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The Research Development of the Response Mechanisms to Magnesium Stresses in Plants

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Abstract

Magnesium (Mg), one of the most core nutrients in plant growth and development, is the most abundant free divalent cation in cells. Shockingly, the Mg content in grains has presented a decrease over time in different periods, and some crops and forages appear Mg deficient symptoms. On the other hand, high Mg content in some soils inhibits plant growth and development, which leads to the Mg toxic symptoms. However, comparing with other nutrients, such as nitrogen, phosphorus or potassium, the responding mechanisms of Mg stress conditions in plants are known little today. Therefore, we integrate the research development recently on plant physiology, magnesium transporters, signaling responding to Mg stresses, and the interactions between Mg and other ions. This review is to attract people's attention and promote the study of the responding mechanisms of magnesium stresses in plants.

Keywords

Plant, Magnesium Deficiency, Magnesium Toxicity, Magnesium Transporter, Signaling, Ion Interaction

植物应答镁营养胁迫机理的研究进展

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摘　要

镁(Magnesium, Mg)是植物生长发育必需的重要营养元素之一，也是细胞中最丰富的游离二价阳离子。人们近期发现：不同时期谷物中的镁含量随时间呈下降趋势，作物和牧草等相继出现了缺镁症；另一方面，由于地球表面部分地区土壤镁含量过高，抑制生物的正常生长发育，导致镁中毒症状。但是，与氮、磷、钾等元素相比，植物应答镁营养胁迫的研究往往被人们遗忘，研究相对滞后。因此，本综述主要从镁胁迫条件下植物生理、信号传递、镁离子转运体，以及镁与其他离子的互作等方面来阐述植物应答镁营养胁迫的研究进展，以期引起人们的重视，推动植物镁胁迫机理的研究。

关键词

植物，缺镁，镁毒害，镁离子转运体，信号传导，离子互作

1. 引言

　　镁在 1925 年就被认为是细胞中最重要的营养元素之一，也是细胞中最丰富的游离二价阳离子[1]。镁具有大的水合半径，能结合 3 到 4 个数量级的水分子，比其它阳离子与水分子的结合更加紧密，并且通过与其它离子相互作用来维持它的水合半径[2]。Mg^{2+}的功能主要是稳定细胞大分子结构(核酸、蛋白、细胞膜、细胞壁等)、维持酶活性(H^+-ATPase、激酶、聚合酶类等)、平衡细胞内活性氧(reactive oxygen species, ROS)和离子[3]，是 300 多种酶(包括羧化酶，磷酸酶，激酶，RNA 聚合酶和 ATP 酶)的配体和激活因子，并以螯合核苷磷酸盐的形式存在[1]。除了上述的功能外，镁在植物叶绿体光合作用中起着关键的作用：叶中镁含量的 1/5 是叶绿素和色素的配体，参与光能的捕获和电子的传递[4]。然而，人们对植物镁生理和分子功能研究的重视度不够，导致其研究水平明显滞后，主要原因是镁在土壤中的含量丰富(第 8 位)、在水中的溶解度大、易被植物吸收，以及镁的生理功能复杂等[5]。另一方面，尽管植物细胞中镁的平衡主要由镁转运体来控制[6]，组学的研究却显示，这些转运体在缺镁[7]和镁毒害[8]条件下的转录水平变化不大，但其他转运体的表达水平变化的比较明显。最近，植物应答镁胁迫信号传导机制的研究获得较大的进展，包括脱落酸(abscisic acid, ABA)和赤霉素(gibberellin, GA)，以及它们的信号因子，如 DELLA 基因(GA 负调控因子)和 ABI1(ABA insensitive 1)应答镁毒害胁迫[9]；活性氧和乙烯等参与缺镁胁迫[7]。尽管如此，植物镁营养胁迫的具体分子机理等进展较慢。本文从植物应答镁营养胁迫、镁离子转运体和镁与其它离子的互作等方面阐述植物镁营养胁迫的研究概况，为相关领域的研究提供比较全面的研究信息。

2. 植物应答缺镁胁迫机理的研究

2.1. 缺镁胁迫严重影响植物的生长和发育

　　植物中镁的含量为 1.5~3.5 g/kg [10]，土壤中有效镁浓度在 125 μM~8.5 mM 之间，能满足植物生长对镁的需求[4]。阳离子交换能力低的酸性土壤和雨量大的热带地区容易导致镁的流失；长期施肥(N-P-K)导致土壤中镁的竞争性耗竭，这些都降低了植物根对镁的可利用度[11] [12]。镁量不足时，植物生长就会

受到抑制、植物老化程度加速、种子产量和品质下降[13]。这些暗示土壤的物化特性对于植物根系利用镁的重要性，改良土壤品质来增加作物的镁含量可能是行之有效的策略之一。

植物镁缺乏(Magnesium deficiency)时，诸如碳代谢，叶绿素合成和碳固定等能力受阻，最终导致植株短根、小芽、矮化、叶片坏死等症状[14]。转录组测序结果显示大量的调控基因首先在根部被调控[7]。当植物重新加入镁离子后，24 小时之内，叶内 1/5 和根内 1/2 差异表达的基因恢复到初始模式，说明根是最早应答镁浓度变化的器官。而叶片中缺镁应答基因在 8 小时后的表达差异逐渐变得明显[15]。缺镁 1天后，镁在芽中的浓度迅速下降[7] [14]，说明芽和叶是应答镁浓度变化的第二器官。缺镁显著抑制蔗糖在韧皮部的转运，导致能源叶中碳化物的积累，重新加入镁能迅速提高韧皮部蔗糖的转运[14] [16]。这些结果说明，镁是参与韧皮部转运蔗糖的重要阳离子。这个过程可能与镁有关，而与光照无关[14]，可能是韧皮部 Mg-ATP 浓度的下降抑制能源叶蔗糖的转运[17]，就像钾、锌不足时叶片中蔗糖的积累，但缺磷没有这些现象[10]。蔗糖在韧皮部的转运是由 H^+/蔗糖协同转运催化，这种由筛管质膜上 H^+-ATP 酶催化的转运需要质子梯度[17]。Mg-ATP 是生物系统最主要的 ATP 复合体[18]，且对 H^+-ATP 酶的功能是必需的[19]。缺镁诱导甜菜(*Beta vulgaris* L.)叶中 *BvSUT1* (Sucrose transporter 1，位于维管系统伴侣细胞的一种韧皮部特异性质子蔗糖同向转运蛋白)的表达[20]。同时，镁是碳水化合物代谢酶的催化剂或辅因子，这些酶的活性受到缺镁的抑制，导致叶中碳水化合物(大部分为淀粉)不能转化为蔗糖而富集，这些酶包括果糖-1,6-二磷酸酶(Fructose 1,6-bisphosphatase, FBPase)，谷氨酸合成酶，UDP-D-葡萄糖焦磷酸化酶、ADP-D-葡萄糖焦磷酸化酶、GDPD-葡萄糖焦磷酸化酶和 UDP-D-葡糖醛酸焦磷酸化酶[14]。过量的淀粉积累反馈抑制光合速率，并抑制 *CAB2* 基因(叶绿素 a/b 结合蛋白基因 2，负责编码叶绿素 a 和 b 蛋白)，从而减少叶绿素的生物合成[14]。此外，光合作用受损导致叶绿体无效电子和吸收能量的积累，促进 ROS 的产生，导致叶绿素的光氧化和叶绿体膜脂质损伤，高光照加重缺镁的症状印证了这一点[21]。这是由于抑制叶绿体中激发能量从 PSII(光合系统 II)转移到 PSI 的缘故[22]。活性氧的产生可能与原卟啉 IX (Protoporphyrin IX)有关，一旦原卟啉 IX 在组织中高度积累，就能导致叶组织坏死[23]。与此同步的是增强了植物的抗氧化酶活性[15] [24]，拟南芥(*Arabidopsis thaliana* L.)缺镁处理后抗氧化剂的量明显增加[15]证实了这一点。最新的研究表明，水稻(*Oryza sativa* L.)在缺镁胁迫条件下，蒸腾速率的降低先于叶中糖的积累和叶萎黄[25]。这些结果说明，植物应答缺镁胁迫是一个复杂的系统，其分子调控机理还不清楚，需要进一步的探究。

2.2. 镁离子转运体在植物细胞内镁离子平衡中的作用

随着拟南芥镁转运体(Magnesium transporters, MGTRs) [26] [27]的发现，镁在植物细胞中的平衡机制得到初步阐述。AtMHX 是一个 Mg^{2+}/H^+交换体，主要位于韧皮部[28]，也是植物中第一个被克隆的 MGTR [27]。AtMHX 顺式调节子[28]-[30]和过表达的分析[31] [32]显示 AtMHX 主要维持细胞内金属离子和质子的稳态，并参与光合作用。最近发现 AtCNGC10 位于质膜[33]，参与镁的摄取和远距离运输，也可能涉及钙和钾的运输[34]。

已知的 MGTRs 大多是 CorA 类转运体，CorA 类 MGTRs 的共性是在第一跨膜结构域的尾端部有一个保守的甘氨酸-蛋氨酸-天冬酰胺(Gly-Met-Asp, GMN)三肽基序[2]。拟南芥中 10 个 CorA 类转运体分为镁高亲和转运体，低亲和转运体和双功能转运体，它们被认为是植物重要的镁转运系统，参与细胞对镁的摄取、分布和体内平衡，定位在质膜、内质网、液泡、线粒体和叶绿体等亚器官[2]。然而，目前只有 *AtMGT*6 (Mao *et al.*, 2014)、*AtMGT*7 [35]的基因沉默植株，和 *AtMGT*1 [36]的过表达植株在缺镁条件下有突变表型；双突变(*AtMRS*2-1/10)和三突变(*AtMRS*2-1/5/10)可通过降低钙离子浓度来恢复缺镁条件下植物的生长发育问题[37]，但确切机制并不清楚。在低镁条件下，*AtMGT*1 和 *AtMGT*7 在根部高表达，且 *AtMGT*7

的基因敲除植株对缺镁敏感，说明这些基因可能参与镁的摄取，但 AtMGT7 定位于内质网[35]，说明其可能调控内质网 Mg^{2+} 的平衡。AtMGT1 定位于质膜[26]，表达于根毛伸长区的维管组织和成熟叶的表皮毛[35]，过表达拟南芥 *AtMGT*1 和水稻 *OsMGT*1 显著提高转基因植株的铝毒害耐性[36] [38]，即胞质溶胶中镁含量的升高可以缓解铝毒害。这些说明 *MGT*1 应答铝毒害，而不是缺镁胁迫。AtMGT6 是质膜 MGTR，参与根部对镁的摄取，缺镁诱导其高表达[39]。AtMGT2 和 AtMGT3 定位在叶肉细胞的液泡膜中，与 AtMHX 类似[27]，参与细胞内镁离子的平衡[35] [40]。此外，拟南芥种子中镁含量与一些 *AtMGTs* [41] 和 *AtMHX* [42]基因的 QTL (quantitative trait loci)共定位可能暗示，*MGTRs* 在不同组织中起着重要的镁转运功能。然而，这些 *MGTRs* 的表达水平在植物应答缺镁的芯片中没有显著的变化，其它的转运体基因却被缺镁上调表达[7] [15]，说明还存在其它的 *MGTRs* 应答植物缺镁胁迫。

另外，AtMGT5 定位于线粒体[43]，与 AtMGT9 [44]类似，影响植物的育性。AtMGT10 定位于叶绿体被膜系统，在基座叶和茎生叶的维管组织中表达[35]，其功能可能是转运镁离子到叶绿体[45]。另一方面，水稻中 II 类 HKT (high affinity K^+ transporter)的两个成员(*OsHKT*2;4 和 *TaHKT*2;1)除转运钾外，还转运镁和钙，但受钾浓度的影响[46]，这也暗示一些其它离子转运体在植物应答缺镁过程中可能充当重要的角色，只是这些 *MGTRs* 的调控信息还非常少，只发现脱落酸(ABA)和生长素参与 *AtMHX* 第一个内含子和顺式调节子的调控[28]-[30]。

2.3. 植物应答缺镁胁迫的信号传递

缺镁阻碍糖从叶到根的转运，促进叶中淀粉的积累，反馈抑制光合作用，增加细胞的 ROS，最终抑制植物的生长[17]。最近的研究说明，植物中存在应答缺镁信号的调控途径。例如乙烯生物合成、ABA 和生物钟相关基因受低镁诱导表达[7] [24]。然而，应答缺镁信号传递的研究还较少。Hermans 等[7]报道，植物缺镁处理后 ABA 的含量变化不明显，尽管部分 ABA 相关基因上调表达。我们的研究发现镁毒害(Magnesium toxicity)处理植株的根和叶中 ABA 含量显著升高[9]。Hermans 等[15]还发现，乙烯在应答缺镁过程中发挥了关键作用，缺镁处理后乙烯生物合成酶基因(例如 At5g43450、At1g06620 和 At2g25450)的表达水平明显上升，且缺镁处理植物的乙烯含量是对照植物的 2 倍。这些结果说明，植物应答缺镁胁迫存在一些独特的信号通路，并且与这些植物激素有关。Niu 等[24]发现，根器官内 ROS、抗氧化酶和 Ca^{2+} 受缺镁胁迫的诱导，最终影响根毛的发育。然而，这些因子的具体作用模式还了解的较少。

3. 植物应答镁毒害胁迫的机理研究

3.1. 植物应答镁毒害的特性

人们虽然对植物缺镁的生理机制了解的相对较多，但对镁毒害引起的生理变化机理却知之甚少，特别是镁毒害胁迫条件下的信号转导途径。植物在蛇纹石(Mg^{2+} > 10 mM，缺乏氮，磷和钾，但是富含铬、镍、铁、锰、钴和镉等重金属)或者火星表层类似土壤(Mg^{2+}占总质量的 10%以上)中的生长非常缓慢[8] [47]。植物在这些土壤中生长需要克服几个问题：1) 怎样调控高浓度镁的吸收和贮存；2) 怎样调控根系统的正常发育；3) 怎样调控叶的正常生长等。人们发现 *A. lyrata* 蛇纹石耐性株系和蛇纹石非耐性株系间的 DNA 具有高度多态性[48]，并采用 *Microseris douglasii* (蛇纹石耐性)和 *M. bigelovii* (蛇纹石敏感)定位了植物应答镁毒害的几个 QTL 位点[49]。这些研究说明植物适应镁毒害的分子机理是比较复杂的。

人们通过对拟南芥的研究，发现了植物适应这些问题的一些作用机制。在富含高硫酸镁的土壤中，转运体 *AtMRS*2-10 和 *AtSULTR*1 (定位在根细胞质膜)的突变体中镁含量并没有降低，而 *cax*1-1 (H^+/Ca^{2+} transporter, CAX)突变体对镁毒害土壤却有很强的耐性[47]。在镁毒害条件下，对野生型拟南芥 *Col*-0 和 *cax*1-1 的根进行转录组分析，发现镁毒害处理 *Col*-0 植物 45 分钟后，显著差异表达的基因主要包括激素

代谢相关蛋白、转录因子、钙结合蛋白、激酶、细胞壁相关蛋白和膜转运蛋白；180 分钟后，约 200 个转运体基因的表达发生了变化，第一个被下调的基因是 *CAX*1。事实上，*Col*-0 和 *cax*1-1 植株在处理 180 分钟后，只有四个转录本发生了明显的表达差异，说明在植物早期应答镁毒害中 *CAX*1 的重要性[8]。另外，在镁毒害条件下，植物叶片淀粉的生物合成酶基因(如 *SS*1、*SS*2、*GBSS*1 和 *APL*1)的转录水平被显著抑制，而淀粉降解酶基因被上调表达，如 *AtAMY*1 和 *BAM*1，叶片淀粉碘染色、糖的测定都暗示了这一点，即镁毒害处理的叶片很难被碘染色，且淀粉和蔗糖含量明显下降[5] [9]。镁毒害时可能上调一些植物 MGTRs 的转录水平，除 *AtMHX* 被下调表达，其他 MGTRs 都不同程度的上调表达，最终导致植物吸收过量的镁[9]。然而，具体的分子调控机理还不是很清楚。

3.2. 植物应答镁毒害的信号传递

镁毒害明显诱导多种植物激素生物合成酶基因的表达量，如脱落酸(9-顺式-环氧类双加氧酶)、乙烯(1-氨基环丙烷-1-羧酸合酶)和茉莉酸(脂肪氧合酶) [8]，这些激素都参与调控植物生物或非生物逆境的应答过程。在拟南芥中，镁毒害导致植物 ABA 含量比对照增加 5 倍多，ABA 的生物合成基因如 *ABA*1 和 *ABA*2 等被上调表达[9]；镁毒害诱导差异表达基因的启动子序列包含 ABA 调控元件[8]，以及生长素和 ABA 诱导维管束中转运体 *AtMHX* 的表达[28]。这些说明 ABA 在植物应答镁毒害中发挥关键的调控作用。与野生植物相比，ABA 非敏感突变体 *abi*1-1 在镁毒害条件下生长较好。外源 ABA 和镁毒害处理都能促进 DELLA 蛋白 RGA 的积累[9]，但 RGA 在 ABA 处理的 *abi*1-1 植物中没有积累[50]。DELLA 蛋白是赤霉素信号转录负调控的核心因子之一，参与许多适应性反应，是几种植物激素信号的核心信号交汇点(core cross-talk nodes) [51]，如赤霉素、生长素、乙烯、脱落酸、油菜素类固醇、水杨酸和茉莉酮酸酯等。因此，我们推断镁毒害可能诱导 ABA 的生物合成，通过 ABI1 增加 DELLAs 积累，进而抑制植物的生长和发育。类似 *abi*1-1 植物，DELLA 四突变体 DELLA-Q (*GAI-T*6 *RGA-T*2 *rgl*1-1 *rgl*2-1)在镁毒害处理条件下生长良好[9]。DELLA-Q 植株可以通过降低淀粉的过度消耗、ABA 的过度积累和调控 *MGTRs* 的表达来改善植物体内的 *MGTRs* 和 ABA 生物合成酶的表达水平，进而降低植物 Mg^{2+}和 ABA 的过度积累[9]。因此，DELLAs 可能是植物适应镁毒害的关键信号因子之一，ABA 信号可能通过 DELLAs 调控植物应答镁毒害胁迫。Mogami 等[52]发现钙调磷酸酶 B 类似互作蛋白激酶(Calcineurin B-like (CBL)-interacting protein kinase, CIPK)基因 CIPK26/3/9/23 等参与 ABA 激活 SRK2D/E/I 等因子的过程，从而调控下游基因，维持高镁条件下植物细胞内的镁离子平衡；Niu 等[24]发现 ROS 和细胞溶质 Ca^{2+}可能是应答镁胁迫的信号因子；Gao 等[53]提出 Ca^{2+}-CBL-CIPK 信号途径与液泡存储应答离子胁迫的模型，包括镁毒害。这些说明 ABA、CBLs、CIPK、DELLAs、ROS、Ca 等因子是植物应答镁毒害的信号因子，其相互间的作用机理还有待深入研究。

4. 植物中镁与其它离子的互作

植物中镁与其他离子存在多种互作关系。高钾和高钙导致植物根部镁的可利用性下降[12]，而若干 *AtMGT* 基因在低钙条件下或 *cax*1/*cax*3 钙转运体双突变体植物中被显著诱导，在缺镁胁迫的植物中并没有这些现象[7] [15]，说明植物细胞可能通过增加镁的转运来弥补低钙，高钙却抑制镁的可利用性。钾除了与镁竞争质外体结合位点外，还可能竞争某些转运体，非洲爪蟾(*Xenopus laevis* L.)卵母细胞表达的 II 类钾转运体 2 个成员(*OsHKT*2;4 和 *TaHKT*2;1)也能转运 Mg^{2+} [46]。蚕豆(*Pisum sativum* L.)叶肉细胞 Mg^{2+}摄取有两个系统，一个是非选择性离子通道，另一个是 H^+/Mg^{2+}的交换器(MHX)，后者在低镁浓度下作用，非选择性离子通道也转运钾和钙[54]，这些可能解释高钾和高钙抑制植物利用镁的现象。铈(稀土元素)能促进叶绿素和光合色素的合成，增加 CO_2 同化和抗氧化防御系统中关键酶的活性，以及减轻缺镁条

件下菠菜(*Spinacia oleracea* L.)叶内丙二醛和 ROS 对细胞的毒害[23] [55]。这些结果说明，铈与镁在一定程度上有相似的功能，但其机理尚不清楚。同理，镧与铈相似，也能减轻缺镁对植物的伤害[56]。

高浓度镁可以缓解重金属和铝对植物生长发育的抑制和毒害。例如，镁处理能显著减轻高浓度铜对大麦(*Hordeum vulgare* L.) [57]、豇豆(*Vigna unguiculata* L.) [58]和葡萄(*Vitis vinifera* L.) [59] [60]的毒害，但在甜菜[61]和生菜(*Lactuca sativa* L.) [62]中没有发现类似的现象，这些说明镁对铜毒害的影响与植物物种相关。镉毒害抑制芥菜(*Brassica juncea* L.)的生长，可被高浓度镁缓解[63]，而缺镁预处理能预防高镉对拟南芥和水稻幼叶的漂白作用，还可提高植株的抗氧化能力，减轻镉对叶绿体的损伤、维持铁的稳态、促进镉的外排或液泡存储[11] [64]。在烟草(*Nicotiana tabacum* L.) [36]和水稻[38]中，镁转运基因(*AtMGT*1 和 *OsMGT*1)的过表达植株明显耐铝毒害胁迫；一些植物如大豆(*Glycine max* L.) [65]、水稻[38] [66]、拟南芥[64]和赤小豆(*Vigna umbellata* L.) [67]，在添加镁和钙时，也能抗铝毒害。铝和镁可能相互争夺膜转运体和酶的金属结合位点[68]，即镁减轻铝毒害的可能原因是通过减少质外体铝的结合位点和降低铝在根质膜的表面活性[69]，反之亦然[38]。不同甘蓝(*B. Oleracea* L.)品种的镁含量有 2.3 倍的浓度差，且这种变异是高度遗传的[70]，这暗示我们能培育出镁高度富集的作物，并耐受铝毒害。低 pH 值(pH < 4.5 或高 H^+)同样抑制植物对镁的摄取[71]、导致镁的浸出和渗漏、增加有害离子的浓度，如铝和锰[38] [72]。另外，增加硝酸根离子的供应能促进镁的摄入，但降低植物体内镁的迁移[73]；增加镁的供应可能逆转氨对植物的毒害[74]。这些结果说明植物中镁和其它离子之间的相互作用非常复杂，很多机理还不清楚。

5. 展望

镁是植物生长发育必需的营养元素之一，过多或缺失都会影响植物的正常生长发育。植物镁营养元素的研究多集中在镁离子转运体的结构和功能、缺镁和镁毒害生理等方面，并在光合作用，碳代谢，减轻铝毒害等方面取得了一定的进展，但对镁胁迫条件下镁离子的吸收规律、信号传递和调控等分子水平的研究相对较少。然而，不同时期植物的镁含量随时间下降[75]和镁毒害[9]等提醒我们，镁营养元素胁迫对人类的影响并不遥远，特别是缺镁胁迫。因此，本综述一方面阐述植物镁营养胁迫的研究进展，为深入研究相关的机理提供文献基础；另一方面希望获得科学家、营养学家、农学家等的重视，加强该领域的研究工作。我们相信近些年的基因组、转录组、蛋白组和非编码 RNA 组等新技术的快速发展，必将加速推动植物镁胁迫生理和信号传递研究的进展。

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