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硅在植物体内的分布和吸收及其在病害逆境胁迫中的抗性作用

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摘要:硅在地壳中含量位居第二位,尽管还没有被列为植物生长的必需营养元素,但它在促进植物生长发育和营养吸收、提高植物对非生物逆境胁迫和生物逆境胁迫的抗性等方面都具有重要作用。综述了近些年来国内外关于硅在植物体内的分布、吸收及其生理效应,重点介绍了硅在病害逆境胁迫中的抗性作用机理。高等植物以单硅酸[$Si(OH)_4$]的形式吸收硅,存在硅的主动吸收和被动吸收机制。硅主要沉积在叶片及叶鞘表皮细胞,形成硅化细胞和角质-硅双层结构,能增强寄主植物细胞壁的机械强度和稳固性,从而延缓和抵御病菌的侵入和扩展。更多的证据表明,硅处理能增加植物叶片保护酶(过氧化物酶、多酚氧化酶、苯丙氨酸解氨酶等)活性和诱导寄主产生次生代谢抗性物质(如植保素、多酚类化合物、木质素),从而激活植物的防御系统,增强对病原菌的抵抗能力。分子水平上的研究显示,硅能诱导与植物防御机制相关的基因表达,参与抗病信号分子(如水杨酸、茉莉酸和乙烯)在信号传导中的作用。

关键词:硅;植物;环境胁迫;抗病性;诱导抗性

Distribution and absorption of silicon in plant and its role in plant disease resistance under environmental stress

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Abstract: Silicon (Si) is the second largest abundant mineral element in the earth's crust. Although Si is still not listed as an essential element for the majority of plant species, it plays important roles in stimulating plant growth and nutrition uptake and enhancing plant resistance to abiotic and biotic stresses. This paper reviewed the distribution and absorption of Si in plant and its physiological functions with focusing on the mechanisms of Si mediated pathogen resistance. Higher plants mainly take up Si in the form of [$Si(OH)_4$], and there are active and passive Si uptake mechanisms. Silicon can deposit in the epidermal cell walls beneath the cuticle, form a cuticle-Si double layer and enhance cell wall mechanical strength and stability, and therefore retard and resist pathogen from penetration and spreading. More research evidence shows that Si-treated plants can significantly increase the activity of protective enzymes such as peroxidase, polyphenol oxidase, phenylalanine ammonia-lyase, etc. in leaves and the production of antifungal compounds such as phenolic metabolism product, phytoalexins, pathogenesis-related proteins, etc., which in turn activate the plant defense system and enhance the plant resistance to pathogen. Studies in molecular level show that Si can induce the expression of defense-related genes as well as interact with disease-resistant signal molecules such as salicylic acid, jasmonic acid and ethylene for signal transduction.

Key Words: silicon; plant; environmental stress; disease resistance; induced resistance

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硅(Silicon, Si)是地壳中含量仅次于氧的元素,位居第2位,也是地球上绝大数植物生长的矿质基质,但是硅的重要性一直没有得到应有的重视,目前还未被列为植物营养需求的必需元素[1-2],部分原因是硅的广泛存在和缺乏时症状不明显以及它在植物中的作用和代谢机理还不完全清楚[1,3-4]。但是随着作物的不断种植和化学肥料(N,P,K)的大量施用消耗了植物必需的土壤中的硅,土壤中硅的缺乏已经作为限制作物特别是高硅积累植物如水稻和甘蔗产量的主要限制因子。国内外关于硅元素对于不同植物种类和品种的生长发育、产量、非生物胁迫抗性和病虫害的抗性方面的显著效果有广泛的研究[1,5]。本文在对硅的分布、植物对硅的吸收和运输、硅的生理效应等进行介绍的基础上,结合国内外的最新研究进展以及我们的相关研究结果,重点从物理屏障、诱导抗性、调控基因表达等方面综述了国内外关于硅提高病害抗性的机理,以便为深入开展硅的理论和实践研究提供参考价值。

1 硅的分布及植物对硅的吸收

1.1 硅的分布

硅在地壳中的含量约为28%。自然界中没有游离态的硅,而主要以氧化物和硅酸盐的形式存在。硅在土壤中的含量因土壤类型不同而异,主要存在于土体和土壤溶液中,或被吸附在土壤胶体的表面[7]。在土壤溶液中,硅主要以单硅酸的形态存在,其含量一般为0.1—0.6 mmol/L[6]。被植物吸收利用的有效硅,指土壤中的单硅酸及易转化为单硅酸的盐类(是当季作物可利用的硅素),数量甚微,一般为50—250 mg/kg。土壤有效硅含量通常作为衡量土壤供硅能力的指标,它受气候条件、土壤pH值、成土母质、土壤粘粒、施用有机肥、土壤水分及土壤温度等因素的影响[8]。

硅主要沉积在植物细胞的细胞腔、细胞壁和细胞间隙[9-10],其存在的主要形态是水化无定形二氧化硅($SiO_2 \cdot nH_2O$)和二氧化硅(SiO_2)[11],其次是硅酸和胶状硅酸[12]。Parry 和 Kelso[13]认为,在泡状细胞、表皮细胞和硅化细胞内,硅的沉积形状为杆状,受代谢严格的调控。Pipemo[10]认为硅体的形状具有物种类别上的相近性。

硅在整个植物界的含量与分布极不均匀,不同种类的植物含硅量差异较大。Takahashi 和 Miyake[14]研究表明,硅是种间含量差异最大的元素。不同植物含硅量的顺序大致是:谷类作物 > 牧草 > 蔬菜 > 果树 > 豆科[15]。另外,植物体内硅的含量还受植物的部位、生育期、种植方式、环境条件等多种因素的影响[8]。

1.2 植物对硅的吸收与运输

不同植物种间硅含量的差异很大,硅含量可以占到植株地上部干重的0.1%—10%[2,6],这种差异主要是由于不同植物根系对硅吸收能力的差异引起的[16-17]。在 $pH < 9$ 时,植物根系从土壤溶液中吸收不带电荷的水溶性单硅酸[18]。单硅酸通过蒸腾流以液态硅酸的形式转运到植株地上部分,然后单硅酸脱水聚合为无定形二氧化硅($SiO_2 \cdot nH_2O$),并沉积在植物组织内[2]。Mitani 和 Ma[19]认为植物对硅的吸收包括至少两个过程:从外部溶液到皮层细胞的径向运输和从皮层细胞释放进入木质部(木质部卸载)。在水稻中,已经证实了硅的径向运输是由一个 K_m 值为0.15 mmol/L的跨膜转运蛋白介导的过程[20-21]。Liang 等[22]首次报道黄瓜对硅的吸收与运输是逆浓度梯度的主动过程,受低温和代谢抑制剂的显著影响。Rains 等[23]研究结果表明,2,4-二硝基酚(DNP)和KCN会抑制小麦对硅的吸收,磷酸根离子则没有显著影响,而Ge离子对小麦硅的吸收有竞争性抑制作用。

对水稻、黄瓜和番茄这3种地上部分硅含量相差大的植物的硅吸收机制研究表明,硅径向运输中高密度的转运蛋白(SIT1,包括Lsi1和Lsi2)含量和木质部卸载中转运蛋白(SIT2,包括Lsi6)的存在是水稻硅含量高的重要因素。黄瓜和番茄较低的硅积累量,可以解释为转运蛋白SIT1的密度低和SIT2的缺失[19]。

植物对硅的吸收和运输的研究近期取得很大进展,其中以日本 Okayama University 的 Ma Jianfeng 课题组最具代表。Ma 等[21,24-25]从野生型水稻经叠氮化钠处理得到的突变株中克隆了与水稻主动吸硅相关的基因 *Lsi*1,*Lsi*1 基因属于水通道家族,该基因位于第2号染色体上,包括5个外显子和4个内含子。其cDNA全长为1409bp,编码的蛋白质含298个氨基酸,包括6个跨膜结构域和2个NPA(Asn-Pro-Ala)高度保守的特征性

序列。*Lsi*1 组成性表达于水稻的根部,主要在主根和侧根中表达,但不在根毛中表达,其编码蛋白 *Lsi*1 分布在根部外皮层和内皮层细胞质膜上。Ma 等[26]随后又克隆出另一个编码硅转运蛋白的基因 *Lsi*2,该基因位于第 3 号染色体上,包括 2 个外显子和 1 个内含子。其 cDNA 全长为 1416bp,编码的蛋白质含 472 个氨基酸,一共有 12 个跨膜结构域。转运蛋白 *Lsi*2 也是主要分布在水稻根部外皮层和内皮层细胞质膜上,但 *Lsi*2 位于相同细胞间的近侧端,而 *Lsi*1 是位于细胞的远侧端。两个蛋白的作用也不同,*Lsi*1 是将植物体外的硅转运到细胞内,而 *Lsi*2 作用刚好相反,是将硅排出细胞外。*Lsi*2 的排硅作用受低温和解偶联剂 2,4-二硝基酚(DNP)、羰基氰化物间氯苯腙(CCCP)、羰基-氰-对-三氟甲氧基苯肼(FCCP)等的抑制,表明排硅过程是需能的。Yamaji 等[27]发现一个调节水稻地上部硅分布的转运蛋白 *Lsi*6,该蛋白表达于水稻的叶鞘和叶片,也表达于根尖,主要位于水稻叶鞘和叶片木质部的薄壁细胞内。*Lsi*6 可以转运出木质部内的 Si,并最终影响硅在叶片的分布。这些研究对进一步深入理解和认识硅的吸收机理具有重要的意义。

2　硅的生理效应及抗性作用

随着人们对硅的重要性的不断认识,近十多年来国内外对硅素的研究取得很大进展。从硅的生理效应上看,硅能促进植物的健壮生长[28-29]和改善植株的矿质营养吸收[6],更重要的是硅在非生物和生物逆境胁迫中的抗性作用。研究表明,硅能提高植物对金属离子毒害的抗性[30-31]、缓解盐胁迫[32-33]、增强水稻抗倒性[1]、抗旱性[34-36]、抗高低温[37-38]和抗紫外线辐射等[39-40]。对于生物胁迫方面,硅在增强植物的抗病性[41-43]和抗虫性[2,44]等方面起重要的作用(表 1)。

表 1　硅对生物逆境胁迫和非生物逆境胁迫的抗性作用

Table 1　Role of silicon in alleviating biotic and abiotic stress

胁迫类型 Stress type	植物 Species	参考文献 References
Cd	水稻 *Oryza sativa* L.,玉米 *Zea mays* L. 白菜 *Brassica pekinensis*	[31,45-49]
Mn	黄瓜 *Cucumis sativus* L. 豇豆 *Vigna unguiculata* L.	[50-52,30]
Al	水稻, 玉米,大麦 *Hordeum vulgare* L.	[53-56,39]
Cr	小白菜 *Brassica chinensis*	[57-58]
盐害 Salt stress	水稻,黄瓜, 大麦	[32,3-4]
干旱 Drought	小麦,玉米,高粱 *Sorghum bicolor* L.	[35,59-60,36]
紫外线胁迫 ultraviolet stress	水稻	40,61]
高低温 Temperature stress	水稻	[37-38,62]
稻瘟病 *Magnaporthe grisea*,纹枯病 *Rhizoctonia solani*, 胡麻斑病 *Cochliobolus miyabeanus*	水稻	[41,63-64,42,65-71]
白粉病 *Blumeria graminis*,*Sphaerotheca fuliginea*	甜瓜 *Cucumis melon* L., 拟南芥 *Arabidopsis thaliana*, 黄瓜,小麦	[72-81]
炭疽病 *Colletotrichum lagenarium*	黄瓜,菜心 *Brassica campestris* L.	[82-83]
灰斑病 *Magnaporthe grisea*	钝叶草 *Stenotaphrum secundatum* 黑麦草 *Lolium perenne*	[84-85]
稻纵卷叶螟 *Cnaphalocrocis medinalis*, 褐飞虱 *Nilaparvata lugens*, 稻螟蛉 *Naranga aenescens*	水稻	[86,2]
茎螟 *Eldana saccharina*	甘蔗 *Saccharum* spp.	[44]

3　硅提高植物抗病性的机理

尽管硅能提高许多植物对不同病害的抗性,但其抗性机理还不完全清楚,也一直处于争论之中。综合国内外研究情况,其可能机理主要包括物理屏障、诱导抗性及调控基因表达等方面。

3.1　物理屏障

这种机理的主要依据是,硅在植物细胞的大量沉积、硅质化,形成硅突,防止病菌菌丝的侵入和扩展,能降

低病菌对细胞壁的酶降解作用,起到类似物理屏障的作用,从而增强病害的抗性。同时,有研究表明,硅的含量与植物病害的抗性存在相关关系[87]。

3.1.1 硅的沉积、硅质化和硅突形成

研究表明,硅能在植物叶片、茎秆、根系的表皮组织内沉积,形成硅化细胞和角质-硅双层结构,使组织硅质化,进而形成机械障碍从而延缓和抵御病菌的侵入[34,42,71,81,88-89]。杨秉耀等[90]发现水稻抗性品种的剑叶表皮硅化细胞数量多。水茂兴等[64]研究表明,施用高效硅肥,水稻叶片细胞壁增厚,剑叶表面硅化细胞增加。利用电镜和原位 X-射线分析, Kim 等[66]发现硅能沉积在叶片表皮细胞壁,硅化的细胞与稻瘟病的抗性密切相关。Liang 等[91]研究表明,叶面喷施和根部施用硅肥均能增加黄瓜对白粉病的抗性,但其机制却不一样。叶面喷施只能通过机械障碍来降低病害感染,而根部施用则通过代谢抗性起作用。郭玉蓉等[92]研究表明,硅化物处理使硅在甜瓜叶面气孔处和表皮层的沉积明显增强,起到了物理屏障作用。对稻瘟病的研究表明,在接种病菌的情况下,加硅处理后硅在叶片表面高度沉积,叶片的硅化细胞数量、长度、宽度和面积有不同程度的增加,气孔硅突数增多,硅化细胞排列更加清晰、致密和整齐[71]。张国良等[69]对硅与纹枯病相互作用关系的研究也有类似结果。Hayasaka 等[93]最新的研究结果表明,沉积在水稻叶表皮的硅参与抵抗稻瘟病菌吸器的附着穿入。

表皮细胞的硅突形成被认为有助于增强植物的抗病性[94,73]。对小麦病害 *B. graminis* f. sp. *tritci.* 、水稻纹枯病的研究表明,加硅处理后,在植物叶片病害侵染点的叶片气孔保卫细胞上的硅突数增多[69,73]。通过扫描电镜观察也发现,在稻瘟病侵染下,硅处理增加了保卫细胞上的硅突数,从而增强了对病害的抗性[71]。

3.1.2 硅的含量与病害抗性的关系

有报道指出水稻抗稻瘟病品种的含硅量比感病品种的含硅量大,而且品种的抗性程度随硅的施用量及其植株中硅的积累量增加而提高[95]。Winslow 等[87]报道水稻不同基因型间病害严重程度与组织含硅量呈负相关。Kim 等[66]发现加硅后水稻对稻瘟病抗、感两个品种的病害严重程度均显著降低,硅含量高的植株有大量的硅化细胞,它们受稻瘟病的危害小;增加硅的施用量会提高植株的抗性。Hayasaka 等[96]研究认为,在水稻苗期施硅,当水稻体内硅含量(SiO_2)达到 5% 以上时,稻瘟病情即显著下降。研究表明,随着施硅浓度的增大,水稻抗稻瘟病的能力增强,植株体内的硅含量也随之增加。杨秉耀等[90]应用扫描电子显微镜对 8 个不同品种的水稻叶片表面硅化细胞的形态结构进行了观察,并用 X 射线能谱分析其硅含量,结果表明水稻叶片硅化细胞和硅含量大小与其抗性存在明显的正相关。张国良等[69]研究表明,加硅处理的水稻叶片硅化细胞和叶片表面的硅元素含量均显著高于缺硅处理,硅在叶片表面一定微区的沉积可以起到物理屏障作用,从而提高水稻抗纹枯病的能力。

但是,有研究认为,在病菌侵染发生后,硅质化表皮以及在侵染过程中形成的硅层就再也不能阻止菌丝的生长[95]。在实际生产中,确实有某些含硅量低的品种抗某些病菌生理小种,而某些含硅量高的品种表现感病,即使抗病品种,也仍然发现真菌会穿透其表皮细胞。因此,硅的抗性机制不仅仅是机械保护。Carver 等[97]和 Chérif 等[98]发现,硅在病害侵染点和表皮细胞的积累和沉积与抗性并没有相关关系。对黄瓜的研究表明,当供硅停止后,硅对白粉病的保护效应就停止,尽管硅依然在植物组织内继续积累[81]。Heine 等[99]研究发现,硅在根细胞的积累并不与番茄对 *Pythium aphanidermatum* 病害的扩展有关。所以尽管物理屏障最早一直被作为抗性机制,近来也有不少证据支持,但却争议不断,还不能完全解释硅的抗性机理。

3.2 诱导抗性

更多的证据显示,硅可能参与植物寄主和病原菌相互作用体系的代谢过程,经过一系列生理生化反应和信号转导,激活寄主防卫基因,诱导产生一系列小分子代谢物从而增强植物的抗病性[7,76,100]。Chérif 等[98,100]指出,硅与其它诱导剂相比,一个显著优势是在病原物侵染之前不改变植物的正常生理代谢,不会因消耗能量而导致作物减产。而其它诱导剂如病原物、草酸、水杨酸等却会改变正常代谢途径,消耗能量,导致不必要的减产。

3.2.1　增强与抗病有关的保护酶活性

植物在受到病害侵染时会引起体内一些与酚类代谢相关的酶活性变化,诱导防御反应,合成并累积系列防御反应物质,从而增强植物抵御病原菌侵袭的能力。常见的与抗性相关的酶包括过氧化物酶(POD)、多酚氧化酶(PPO)、苯丙氨酸解氨酶(PAL)、过氧化氢酶(CAT)等。这些酶除了参与酚类物质代谢外,还参与木质素、植保素等次生抗性物质的形成和积累,可作为整个代谢途径的调节子,常被看作植物抗病性的生化指标之一[101-102]。其中 POD 参与植物细胞壁木质素的合成[103];PPO 具有把多酚氧化成对病原物有高度毒性的醌类物质的作用;PAL 是植物抗病代谢(莽草酸途径)的关键酶和限速酶,可催化 L-苯丙氨酸还原脱氢,为合成植物保卫素和木质素提供苯丙烷碳骨架或碳桥,从而在抗病性中起作用[104]。

研究发现,在黄瓜无土栽培营养液中加入可溶性硅,可显著减轻由腐霉菌(*Pythium* spp.)造成的根腐病,其防治效果与植株体内 POD 和 PPO 活性增强有关[100]。对小麦、黄瓜、瓠瓜、甜瓜、长豇豆等的白粉病研究表明,硅处理能增强感病植株叶片的 POD、PPO、PAL、CAT 和几丁质酶(CHT)等的活性,从而降低病害的发病率[74,79-80,91-92,105,112]。研究表明,在接种稻瘟病菌后,无论是抗病还是感病材料,硅处理的植株叶片 POD、PPO、PAL 活性与不加硅相比均显著增加[71]。李国景等[106]的研究也表明,外源加硅可明显提高长豇豆感病和抗病品种接种锈菌后的 POD、CAT 和超氧化物歧化酶(SOD)等抗氧化酶活性,降低丙二醛含量,未接种时硅对上述参数无明显影响。

然而也有研究认为,加硅处理在接种炭疽病菌后对黄瓜叶片 POD、PPO、PAL 活性和木质素含量没有显著影响,对抗炭疽病效果也不显著[82,107]。张国良等[69]研究表明,接种纹枯病菌后,尽管硅处理后叶片的 POD 和 SOD 活性显著增加,但 PPO 活性则降低,PAL 活性则没有影响。因此,硅对不同作物、不同真菌引起的病害的抗病效果和机理可能各不相同,要完全弄清其机理有待于深入研究。

3.2.2　诱导次生代谢产物

与硅提高植物体内的保护酶活性相对应的是,硅可通过诱导产生次生抗菌物质如植保素、木质素、酚类物质和病原相关蛋白[68,76,100,108]来提高寄主对病害的抗性。

Fawe 等[76]在加硅处理且受白粉菌侵染的黄瓜叶片提取物中得到了黄酮类植保素物质 Flavonol Aglycone Rhamnetin (3,5,3′,4′-tetrahydroxy-7-O-methoxyflavone, 即 3,5,3′,4′-四羟基-7-O-甲氧基黄酮)。并且认为硅参与了受侵寄主的抗菌活动,使植物产生了一些小分子代谢物质(酶类、黄酮醇类),与水杨酸或茉莉酸诱导植物抗性相比,可溶性硅充当了诱导植物抗性的调节子,使植物更快或更有效地抵御病原体的攻击,硅起了预防作用但没有直接影响植物的代谢。Rodrigues 等[68]通过超微结构观察,首次提供了硅介导水稻抗稻瘟病菌的细胞学证据,发现接菌后加硅处理的水稻体内大量生成酚醛类物质抵御稻瘟病菌的生长。进一步研究发现,在接菌后施硅能提高水稻叶片的植保素含量(主要是稻壳酮 A 和 B)2—3 倍,从而增强水稻对稻瘟病菌的抗性[109-110]。Bélanger 等[73]通过组织学及超微结构分析发现,加硅处理的小麦表皮细胞对白粉菌有特殊的防御反应,包括乳突形成、胼胝质产生,并释放酚类物质;酚类物质不仅积累在细胞壁,而且能以类似于其他已报道的植保素的方式改变病菌吸器的完整性,从而抵御病菌的入侵。在硅减轻黄瓜和长豇豆的白粉病的研究中发现,施硅处理的植株叶片中酚类物质的含量显著高于不加硅处理[80,105],而未接种时,加硅处理对酚类物质含量大小没有显著影响。

此外,寄主感染病原菌后木质素含量的增加与病害的降低关系密切[111]。木质素通过保护植物细胞壁物质不被真菌降解,并使侵入的菌丝细胞木质化从而增强对病原菌的抗性。魏国强等[112]研究表明,与不加硅相比,在接种白粉病菌条件下,加硅处理的瓠瓜叶片木质素含量是不加硅处理的 1.43 倍。研究也证实,在稻瘟病侵染条件下,加硅能显著提高水稻感病材料叶片的木质素含量[71]。

3.3　分子方面的机理

与大量生理生化方面的机理研究相比,从分子水平上揭示硅提高植物的抗病性机理还很薄弱[113]。有研究表明,在未受到逆境胁迫时,硅处理对基因表达没有影响[114]。Kauss 等[115]在对硅介导黄瓜的系统诱导抗

性发现,病菌感染位点细胞壁抗性的增强与一个新的编码富含脯氨酸的蛋白被激活关系密切。Rodrigues 等[110]首次在分子水平上研究了硅的抗病机制。加硅处理能促进水稻品种对稻瘟病菌产生过敏性反应,诱导表达编码 PR-1、POD 等基因,并积累大量的酚类物质和木质素,从而抵制菌丝生长与侵入表皮细胞。

Fauteux 等[78]通过定量 PCR 方法研究了硅对拟南芥白粉病病菌的抗性作用。结果表明,在接种、未加硅的拟南芥植株中,菌丝大量生长、繁殖,而加硅后明显地降低了菌丝的密度从而显著降低病害的侵染。不接种只加硅处理的拟南芥只有 2 个基因的表达量受影响,而无论加硅与否,接种处理的拟南芥都有将近 4000 个基因的表达量发生变化。对这些基因进行功能分类,其中许多的上调基因与抗性相关,同时与植物防御机制相关的基因在植物-病原菌相互作用中通过识别、信号传递和诱导,使植物自身的防御系统被激活,防御反应基因得以被调控表达,而很大比例的下调基因则是与初级代谢相关。Li 等[116]认为,受逆境胁迫的植株产生了一种有序的极其重要的应对胁迫条件的响应,降低了信使 RNA 的变化,这种变化与加硅处理的植株间有显著的不同。

4 结语

硅能显著提高植物对病害的抗性,硅肥施用为植物病害的防治提供了一条新的思路。但硅在增强植物抗病性中的作用机理还不是完全清楚,存在一些争议[43,113]。如(1)硅是否对病原菌直接产生毒害作用、硅对病原菌的抗性以物理屏障为主还是以诱导抗性为主,还是同时存在?(2)硅在不同植物与病原菌互作系统中的抗病机理是否相同?(3)硅与系统抗性的信号分子水杨酸、茉莉酸、乙烯等的关系如何?(4)硅如何调控信号传导和基因表达?(5)硅在高等植物体内的吸收和运输机制如何等?最近在水稻中克隆了与水稻主动吸硅相关的基因 *lsi*1、编码硅转运蛋白的基因 *lsi*2 和 *Lsi*6[21,24-27],这些成果预示着硅的研究与实践应用曙光的到来。

与此同时,国际上对硅的研究与生产应用也日益活跃。1999 年 9 月、2002 年 8 月、2005 年 10 月、2008 年 10 月分别在美国、日本、巴西、南非召开了四届硅在农业中的应用国际大会。通过对硅的深入研究,有助于揭示硅提高植物对逆境胁迫的抗性机制,以便更好地为农业生产应用提供理论基础。

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