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钼提高植物抗逆性研究进展

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摘要 钼(Mo)作为植物必需的微量元素,在促进植物生长发育和增强植物抗逆性方面发挥着关键作用。植物对钼的吸收转运主要受到钼酸盐转运蛋白基因*MOT1*和*MOT2*调控,钼进入植物体内以含钼酶形式参与植物生长代谢,其中对植物抗逆性方面的调控主要表现为:钼通过含钼酶硝酸还原酶、醛氧化酶、黄嘌呤脱氢酶影响植物体内的光合碳氮代谢、激素合成和活性氧代谢进而调控植物抗寒性;钼通过硝酸还原酶和醛氧化酶介导的信号转导过程调控根系发育、养分水分利用及抗旱基因表达,进一步影响脂质合成与代谢调控植物抗旱性;最新研究还发现钼在植物适应盐胁迫、缓解重金属胁迫方面也具有重要作用。这些研究结果为通过钼营养调控提升植物的抗逆性提供了新思路。

关键词 钼; 钼酶; 转运蛋白; 抗寒; 抗旱; 抗盐; 重金属抗性

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农业生产会受到多种环境胁迫(如寒冷、干旱、盐碱、重金属等)的影响,如何通过营养调控提高植物的抗胁迫能力一直是科学家们关注的热点^[1]。大量元素磷、钾提高作物抗逆性的效应及机制较为明确,而微量元素与作物抗逆性的关系报道较少。钼是植物体必需的微量元素,它在植物体的生理功能主要通过含钼酶来实现。较早的研究发现低温处理下施钼增加了硝酸还原酶和黄嘌呤脱氢酶的活性,进而提高植物的低温耐受性^[2]。近年来,越来越多的研究证实钼不仅可提高植物抗寒性,还能提高植物抗旱、抗盐胁迫及抗重金属胁迫的能力。本文以钼的吸收和转运、含钼酶调控的代谢过程为主线综述钼提高植物抗逆性的生理及分子机制,旨在为通过钼营养调控提升植物的抗逆性提供理论依据。

1 植物对钼的吸收和转运

钼在土壤含量相对较低(0.2~36 mg/kg),其中有效钼含量低于0.15 mg/kg的土壤则被认为处于缺钼水平^[3]。据报道世界范围内缺钼现象普遍存在,我国缺钼耕地面积更是达4 467万 hm²^[4]。在pH>4.3的土壤溶液中,钼主要以钼酸根阴离子(MoO₄²⁻)

形式存在,而pH<4.3的土壤溶液中,则主要为HMoO₄⁻或Mo₃(H₂O)₃形态的钼^[5]。土壤钼以MoO₄²⁻形态进入植物根系,并通过影响含钼酶的活性而影响植物体内的碳代谢、氮代谢、谷胱甘肽循环、次生代谢和活性氧代谢等过程^[5]。钼作为植物必需营养元素之一,其吸收方式一直存在着争论^[6]。部分学者认为植物吸收钼是被动吸收,然而大多数学者认为植物吸收钼可能是一个主动吸收的过程。真核生物中第一个高亲和钼转运蛋白基因*MOT1*首先在绿藻中被克隆^[7],随后在拟南芥上也鉴定出高亲和钼酸盐转运蛋白*MOT1*,发现其在根和茎中均有表达并被定位在质膜上^[8]。Minner-Meinen等^[9]进一步利用*mot1.1*和*mot1.2*拟南芥双敲除突变体研究了*MOT1.1*和*MOT1.2*的功能,发现*AtMOT1.1*不参与叶肉细胞中钼酸盐的输入,与钼辅因子合成蛋白没有相互作用,而*AtMOT1.2*则通过与钼插入酶Cnx1的直接相互作用调控钼辅因子合成。最近,研究人员采用全基因组关联分析及QTL定位方法鉴定出水稻*OsMOT1;1*并发现该基因主要在根中表达,敲除后根和茎秆中钼含量降低,推测*OsMOT1;1*为控制秸秆和籽粒中钼浓度的关键基因^[10-11]。在豆科

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作物中,定位于百脉根质膜上的钼酸盐转运蛋白LjMOT1可能参与了钼的运输^[12],而在苜蓿中发现的质膜钼转运蛋白MtMOT1.3负责将钼酸盐转运至根瘤细胞内,参与固氮酶的生物合成^[13]。

相比于MOT1家族,对钼转运蛋白MOT2家族基因功能研究尚少,Gasber等^[14]在拟南芥中发现了1个钼酸盐转运蛋白AtMOT2,将它定位于液泡膜上,负责液泡中钼酸盐的向外转运和钼在植物器官内的再分配,对提高拟南芥籽粒中钼含量至关重要。最近有研究发现水稻*OsMOT2;1/OsCd1*参与其根系对镉(Cd)的吸收和转运过程,敲除*OsMOT2*会降低水稻根、茎和籽粒中镉的积累,但AtMOT2是否具有钼转运功能尚未进一步证实^[15]。Hibara等^[16]在水稻中发现了1个衣藻钼转运基因*CrMOT2*的同源基因*OsASY*,也被认为是*OsMOT2;2*,在水稻早期发芽过程中发挥着重要作用,推测它参与水稻中钼的转运^[5]。拟南芥钼酸盐转运AtMOT2家族蛋白参与植物叶片和繁殖器官钼的转运,最近被证实具有高尔基S-腺苷甲硫氨酸的转运功能;同时在液泡中检测到谷胱甘肽-钼酸盐复合物,为MOT2家族蛋白调节植物体内钼稳态提供了直接证据^[17]。

2 植物钼辅因子与含钼酶

钼辅因子是真核生物钼酶的重要组分,在小麦、大麦、烟草、拟南芥等植物中都确证有钼辅因子的存在^[18]。钼辅因子合成后进一步形成含钼酶,目前能确定存在于植物中的含钼酶有5种:硝酸还原酶(nitrate reductase, NR)、黄嘌呤脱氢酶(xanthine dehydrogenase, XDH)、醛氧化酶(aldehyde oxidase, AO)、亚硫酸盐氧化酶(sulfite oxidase, SO)和线粒体氨羟还原蛋白(mitochondrial oxime reducing protein, mARC),这些含钼酶都直接或间接参与植物抗逆性的调控。

NR是植物氮同化的关键酶之一,对植物氮代谢和碳代谢具有重要影响^[19]。最近研究发现,NR除了影响氮同化外,还参与信号传导过程,进而影响植物的抗逆性。NR突变的拟南芥(*nia1/nia2*)可以诱导一氧化氮的产生,并增加脯氨酸的积累从而增强植物耐寒性^[20],硝酸还原酶基因*NIA1/NIA2*还参与拟南芥生长素生物合成和信号传导的正向调控^[21]。水稻中的*OsNR1.2*基因可以编码1种NADH依赖性硝酸还原酶,这种酶通过抑制硝酸盐同化过程而提高其抗旱性^[22]。此外,NR诱导产生的NO还可以通过

增强抗坏血酸-谷胱甘肽(AsA-GSH)循环和抗氧化酶活性来增强植物耐盐性和耐重金属胁迫能力^[23-24]。

黄嘌呤脱氢酶(XDH)主要参与细胞分裂素代谢产物的氧化分解以及脱落酸(ABA)和吲哚乙酸(IAA)的间接合成^[25]。黄嘌呤脱氢酶RNA干扰使拟南芥转基因植株的生物量降低、过氧化氢(H₂O₂)含量增加,抗旱能力减弱^[26]。水稻XDH失活突变体ESL1中H₂O₂、丙二醛(MDA)含量和过氧化物酶(POD)活性显著高于野生型,内源ABA和叶绿素含量明显降低,在分蘖起始阶段表现出生长迟缓和叶片衰老的表型^[27]。大豆缺失*GmXDH*突变体表现出黄化等氮缺乏症和根瘤早期衰老,根瘤中固氮酶活性降低,根瘤内部呈现绿白色且豆血红蛋白减少^[28],说明XDH可能介导了植物活性氧的清除、生长素的合成调控及生物固氮过程。

醛氧化酶(AO)参与植物体内激素合成,并以脱落醛、吲哚-3-醛、吲哚-3-乙醛和苯甲醛为底物催化合成ABA和IAA,因此,AO与植物抗逆性关系密切。冬小麦通过AO影响ABA合成进而调控植物抗寒性^[29];干旱条件下,水稻*OsAO3*过表达时,植株体内ABA含量升高,水分损失减少,提高植株耐旱性^[30];拟南芥*AtAO3*基因功能缺失会导致植株ABA水平的降低且对干旱胁迫更敏感^[31]。

亚硫酸盐氧化酶(SO)能够氧化亚硫酸盐转化为硫酸盐,在半胱氨酸和蛋氨酸的分解代谢及亚硫酸盐和二氧化硫的解毒中起重要作用。Sharma等^[32]使用亚硫酸盐处理番茄果实和叶片,SO活性受损的植株生长受抑制,而SO过表达植株具有良好抗性。最近有报道指出玉米*ZmSO*启动子能够诱导植株ABA合成而使作物表现出较强抗旱性,SO在增强植物耐旱性中的作用有待进一步研究^[33]。

线粒体氨羟还原蛋白(mARC)是较晚发现的1种含钼酶,它附着在线粒体外膜上,与Moco硫化酶(HMCS)的C-末端结构域具有高度的序列同源性,属于钼酶SO家族^[34]。在动物中发现mARC蛋白能够催化硝态氮形成NO,衣藻中mARC蛋白也能够与NR形成NR-mARC系统诱导硝态氮还原为NO^[35]。拟南芥ARC1和ARC2都能还原N-羟基化合物,2种ARC酶都通过细胞色素b5还原酶和细胞色素b5接受来自NADH的电子,但只有ARC2能够接受来自硝酸盐还原酶的电子^[36]。关于ARC生理学功能的研究报道仍十分有限,其结构与功能揭示还需进一

步的研究。

3 钼提高植物抗寒性的生理与分子机制

1988年,德国科学家报道在酸性土壤上施钼可提高冬小麦的抗寒性^[2]。1989年王运华等在湖北省武汉市新洲区发现冬小麦缺钼黄化死苗现象,观察了小麦缺钼症状发生发展过程,提出了越冬期低温是冬小麦施钼有效的4个条件之一,进一步明确了施钼可提高冬小麦抗寒性^[37-39]。随后,在杨树^[40]、拟南芥^[41]和花椰菜^[42]等植物上都观察到施钼可提高植物的抗寒性。施钼引起的植株抗寒性增强主要表现在以下几个方面:一是植株叶绿素含量增加及光合能力增强。缺钼影响冬小麦叶片中 δ -氨基酮戊酸(ALA)向尿卟啉原Ⅲ(UroⅢ)的转化,导致叶绿素合成受阻含量下降,施钼则显著提高低温胁迫下2个冬小麦品系叶片的净光合速率和气孔限制值,显著降低叶片气孔导度、胞间CO₂浓度和蒸腾速率^[43-44],而施钼可显著提高冬小麦叶绿素含量^[45-46]。二是增强了植株抗氧化能力。低温胁迫下施钼显著降低超氧阴离子产生速率,提高了超氧化物歧化酶(SOD)、过氧化氢酶(CAT)、过氧化物酶(POD)和抗坏血酸过氧化物酶(APX)活性,说明钼通过调控活性氧代谢过程来影响冬小麦的抗寒性。三是植物膜系统稳定性强。脂质是细胞膜的关键结构成分,在维持膜完整性以及在介导植物对胁迫反应的细胞信号传导中起着至关重要的作用^[47]。施钼后冬小麦叶片膜脂肪酸组成以亚麻酸为主,膜脂饱和度增大,细胞器和膜结构比缺钼完整^[48],低温胁迫下,类囊体膜中亚麻酸(C18:3)含量和总不饱和脂肪酸(TUSFA)含量升高,从而提高了冬小麦抗寒性^[49]。

从调控机制上看,钼主要通过含钼酶来调控植物的抗寒性,可能途径主要包括:(1)钼通过硝酸还原酶(NR)影响植物光合碳氮代谢及其耦联过程。NR被认为是光合氮与光合碳代谢耦联关系的重要结点^[50-51]。在酸性土壤上施钼可以大幅提高低温胁迫下冬小麦硝酸还原酶(NR)、亚硝酸盐还原酶(nitrite reductase, NiR)和谷氨酰胺合成酶(glutamine synthetase, GS)的活性^[52]。钼通过硝酸还原酶影响冬小麦体内的氮的吸收^[53]、无机氮组分^[54]、氨基酸和蛋白质组分^[55-56]。低温胁迫下缺钼引起冬小麦最大硝酸还原酶活性(NRA_{max})、实际硝酸还原酶活

性(NRA_{act})及平均硝酸还原酶活性(NRA)显著下降,进而引发植株光合氮、碳代谢的失衡。蛋白质组学分析表明,低温胁迫下钼主要通过影响光合作用光反应过程和暗反应过程相关蛋白的表达影响冬小麦光合碳代谢,低温胁迫缺钼诱导了核糖-1,5-二磷酸羧化酶大亚基、磷酸甘油酸激酶、cp31BHv、叶绿素a/b结合蛋白、核糖-1,5-二磷酸羧化酶小亚基、核糖体蛋白P1等6种蛋白的差异表达。施钼显著提高了冬小麦光合速率、最大净光合速率、表观量子产率和羧化效率^[57]。这些结果表明低温胁迫下施钼通过增强冬小麦光合作用为抗寒性的形成提供了物质基础。(2)钼通过醛氧化酶(AO)调控ABA合成,进而影响植物抗寒基因表达。在醛氧化酶催化ABA合成的最后一步,LOS5/ABA3基因编码1种钼辅因子(MoCo)磺化酶,它催化磺化钼辅因子的产生,而磺化钼辅因子是植物ABA合成的最后一步中AO所必需的。LOS5/ABA3基因在植物的不同部位表达,其表达水平影响ABA的含量,进一步的研究表明LOS5/ABA3基因调控ABA合成和胁迫应答基因,拟南芥LOS5突变体的抗寒力、抗旱力和对盐胁迫的抵抗力受损,和另外一种ABA缺失突变体ABA1相比,LOS5突变体对低温应答基因的调控更具有专一性^[41]。低温胁迫下施钼显著增加了AO活性、ABA含量以及bZIP转录因子基因(*Wlip19*和*Wabi5*)和ABA依赖性COR基因(*Wrab15*、*Wrab17*、*Wrab18*和*Wrab19*)的表达,通过基因表达的时序性分析推测钼可能通过以下途径调节ABA依赖性COR基因的表达:Mo→AO→ABA→bZIP→冬小麦ABA依赖性COR基因^[29]。也有报道指出,钼也可能通过介导低温信号传递,激活CBF/DREB1(dehydration responsive element binding,冷诱导的结合因子)转录因子,进而影响下游COR基因(*Wcs120*、*Wcs19*、*Wcor14*和*Wcor15*)的表达^[42, 58]。(3)钼通过XDH调控嘌呤代谢和活性氧代谢,影响基因表达及信号传导。XDH与嘌呤代谢、活性氧代谢和衰老过程关系密切^[59]。在豌豆叶片中,随着超氧化物歧化酶含量的升高,黄嘌呤脱氢酶含量也急剧升高,其他与活性氧代谢相关的酶活性也同时升高^[60]。通过对水稻中含钼酶XDH的编码基因*es11*进行克隆,发现*es11*突变体水稻对非生物胁迫的敏感性增加,说明钼可以通过提高XDH活性而增强植物抗寒性^[27]。

4 钼提高植物抗旱性的生理与分子机制

钼与植物抗旱性之间的关系密切,施用钼肥能够增加干旱胁迫下冬小麦的光合速率、光合产物的积累、冬小麦的千粒重、穗粒数和产量^[61-62]。在模拟干旱胁迫条件下,施用钼显著提高了钼低效和钼高效小麦品种的SOD、CAT、POD、APX等抗氧化酶的活性,以及抗坏血酸、还原型谷胱甘肽、类胡萝卜素等非酶抗氧化剂的含量,并降低了丙二醛含量^[63],表明钼的施用增强了植物清除活性氧的能力。喷施纳米钼肥也能显著提高豌豆^[64]、油菜^[65]等作物的抗旱性。

钼调控植物抗旱性的途径主要包括:(1)钼通过NO介导的信号转导过程调控根系发育及养分水分利用。NR不仅介导NO₃⁻还原为NO₂⁻,而且还将NO₂⁻还原为NO,这是高等植物产生NO的重要途径。Wu等^[66]研究表明,NO信号参与了钼对干旱胁迫下小麦根系生长的调控。主要表现在施钼和NO供体通过增加NO的产生进而提高了侧根长度和根尖数量。Imran等^[67]进一步证明施钼通过促进NO积累和硝酸盐转运蛋白基因*NRT*的表达促进了冬小麦根系生长。施钼改善了水通道蛋白AQP_s的表达,特别是*TaPIP*的表达。施钼降低了小麦叶片蒸腾速率,但增加了根系渗透调节离子K⁺、Ca²⁺和Mg²⁺的浓度,表明离子浓度增加引起的根系渗透压是钼增加小麦水分吸收的动力,而不是蒸腾作用引起的蒸腾拉力^[66]。(2)钼通过ABA介导的信号转导过程调控抗旱基因表达。Shi等^[30]在水稻上发现醛氧化酶*O_sAO3*基因的突变和过表达分别降低/增加了水稻幼苗地上部/根部的ABA水平,ABA在缺水条件下激活干旱反应基因的表达,进一步参与调控水稻的生长、产量和抗旱性^[68]。Wu等^[69]通过添加AO抑制剂、ABA合成抑制剂等互补试验证明施钼提高了小麦的AO活性进而调控了ABA合成。干旱胁迫下施钼显著提高了2个冬小麦品种97003和97014依赖ABA型转录因子基因*Wabi5*的表达量,以及抗旱基因*Wrab17*、*W55a*和*Wrab19*的表达量,表明钼可能主要通过ABA介导的信号转导过程调控抗旱基因的表达^[70]。(3)钼通过脂质代谢调控植物抗旱性。脂类物质是细胞膜、叶绿体膜、线粒体膜的关键组分,在维持膜结构稳定并通过信号传导调控植物干旱胁迫响应过程中起着非常重要的作用^[71]。Wu等^[72]采

用脂质组学和转录组学相结合的方法研究了施钼对干旱胁迫条件下冬小麦脂质合成及代谢的影响,发现施钼增加了脂肪酸合成、甘油酯合成与去饱和化相关基因转录水平,而抑制了脂质氧化相关基因的表达,提高了叶片双半乳糖甘油二酯(DGDG)、单半乳糖甘油二酯(MGDG)、磷脂甘油(PG)和磷脂酰乙醇胺(PE)水平及不饱和度,增加了C36:6、C34:4和C34:3等甘油酯类物质的积累,脂质组成的变化将有助于维持细胞膜的完整性和保护光系统的稳定性,从而协同调控植物耐旱性。

5 植物钼营养与其他抗逆性

1)植物钼营养与抗盐性。施钼可提高小白菜^[73]、冠毛麦草^[74]和盐角草^[75]等植物的耐盐性,其调控机制主要与施钼提高了盐胁迫下植物体内含钼酶(NR、AO和XDH)活性有关。NR是受盐胁迫影响较大的钼酶之一,拟南芥Ler和Col-0生态型在抗盐胁迫上的差异主要取决于两者体内硝酸盐含量和硝酸还原酶基因*NIA2*表达上的差异^[76]。近期的研究还发现,植物中的*AtMOT1;3*等位基因和*AtMOT1;1*弱等位基因在宿主适应盐碱生境的过程中发挥着关键作用,*AtMOT1;1*弱等位基因通过增强*COPT6*的表达以调控钼辅因子(Moco)和ABA的生物合成,在植物适应局部盐胁迫环境中发挥作用,然而,目前关于*AtMOT1;1*促进Moco和ABA的生物合成的机制尚不清楚^[5]。

2)植物钼营养与重金属抗性。外源钼添加能增强油菜、水稻和蓖麻等植物对镉胁迫的抗性,促进植物生长,其原因多与诱导抗氧化防御系统减轻作物氧化损伤有关^[77]。Qu等^[78]最近研究表明,施钼可促进铬(Cr)胁迫下烟草的生长,降低其活性氧含量和铬迁移系数,硒和钼的联合施用可增加烟草谷胱甘肽(GSH)和植物螯合蛋白(phytochelatins, PC)的水平,提高细胞壁和细胞器中铬分配比例以缓解铬毒害,推测硒和钼的联合施用上调了*PCS1*基因表达,促进更多PC与铬离子螯合,并将铬离子固定在根细胞壁和液泡中,从而降低铬的毒性。砷(As)胁迫下钼添加可提高蚕豆幼苗的氮代谢速率,硝酸还原酶、亚硝酸盐还原酶和谷氨酰胺合成酶活性,进一步的研究发现钼主要通过硝酸还原酶诱导内源性NO的产生,提高作物叶绿素代谢、渗透调节物质的积累和抗氧化系统共同增强对砷的抗性作用^[79]。这些结果说明钼能在一定程度上提高植株对重金属的抗性,

缓解重金属的毒害,但这些研究多在缺钼条件下开展,因此,推测其抗性作用机制多与植物体内钼营养失调有关,而钼能否作为重金属吸收的阻隔剂以降低植物体内尤其是可食用部位重金属含量有待进一步的研究确证。

6 展 望

钼作为植物必需的微量元素,越来越多的证据表明,钼能提高植物的抗逆性(抗寒、抗旱、抗盐胁迫、抗重金属胁迫等),其调控机制与含钼酶的生理功能关系密切,含钼酶多通过影响植物碳氮代谢、抗性基因表达、活性氧清除能力以提高作物的抗逆性。未来应进一步围绕钼在植物体内的吸收同化过程、含钼酶调控的信号转导过程开展研究,重点关注:(1)植物体内新的钼转运蛋白基因的克隆鉴定及其与植物抗逆性的关系;(2)钼辅因子合成关键基因、关键酶或蛋白与植物抗逆性的关系;(3)新的含钼酶的发现及其对植物抗逆性的调控作用;(4)钼调控植物抗逆性(抗寒、抗旱、抗盐及抗重金属胁迫等)的共性机制与差异机制。

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Progress on improving plant stress resistance with molybdenum

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Abstract Molybdenum (Mo), as an essential trace element in plants, plays a crucial role in promoting the growth and development of plant and enhancing plant stress resistance. The absorption and transportation of molybdenum in plants are mainly regulated by the molybdate transporter genes *MOT1* and *MOT2*. Molybdenum enters the plant and participates in the growth and metabolism of plant in the form of molybdenum containing enzymes. The regulation of plant stress resistance is mainly manifested as follows: molybdenum affects the photosynthetic carbon and nitrogen metabolism, hormone synthesis, and reactive oxygen species metabolism in the plant through molybdenum containing enzymes including nitrate reductase, aldehyde oxidase, and xanthine dehydrogenase, thereby regulating plant cold resistance. Molybdenum regulates root development, nutrient and water use, and drought resistance gene expression through signal transduction processes mediated by nitrate reductase and aldehyde oxidase, further affecting lipid synthesis and metabolism to regulate plant drought resistance. The recent studies have found that molybdenum plays an important role in plant adaptation to salt stress and alleviating heavy metal stress as well. It will provide new insights into improving plant stress resistance via regulating molybdenum nutrition.

Keywords molybdenum; molybdoenzymes; transport proteins; cold resistance; drought resistance; salt resistance; heavy metal resistance

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