可通过光呼吸过程中由GOX催化乙醇酸氧化产生[103]. 此外, 研究表明, 干旱条件下质外体产生的活性氧可激活$Ca^{2+}$通道, 导致细胞溶质中$Ca^{2+}$和ROS浓度升高[104,105], 同时, ROS激活$Ca^{2+}$通道可能是ROS参与信号转导网络的关键步骤[106]. 有研究证明, 当植物缺K时, ROS在拟南芥根细胞中被强烈诱导和积累[107,108]. 因此, 干旱胁迫下植物体ROS的产生是质外体和细胞内共同作用的结果. 一方面, 干旱胁迫引起质外体产生的ROS作为信号分子, 激活$Ca^{2+}$通道导致细胞内ROS浓度升高[89,104~106], 另一方面, 干旱胁迫又可引起细胞内不同器官(叶绿体[13,109]、线粒体[110~113]和过氧化物酶[114,115]等)中ROS的产生和积累.

## 2.2 植物体抗氧化系统对ROS的清除

为防止ROS的过度积累引起氧化应激及对植物细胞造成氧化损伤, 其产生必须得到有效的控制, 因此, 植物细胞已经进化出多种抗氧化机制(酶促系统和非酶促系统)以清除ROS存在所带来的毒害[14,15,116]. 酶促清除系统主要包括超氧化物歧化酶(superoxide dismutase, SOD)、过氧化物酶(peroxidase, POD)、过氧化氢酶(catalase, CAT)、抗坏血酸过氧化物酶(ascorbate peroxidase, APX)、脱氢抗坏血酸酶(dehydroascorbate reductas, DHAR)、单脱氢抗坏血酸酶(monodehydroasorbate reductase, MDHAR)、谷胱甘肽过氧化物酶(glutathione peroxidase, GPX)、谷胱甘肽还原酶(glutathione reductase, GR)、愈创木酚过氧化物酶(guaiacol peroxidase, GOPX)等. 非酶促抗氧化物剂主要是一些相对分子质量较小的有机物, 如脯氨酸、抗坏血酸(ascorbic acid, ASA)、谷胱甘肽(glutataione, GSH)、生育酚、类黄酮、酚类化合物和非蛋白质氨基酸等.

干旱条件下, ROS在不同细胞区室中均可产生. SOD作为ROS清除的第一道防线, 可将$O_2^-$转化为$O_2$和$H_2O_2$(图3). CAT作为一种多功能酶(CAT1, CAT2和CAT3), 主要负责过氧化物酶体中$H_2O_2$的清除(图3). 研究发现, 存在于乙醛酸循环体中的CAT可清除光呼吸过程或脂肪酸β-氧化反应产生的$H_2O_2$[118]. 抗坏血酸在不同植物及不同组织中广泛存在, 它在线粒体中合成并转运到植物的其他组织[119,120], 抗坏血酸过氧化物酶(APX)以抗坏血酸为底物, 在抗坏血酸-谷胱甘肽循环中将$H_2O_2$还原为$H_2O$, 产生单脱氢抗坏血酸. 谷胱甘肽过氧化酶(GPx)在清除脂类和烷基过氧化物的氧化代谢方面具有重要作用[121].

干旱胁迫下, 植物体内的非酶物质(脯氨酸、抗坏血酸、谷胱甘肽、生育酚、类黄酮、酚类化合物等)可以与ROS直接反应或作为酶的底物出现在ROS清除机制中, 如胡萝卜素和维生素E对$O_2^-$, ·OH, $^1O_2$具有清除作用, 同时也能有效地抑制脂质过氧化的连锁反应[122]. 还原型谷胱甘肽(GSH)可与·OH等多种自由基直接发生反应, 将有机自由基R·还原为RH, 对多种酶起稳定作用. 抗坏血酸(ASA)作为小分子物质一方面能直接清除包括$HO_2^-$, $O_2^-$和$^1O_2$等ROS, 另一方面ASA使α-生育酚处于还原状态[123]. 多种胁迫条件都会造成植物体脯氨酸的积累, 其可以通过与$^1O_2$和·OH熬合来减轻ROS对植物的伤害, 也可以通过激发体内POD, CAT及SOD等的活性来清除活性氧[118]. 一些研究表明, 类黄酮可以与$O_2^-$, $H_2O_2$, $OH^-$或$^1O_2$等发生反应, 从而直接清除植物细胞中的ROS; 存在于植物细胞内囊体膜的α-生育酚可通过淬灭或清除$^1O_2$, $O_2^-$和·OH等防止膜质过氧化[124]. 此外, 植物除了拥有清除已产生ROS的这些抗氧化机制之外, 也进化出了许多有效的措施来避免或减轻ROS积累对植物造成的毒害, 主要包括解

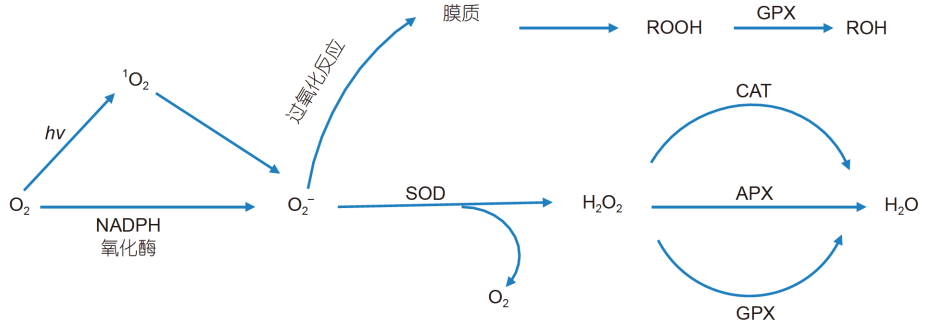



**图 3** (网络版彩色)植物体内ROS的清除[117]
**Figure 3** (Color online) Diagram of ROS scavenging in plants[117]

剖学和形态学上的适应和改变，例如叶片运动和卷曲、$C_4$途径或CAM(景天酸代谢)、叶绿素的运动、光合作用的抑制以及光系统(PSI和PSII)的响应等[12].

## 3 植物体ROS的信号转导作用

植物对外界胁迫信号的感知和传递是植物响应外界胁迫的最基本反应之一，植物体内庞大而复杂的信号传导网络(主要包括ROS, CaM, G蛋白, MAKP, 植物内源激素，TFs，miRNA及NO等)有助于植物实现这一目标(图4). 随着对干旱胁迫机制及信号网络研究的深入，我们知道这些信号网络之间不是线性的、单向的，而是复杂的、动态的[12]. 因此, 干旱胁迫的初级信号很可能被多个信号感受器感知，然后通过一系列不同的次级信号传导网络(如植物内源激素, $Ca^{2+}$, MAKP及氧化还原平衡等)启动和放大，这些次级信号通过调节基因表达、转录因子激活、蛋白质修饰及激素代谢来参与植物对外界胁迫的响应.

ROS作为大部分需氧生物有氧代谢的重要产物，早期的研究主要集中在ROS对植物的毒害方面，但近年来研究发现，ROS作为重要的信号分子在植物的生长发育、分化、细胞程序性死亡(PCD)、激素代谢、根的生长和向地性以及生物胁迫和非生物胁迫方面起着重要作用[15,16,88,125~127]. 活性氧作为植物响应外界刺激的信号分子，其主要功能包括：(1) 参与植物的生长、发育、分化; (2) 参与植物对生物胁迫和非生物胁迫的应答; (3) 调控基因表达、转录因子激活及蛋白质修饰; (4) 参与细胞的防御反应和细胞程序性死亡; (5) 参与激素代谢; (6) 与其他信号分子(CaM，G蛋白，MAKP，miRNA及NO)构成植物体复杂的信号网络. 研究发现, 对植物进行一定的体外ROS处理, 可显著改善植物的生长特性[122]，这对植物调节许多生理生化过程有益[123,128~136]. 干旱胁迫条件下，ROS在不同细胞区室中广泛产生，$O_2^-$，$H_2O_2$作为主要的ROS在不同亚细胞产生会引起不同的反应. 有研究表明叶绿体中产生的$H_2O_2$能够激活早期信号反应，包括参与次级信号转导、TFs激活及调控基表达等; 过氧化物酶体中产生的$H_2O_2$可参与蛋白质的修饰[137]. 质外体NADPH氧化酶产生的ROS可作为植物响应生物胁迫和非生物胁迫的信号分子[138,139]. 也有研究表明，ROS在信号转导过程中可与蛋白质相互作用，从而引起蛋白质物理化学性质、构象及活性的改变[140~142]. 另一种新的观点认为活性氧引起的氧化应激并不是直接杀死细胞，而是ROS触发细胞生理死亡的自然过程[143,144]，如果将细胞ROS水平降低至特定阈值以下可能会导致细胞增殖受到抑制，并对植物细胞的分化和防御反应产生负面影响[140,145].

与此同时，ROS作为信号分子与其他信号分子之间相互作用形成一个复杂的信号调节网络来直接或间接地参与植物对干旱胁迫的响应(图4). 有研究表明, ROS作为植物响应干旱胁迫最早和最常见的胁迫信号响应分子之一，可能在各种信号转导途径中作为一个关键的信号枢纽点[12,125,130,134,146]. 干旱胁迫发生时，质外体产生的ROS可作为首要信号分子激活相关离子通道(如$Ca^{2+}$通道), 导致细胞内ROS浓度升高[92,104~106]. 同时，干旱胁迫又引起细胞内不同器官(叶绿体、线粒体和过氧化物酶等)中ROS的产生和积累[93~98]，细胞内ROS的这些变化将破坏细胞中ROS平衡，并转化为氧化还原信号. 一方面, 这些信号通过短距离运输在不同的调节水平和不同的亚细胞区室中引发特异性反应[94,147]; 另一方面, 氧化还原信号又与植物细胞内其他信号分子相互作用引起一系列次级信号网络(植物激素、$Ca^{2+}$、蛋白激酶和磷酸酶等)的启动. 在干旱条件下，叶绿体氧化还原状态的变化可调控叶绿体中相关蛋白的表达，细胞氧化还原稳态与线粒体状态密切相关[139,148~150]; 同时, 叶绿体、线粒体、过氧化物酶体及乙醛酸体中产生的ROS也可作为信号分子传递到细胞核，调控核基因的表达，这些事实表明，细胞可通过ROS的变化在细胞水平来调控植物对干旱胁迫的应答[88,139,151,152]. 此外，ROS与其他关键信号组分(包括NADPH氧化酶, $Ca^{2+}$, MAPK, 植物激素, TFs, miRNA等)也有其明显的相互作用(无论上游或下游)[12]. 研究表明，NADPH氧化酶的激活可能是应激条件下质外体ROS产生和积累的主要原因[92]. 也有研究表明，NADPH氧化酶产生的ROS在ABA调控气孔关闭的下游起重要作用[153]; $Ca^{2+}$作为植物细胞中广泛存在的第二信使可感知或转导植物对干旱胁迫的刺激，$Ca^{2+}$在ROS的上游[154]或下游起作用[104,155]. MAPK作为细胞内重要的信号转导分子能够受$H_2O_2$的激活[156]. 而ROS对TFs的影响是多方面的，ROS可直接激活TF，也可增强TF表达或增加TF的稳定性等; miRNA作为一类小的非编码RNA，是基因表达的关键调控因子[157~159]. 据报道, $H_2O_2$可响应miRNA的靶标, 从而参与不同的细胞反应和代谢过程，如转录调控、物质转运和细胞程序性死亡等[160]. 因此，ROS的介导的信号转导与miRNA和

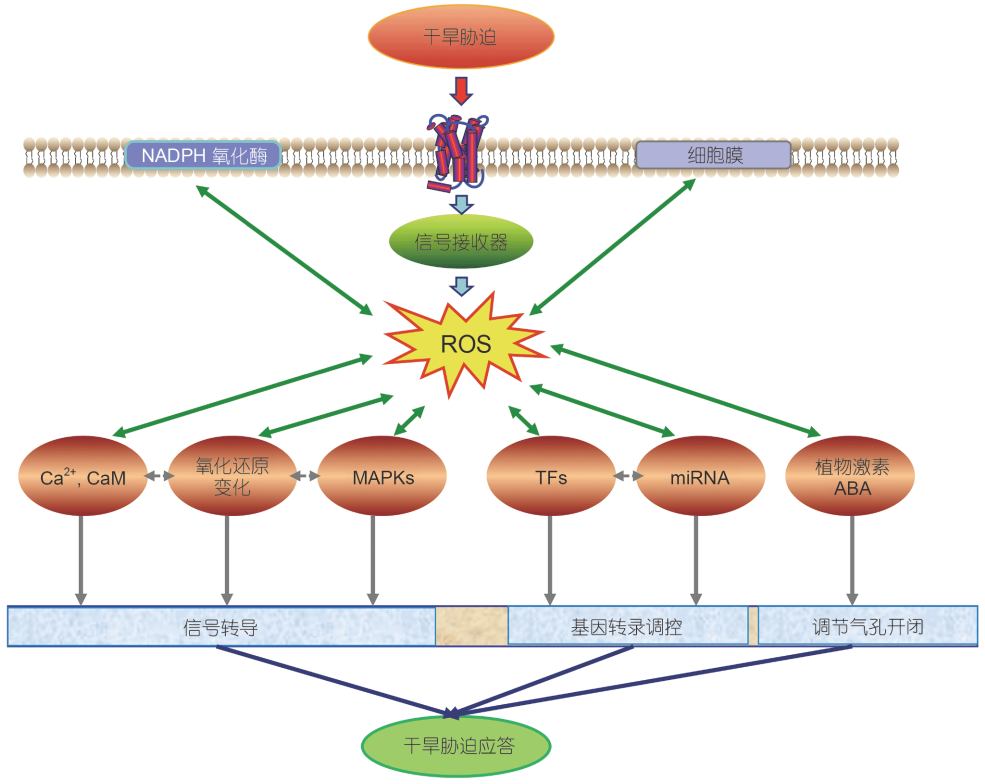



**图 4** 干旱条件下植物体内ROS的信号转导网络. 实线箭头表示ROS与其他信号分子之间有直接的相互作用, 虚线箭头表示可能存在相互作用
**Figure 4** The signaling networks of ROS in plants under drought stress. Solid arrows for direct ROS interactions with other signaling components, dashed arrows for expected indirect interactions

TFs在基因调控表达层面参与植物对干旱胁迫的响应. 尽管已经在ROS信号转导方面取得了重大进展, 但ROS引起的氧化应激机制以及干旱条件下ROS与其他信号分子之间的关键作用机制仍未明确.

## 4 结论和展望

ROS作为地球上所有需氧生命体有氧代谢必不可少的代谢产物, 涉及植物生长、发育、分化、物质的代谢运输、防御反应、细胞程序性死亡及生物胁迫和非生物胁迫应答的各个方面. 植物体内ROS成像技术对了解活性氧在植物细胞或组织中的信号转导作用有很重要的贡献, 但目前对植物体内活性氧的产生和清除的调控仍缺乏有效的策略. 植物体各种亚细胞区室和不同细胞环境都可产生活性氧, 细胞内区室之间氧化还原的状态和信号传递对植物的应激反应和生长发育十分关键. 然而, 目前对活性氧在不同的细胞及各亚细胞区室之间的代谢机制的研究相对较少. 研究表明, $H_2O_2$和$O_2^{\cdot-}$在不同细胞区室中的积累存在差异, 单线态氧介导信号在不同细胞和亚细胞之间的传递中起着重要作用. 这些研究表明, 不同类型的ROS以及细胞内不同ROS产生的信号整合对植物的应激反应和生长发育具有重要影响.

从信号转导角度来看, ROS作为植物响应不同生物和非生物胁迫应答的信号分子, 研究认为其处于信号转导网络的核心位置. ROS与其他关键信号分子(如NADPH氧化酶, G蛋白, $Ca^{2+}$, MAPK, SA, JA, ABA, 乙烯, TFs, miRNA及NO等)具有明显的相互作用. 在ROS家族中, 由于$H_2O_2$相对稳定且扩散能力较强, 其信号传导作用得到了较为彻底的研究, 已经证明$H_2O_2$在植物的生长、发育、代谢和衰老中起着不同的作用[161~163]. 与$H_2O_2$相比, 由于超氧阴离子不太稳定并且不能穿过膜, 其信号转导作用的研究相对较少. 毫无疑问, ROS作为信号分子已得到了证明, 但仍有许多问题待解决: (1) 植物细胞如何感知ROS? (2) 质外体产生的ROS是否能够跨膜进入细胞内? ROS信号如何在不同亚细胞区室之间传递? (3) 不同的亚细胞区室中ROS的浓度是多少? ROS作为信号分子参与植物响应干旱胁迫应答的阈值水平是多少? (4) ROS作为信号分子如何

与其他信号网络相互作用来参与植物对干旱胁迫的应答?

这些问题的研究对于阐明ROS作为信号分子参与干旱胁迫应答至关重要, 因此对ROS的信号作用机制以及与其他信号之间的相互作用的研究可能是未来工作的重点.

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Summary for “干旱胁迫下植物体内ROS的作用机制”

# Mechanisms of reactive oxygen species in plants under drought stress

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Stress is one of the main issues in agricultural production. Drought stress has a significant impact on plant growth and development, reduces crop yield, and can result in environmental degradation. Plants have evolved a series of adaptations to natural environmental stress at morphological, physiological, biochemical, cellular, and molecular levels, such as stress escape, stress tolerance, and stress resistance. Therefore, it is very important to understand the effects of drought stress on plants, and plant sensing, transduction, and response to drought signals, for improving crop yields. ROS, as an essential metabolite of aerobic metabolism in all aerobic organisms on earth, mainly exists in the form of free radicals and non-free radicals, including hydrogen peroxide ($H_2O_2$), superoxide anion radicals ($O^{2-}$), hydroxyl radicals (·OH), singlet oxygen ($1O_2$), organic oxygen radicals (RO· and ROO·). In plants, ROS is widely involved in plant growth, development, differentiation, metabolic transport of substances, defense response, programmed cell death and biological and abiotic stress responses as a byproduct of aerobic energy metabolism and plant exposure to various biological and abiotic stresses. Under normal environmental conditions, ROS produced can be maintained at a relatively stable level through the antioxidant enzyme system *in vivo* in plant cells. When plants are stimulated by drought stress, this balance is destroyed. Plant cells may be oxidative stress due to the consumption of antioxidant enzymes or excessive accumulation of ROS. Reactive oxygen species (ROS) play an important dual regulatory role in plant growth and development processes as intracellular by-products of aerobic metabolism. Under normal conditions, the production and elimination of ROS maintain dynamic homeostasis in plants. However, this situation can be broken when plants are subjected to drought stresses, leading to ROS production and metabolism disorders. ROS-mediated oxidative stress can cause many adverse cytological effects such as plasma membrane peroxidation, nucleus impairment, photosynthesis retardation, and abnormal respiratory. On the other hand, ROS, as an important signal molecule, interacts with other signal molecules, such as CaM, G protein, MAKP, miRNA, and NO to form a large and complex signal network, which plays a very important regulatory role in plant growth and development, physiological and biochemical reactions, programmed cell death, hormone metabolism, and biotic and abiotic stress responses. In addition, plant cells have evolved a variety of antioxidant mechanisms (enzymatic and non-enzymatic systems) to eliminate toxicity in order to prevent oxidative damage to cells arising from over accumulation of ROS. Enzymatic scavenging system mainly includes superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX), glutathione peroxidase (GPX), guaiacol peroxidase (GOPX), etc. Non-enzymatic antioxidants are mainly some organic compounds with relatively small molecular weight, such as proline, ascorbic acid (ASA), glutathione (GSH), tocopherols, flavonoids, phenolic compounds and non-protein amino acids and so on. In this paper, the effects of drought stress on plant growth and development, morphological structure, and physiological and biochemical characteristics, and the relationships between plant responses to drought stress are summarized. The possible signaling network between ROS as a second messenger and other signaling molecules is also discussed. A theoretical basis is provided to further understand the mechanisms of ROS and improve plant stress resistance.

**drought stress, reactive oxygen species (ROS), NADPH oxidase (NOX), oxidative stress, second messenger**

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