

高等植物对有机氮吸收与利用研究进展

莫良玉, 吴良欢*, 陶勤南

(浙江大学环境与资源学院, 杭州 310029)

摘要: 主要综述植物氨基酸营养生理生化和分子生物学研究方面的最新进展。长期以来, 人们一直认为植物只能吸收无机态 N, 有机 N 必须矿化为无机 N 后才能被植物吸收利用, 而近年来越来越多实验证明植物能吸收有机 N, 特别是氨基酸, 其吸收能力因植物种类而异。生长在有机 N 丰富的北极、高山和亚高山生态环境中的植物甚至嗜好氨基酸。因此, 不应过分夸大有机 N 矿化的重要性。迄今一些植物细胞质膜上的氨基酸转运子基因已被描述并加以克隆。

关键词: 高等植物; 有机 N; 氨基酸吸收; 转运子

Advances in Study of Plant Organic Nitrogen Nutrition

MO Liang-Yu, WU Liang-Huan, TAO Qin-Nan (College of Environment and Resource Science, Zhejiang University, Hangzhou 310029, China). *Acta Ecologica Sinica*, 2002, 22(1): 118~124

Abstract: Traditional models of nutrient cycling assume that soil microorganisms must decompose organic matter, releasing inorganic N, before that N becomes available for plant uptake. But, there is a growing evidences that plant can take up organic N.

In the moist tundra of arctic tundra, most wetland are poor inorganic, plant-available nutrients because mineralization is restricted due to low temperatures and anoxic soils. But tundra soils have higher concentrations of water-extractable free amino acids than of inorganic N. Two tundra sedges, *Eriophorum vaginatum* and *Carex aquatilis*, take up amino acids at least as rapidly as they take up NH_4^+ over a range of concentrations, and compete well for glycine and aspartate N relative to NH_4^+ . *Eriophorum vaginatum*, a non-mycorrhizal sedge that dominantes moist upland tundra throughout the circumpolar Arctic, can absorb free amino acids, accounting for at least 60% of the nitrogen absorbed by this species in the field, and grow on them as its sole N source. So the dynamics of labile organic, rather than of inorganic N, appears to be the critical component of the tundra N cycle, at least in terms of controlling plant uptake and growth.

Alpine and arctic ecosystems are similar in that N mineralization rates are heavily constrained by climate, and plant N demands cannot be met through the uptake of inorganic ions. In the ecosystems where sedge commonly occurs, amino acids were present in the soil pore water, but in highly variable amounts. Amino acid concentrations in soil pore water are 13 ~ 15 $\mu\text{mol/L}$ in alpine dry meadow sits and 15 ~ 20 $\mu\text{mol/L}$ in a subalpine fen habitat. The alpine and subalpine *Cyperaceae* species exhibited higher rates of glycine uptake relative to NH_4^+ and NO_3^- uptake, compared to species from the more temperate habitats. A alpine sedge (*Kobresia myosuroides*) lacks the ability to take up NH_4^+ . This may reflect specialization toward the uptake of organic N in the alpine and subalpine species.

Mycorrhizae can enhance the capacity of the plant to absorb amino acids. Deciduous shrubs, which are ectomycorrhizal, have the highest rates of amino acid absorption (particularly of glycine); evergreen species with ericoid mycorrhizae are intermediate; and graminoids, which are largely nonmycorrhizal, tend to have low rates of amino acid absorption. Mycorrhizal endophyte associated with ericaceous species can absorb and then releases free amino acids that are subsequently taken up by the host plant without ammonification suggests that plants take a more active role in nutrient acquisition and element cycling. At concentrations of free amino acids in arctic tundra, these plant's uptake rates of the three amino acids

基金项目: 国家重点基础研究专项经费(G1999011707)及国家自然科学基金项目(No. 39970432)资助

作者简介: 莫良玉(1968~), 男, 壮族, 广西宜州市人, 博士, 讲师。主要从事有机营养研究工作。

*通讯作者 万方数据

(glycine, aspartatic acid, and glutamic acid) together may account for between 10 and 82% of the total N uptake in the field, depending on species.

The dominant plant species in the boreal forest where climate is similar to that in arctic, irrespective of their type of mycorrhiza, all compete well for, and use, glycine as a N source. At least, 91, 64 and 42% of the N from the absorbed glycine was taken up in intact glycine by the dwarf shrub *Vaccinium myrtillus*, the grass *Deschampsia flexuosa* and the trees *Pinus sylvestris* and *Picea abies*, respectively. Rates of glycine uptake of these plants were similar to those of NH_4^+ .

In agricultural systems, organic N potentially is important for plant N acquisition. Agricultural plants are also shown to absorb amino acids in laboratory studies and in the field. Four agricultural plants (*Phleum pratense*, *Trifolium hybridum*, *T. pratense*, and *Ranunculus acris*) can take up glycine in the form of intact amino acid. A minimum of 19%~23% of the glycine-derived N is take up as intact amino acid by these species. Rice also can take up glycine-N in sterile sand-culture and the contribution of glycine-N uptake to the plant's N budget is dependent largely on the relative levels of glycine-N in a mixture solution. The contribution of glycine-N increases with increasing the level of glycine-N and the uptake of glycine-N may account for up to 55.7% of the total N taken up by roots.

Plant roots are able to release amino acids into rhizosphere by passive diffusion at root tips. The free amino acids exuded into the rhizosphere may be re-absorbed by roots, and also accessed by microorganisms. Under sterile solution culture, *Zea mays* L. roots are capable of re-sorping over 90% of the amino acids exuded. The rates of amino acid transport are similar both for plants and microorganisms indicating that there will be intense competition for amino acid N within the rhizosphere. Studies in natural ecosystems have shown that plants compete well for organic N. So the limiting factor to organic N uptake is likely to reside in the availability of amino acids in the soil.

There is now a great deal of physiological and biochemical evidence for specific amino acid carriers involved in the active transport of different amino acids into plant cells. They are electrogenic transporters that are driven by either transmembrane proton or electrical potential differences. Many amino acid transporter genes have been isolated from higher plants, and it has been revealed that there exist multiple isoforms for each transporter. An extensive molecular characterization of amino acid carriers has been carried out in *Arabidopsis* where evidence has been presented for a multi-gene family of amino acid permeases (AAPs), the members of which differ in their tissue distribution and substrate specificity. The mutants of *Arabidopsis* that lack the activity of a basic-amino-acid transporter have been found. But these transporters have very broad and overlapping specificities, although each transporter exhibits a preference for amino acids possessing a particular molecular geometry or charge.

Recent work indicates that there are several different amino acids carriers present in *Ricinus* which may be involved in a variety of physiological processes. Several amino acid carriers have been resolved in *Ricinus communis* roots.

In summary, growing evidences demonstrate that plants can short-circuit N mineralization by directly absorbing amino acids, then accelerate N turnover and exert greater control over N cycling.

Key words: higher plant; organic N; amino acid absorption; transporter

文章编号:1000-0933(2002)01-0118-07 中图分类号:Q948 文献标识码:A

自从李比希(Liebig)1840年创立矿质营养学说以来,人们一直认为植物只能吸收无机态N而不能吸收有机态N,土壤中的有机态N必须经土壤微生物矿化为无机态N后植物才能吸收。因此,对植物无机态N作了大量研究^[1~4]。然而,随着研究手段的改进和研究内容的不断深入,越来越多证据表明植物也能吸收有机态N,特别是氨基酸。植物有机营养试验最早可上溯到1868年^[5],进入20世纪90年代后,植物有机N营养研究逐渐增多,特别是近年来在植物吸收氨基酸态N营养方面取得了较大进展,本文对高等植物吸收与利用有机氮的生理生化和分子生物学方面的进展综述于下。

1 嗜氨基酸植物

1.1 北极苔原及寒带森林地带嗜氨基酸植物

1.1.1 北极及北方寒冷地带土壤中氨基酸含量 北半球北极及北方寒冷地带常年低温,微生物活性低,

有机质矿化缓慢,土壤无机 N 含量低。养分主要来自降水、微生物固 N、周围分水岭(surrounding watersheds)和地下水。据估计每年每平方米通过降水和微生物固 N 进入北极土壤中的 N 为 30 ~ 250 mg^[6]。由于土壤无机 N 少,如北极苔原土壤无机 N 仅 0.5 ~ 1.0 mg N/kg,有机 N 矿化仅能满足植物需 N 量的一半左右,而微生物体也吸收较多 N,使得能为植物吸收的无机 N 更少但土壤有机 N 含量可达 2 ~ 8 mg N/kg,在白毛羊胡子草(*Erophorum vaginatum*)和苔草(*Carex aquatilis*)生长的湿地中,氨基酸浓度常高出无机 N 的好几倍^[6~8];北方森林土壤的氨基酸 N 含量也高出无机 N 几倍,前者约为 1.0 kg/hm²,后者为 0.3 kg/hm² 左右^[9]。因而氨基酸对生长于这一地带的植物可能很重要。

1.1.2 北极苔原嗜氨基酸植物 Chapin 等报道,北极苔原无菌根的白毛羊胡子草吸收氨基酸 N 的量至少占总吸收 N 量的 60%,这是首次发现无菌根的维管植物喜欢吸收氨基酸;白毛羊胡子草在以氨基酸作 N 源培养时吸收的 N 和形成的生物量均比以无机 N 作 N 源时的多,而适应无机 N 环境生长的小麦在以氨基酸作 N 源时吸收的 N 和形成的生物量则比以无机 N 作 N 源时的少近一半^[8]。Schimel 和 chapin 研究苔原莎草原位(*in situ*)吸收氨基酸时发现,白毛羊胡子草及苔草吸收氨基酸的速率不低于 NH₄⁺;在生长高峰季节供给高浓度氨基酸(25 mg N · kg⁻¹),其吸收速率甚至高于 NH₄⁺,而在生长后期给以低浓度氨基酸(2 ~ 4 mg N · kg⁻¹),其吸收速率近似于 NH₄⁺^[10]。Kielland 发现,生长在北极 4 个生态系统即干性石南灌丛、草丛苔原、灌木苔原和湿草甸的维管植物也能直接吸收氨基酸,但吸收氨基酸能力因植物种类而异,吸收的氨基酸态 N 可占植物总吸 N 量的 10% ~ 82%,植物对氨基酸的吸收能力与氨基酸分子量呈负相关^[7]。

1.1.3 菌根对植物吸收有机氮的促进作用 与真菌形成菌根可以提高植物吸收有机 N 的能力,菌根吸收氨基酸后能释放自由氨基酸供宿主植物直接吸收^[6,7,11]。研究表明,北极地带具有外生菌根的落叶灌木吸收氨基酸速率最高,具石南型(内生)菌根的常绿植物居中,而不具菌根的禾草类最低^[7]。Nasholm 等将带双标记甘氨酸(U-¹³C₂、¹⁵N-glycine)或¹⁵NH₄⁺注射到瑞典北方森林中晚期演替的针叶林的粗腐殖层中,研究有外生菌根的树木欧洲赤松(*Pinus sylvestris*)和挪威云杉(*Picea abies*),有石南型菌根的矮灌木欧洲越桔(*Vaccinium myrtillus*)以及有丛枝菌根的曲芒发草(*Deschampsia flexuosa*)在野外吸收氨基酸情况,通过测定根¹³C 和¹⁵N 百分超比值明显地表明这些植物能直接吸收氨基酸,6 h 后至少有 91%、64% 和 42% 的甘氨酸分别被矮灌木、草和树木吸收^[9]。

1.2 高山地带嗜氨基酸植物

1.2.1 高山土壤的氨基酸含量 高山由于海拔高,其气候特点与北极相似,常年低温,有机质矿化受抑制,因而土壤有机 N 含量高。在高山干草甸土壤孔隙水中氨基酸浓度为 13 ~ 158 μmol/L,甘氨酸为主要成分,在亚高山沼泽地土壤孔隙水中氨基酸浓度为 15 ~ 20 μmol/L,天冬氨酸为主要成分,而在矮草草原土壤孔隙水中氨基酸浓度为 25 ~ 45 μmol/L,谷氨酸为主要成分。这些土壤中的高浓度氨基酸主要来自土壤蛋白酶对土壤蛋白质的水解作用及土壤对氨基酸的吸附作用^[12]。

1.2.2 嗜氨基酸高山植物 Raad 等从 5 个生态系统中收集不带菌根的 13 种莎草,其中 3 种为高山莎草、4 种为亚高山莎草,2 种为矮草草原莎草、1 种为温带沼泽莎草,3 种为干燥热带森林莎草,进行有机 N(甘氨酸)和无机 N(NO₃⁻、NH₄⁺)吸收研究,发现除一种干燥热带森林莎草(*Gahnia gahniiformis*)不能吸收甘氨酸外,其余的均能吸收甘氨酸,而且发现有一种高山莎草(*Kobresia myosuroids*)不能吸收 NH₄⁺,对 NO₃⁻ 虽能吸收,但吸收速率低于氨基酸;与温带、热带莎草相反,高山、亚高山莎草吸收甘氨酸的速率比吸收 NH₄⁺ 及 NO₃⁻ 的大;温带莎草吸收氨基酸、NH₄⁺ 及 NO₃⁻ 的速率均比高山、亚高山莎草的大,这可能是温带莎草生长量大,对 N 需求量大缘故^[12]。

2 作物对氨基酸的吸收

20 世纪 90 年代以来,已有严密的无菌培养试验结果证明作物能吸收利用如氨基酸等有机 N。在无菌水培条件下,等 N 量(10 mg/L)有机、无机 N 对水稻的营养效果依次为甘氨酸态 N>谷氨酸态 N>铵态 N^[13];在甘氨酸态 N 与铵态 N 配施条件下,以吸 N 总量为基础计算的甘氨酸态 N 营养贡献率可达 55.66%^[14]。万方数据

作物在田间条件下也能吸收氨基酸态 N。Nasholm 等用梯牧草(*Phleum pratense*),杂种车轴草(*Tri-*

folium hybridum), 红车轴草 (*T. Pratense*) 和毛茛 (*Ranunculus acris*) 等作物为试验材料, 用注射方法供给带双标记的甘氨酸 ($\text{U-}^{13}\text{C}_2^{15}\text{N}$ glycine), 21 h 后测定根中的 ^{13}C 和 ^{15}N 含量, 发现这 4 种作物在田间均能吸收分子态甘氨酸, 被吸收的甘氨酸中有 19% ~ 23% 以上是以分子态的形式被植物吸收, 这暗示有机 N 也可能是农业上大田作物的重要 N 源^[15]。

3 植物对根际氨基酸分泌物的再吸收

大多数陆生植物的根能向根际分泌含碳化合物, 这样损失的碳可占植物总固碳量的 1% ~ 40%, 而 N 损失可占植物总固 N 量的 10% 左右^[16]。根分泌物成分复杂, 含有多种含碳化合物, 其中糖类、有机酸类和氨基酸类为主要成分^[17,18]。已发现植物能再吸收这些分泌物。Jones 和 Darrah 报道, 玉米在无菌水培时其根被动分泌氨基酸, 但又主动吸收被分泌的氨基酸; 根细胞质中氨基酸浓度 (9.5 mmol) 与土壤溶液中氨基酸浓度 (0.03 mmol) 形成较大浓度差, 特别是在根尖处, 说明氨基酸主要在根尖处被动分泌, 他们推算的分泌速率为 0.27 nmol/(cm root · h)^[19]。Jones 和 Darrah 还报道, 无菌水培每天更换根洗液 (root-bathing solutions) 时玉米根分泌氨基酸速率为 418 ~ 616 ng/(mg root · h), 静态培养 (不更换根洗液) 当根分泌和再吸收氨基酸达平衡后根洗液中氨基酸浓度很低 (约 50 μmol), 而大田中植物根的氨基酸净分泌率为 0.14 ~ 1.4 ng/(mg root · h), 这表明根细胞质膜上氨基酸转运子对氨基酸有很高亲和力^[18,20]。当用质子门抑制剂 CCCP (carbonyl cyanide *m*-chlorophenyl-hydrazone, 碳酰氰邻氯苯酚脲) 加入根洗液后可抑制根对氨基酸的吸收, 而根分泌氨基酸不受抑制, 使氨基酸在根洗液中积累, 另外低温 (5 $^{\circ}\text{C}$) 也可减少根对氨基酸的吸收而对分泌影响不大, 也造成氨基酸在根洗液中累积, 这表明根吸收氨基酸为主动吸收, 需有质子梯度推动, 根对氨基酸的吸收受无机 N 存在的影响^[19]。无菌条件下玉米吸收甘氨酸、甲硫氨酸的速率比吸收 NO_3^- 的大, 前者为 1.7 ~ 4.0 $\mu\text{g}/(\text{mg root DW} \cdot \text{h})$, 而后者为 1.5 ~ 1.6 $\mu\text{g}/(\text{mg root DW} \cdot \text{h})$ ^[20]。

植物根分泌氨基酸主要集中在根表处, 氨基酸在土壤干燥中的扩散距离仅几个 μm , 而且在根尖处微生物数量少, 因而有利根对氨基酸再吸收。Gordon 和 Jackson 报道, 死根和活根 N 浓度相近, 说明 N 不能从老根转移, 由于根细胞氨基酸浓度高, 当根衰老组织死亡降解后能增加根际的氨基酸浓度, 也利于根的再吸收^[21]。

4 植物和微生物对土壤氨基酸营养的相互竞争

土壤中的 N 90% 以上是以有机 N 形式存在, 这些有机 N 的 30% ~ 50% 可以被微生物分解为氨基酸。土壤氨基酸除来自有机质分解外, 降雨也可以提供, 因为雨水中氨基酸浓度为 1 ~ 15 $\mu\text{mol/L}$ ^[22]。一般耕作土中氨基酸含量为 0.31 ~ 4.72 mg/kg^[23]。而 Ostle 等通过测定土壤 N 的自然丰度 ($\delta^{15}\text{N}$) 测得草原和耕作土的氨基酸含量为 350 ~ 1980 mg/kg^[24]。植物和微生物吸收氨基酸迅速, 施入土壤的氨基酸半衰期 (half-life) 为 1 ~ 12 h^[25], 因而植物和土壤中的微生物竞争吸收氨基酸。Jones 和 Hodge 通过比较植物和微生物对氨基酸吸收的动力学和简单的根际计算后发现, 植物吸收氨基酸的速率与微生物的相似, 表明它们在根际中竞争剧烈^[26]。Hodge 等给黑麦草施带 ^{15}N 、 ^{13}C 双标记有机 N 后, 植物吸收 11% ~ 54% 的 N, 而微生物吸收 7% ~ 13% 的 N, 表明植物竞争 N 素养分能力比微生物强^[27]。Hu 等也报道, 植物吸收 N 的能力比土壤中的微生物强^[28]。但短期试验却表明微生物是强竞争者, 有 40% ~ 70% 的 ^{15}N 留在微生物体中^[10]。

5 植物细胞吸收和转运氨基酸的机理

5.1 植物细胞对氨基酸的主动吸收和转运

植物细胞能通过质膜上的特异性载体蛋白主动吸收氨基酸, 该载体为质子偶合运输蛋白或称质子偶合共运输^[29], 它由质膜 H^+ -ATPase 催化产生的 H^+ 电化学势梯度推动上向运输。Bush 和 Langston-Unkefer 给密生西葫芦 (zucchini) 纯化质膜囊泡加上质子电化学势首次描述了高等植物细胞的质子偶合氨基酸运输^[30]。之后, Li 和 Bush 研究纯化的甜菜叶质膜囊泡发现氨基酸运输属电产生的, 由 ΔpH 和膜电势 ($\Delta\psi$) 驱动, 质膜上至少有 4 种氨基酸转运子: 一种是酸性氨基酸转运子, 一种是碱性氨基酸转运子, 另两种是中性氨基酸转运子, 前者称为中性系统 I 和中性系统 II, 虽然某一转运子对某组氨基酸具有专一性, 但每一转运子均能对另一组氨基酸表现出交换专一性 (crossover specificity)^[31~33]。这表明一个转运子可运输多种

氨基酸。近年来对蓖麻、拟南芥质膜的氨基酸转运子研究较多^[34~37]。Weston 等研究蓖麻(*Ricinus communis* L.)根的纯化质膜囊泡的氨基酸运输后发现,谷氨酰胺、异亮氨酸、谷氨酸和天冬氨酸跨膜运输由跨膜 pH 梯度和跨膜电势推动,表明这些氨基酸吸收与质子共运输,而赖氨酸和精氨酸等碱性氨基酸的运输仅由膜电势(内膜为负)驱动,表明碱性氨基酸运输为电压驱动单向运输,但在其他植物,这些碱性氨基酸是与质子共运输,这可能是植物或组织不同,其吸收氨基酸的机制不同^[31,36]。氨基酸竞争吸收实验表明,蓖麻根质膜上至少有 3 种载体,两种对中性氨基酸具高亲和力而对碱性和酸性氨基酸具低亲和力(其中一个对天冬酰胺不具高亲和力而另一个对异亮氨酸和缬氨酸不具高亲和力),一种对碱性氨基酸和一些中性氨基酸具高亲和力而对酸性氨基酸具低亲和力,此外,虽然谷氨酸在低 pH 时能通过谷氨酰胺转运子运输,但可能有一个独立的专门运输酸性氨基酸载体存在质膜上^[36]。

Chen 和 Bush 将拟南芥(*Arabidopsis*)EST cDNAs 克隆至缺失氨基酸转运子的酵母中表达,发现拟南芥细胞质膜存在转运赖氨酸和组氨酸的专一性转运子(LHT1),其对赖氨酸和组氨酸的 K_m 值分别是 175 μmol 和 400 μmol ^[37]。此外,拟南芥还至少有 5 个氨基酸转运子 AAP1~5, AAP1 主要运输带负电荷和中性的氨基酸, AAP2 和 AAP4 主要运输脯氨酸、苯丙氨酸和缬氨酸, AAP3 和 AAP5 主要运输精氨酸、赖氨酸等^[37]。盐胁迫能诱导拟南芥产生两个脯氨酸转运子^[38]。

氨基酸转运子可能以固定的 H^+ :氨基酸比转运氨基酸。Boorer 和 Fisher 将在根中表达量多的拟南芥氨基酸转运子 AAP5 克隆到爪蟾(*Xenopus*)卵母细胞内表达,发现 AAP5 能转运中性、酸性和碱性等多种氨基酸,尽管转运子对各种氨基酸的表现亲和性($K_{0.05}$)和最大转运速率(V_{\max})不同,但转运氨基酸以固定的 H^+ :氨基酸=1:1 进行^[39]。

目前已发现有缺失氨基酸载体的大麦及拟南芥突变体存在。Heremans 等报道,在 0.1 ~ 0.4 mmol 范围内,赖氨酸进入缺失碱性氨基酸转运子(*ritll* 或 *racl*)的拟南芥突变体离体幼根流量仅为进入野生型植株的 7%,这是由于缺失了低亲和吸收系统,他们推测拟南芥根质膜上可能有 4 种吸收系统参与赖氨酸吸收,两种均为高亲和系统,其中一种对缬氨酸亲和力高而另一种对缬氨酸亲和力低;一种为低亲和系统,对碱性氨基酸有专一性;另一种为不饱和吸收系统^[40]。缺失碱性氨基酸载体的大麦突变体对碱性氨基酸(如赖氨酸、精氨酸、鸟氨酸)吸收减少,而中性氨基酸和酸性氨基酸的吸收不受影响^[41]。

5.2 植物细胞质膜氨基酸转运子基因

一些植物的氨基酸转运子基因已被分离。植物的第一个氨基酸转运子基因(拟南芥 AAP1/NAT2)的克隆和鉴定是采用使植物 cDNA 在缺失某一氨基酸转运子酵母突变体上表达而进行功能互补。因缺失某一氨基酸转运子的酵母不能吸收该氨基酸,而将植物的该转运子基因导入酵母中表达后该酵母就可以吸收该氨基酸。拟南芥 AAP1/NAT2 可转运多种氨基酸,但更倾向转运中性氨基酸,它有 486 个氨基酸残基,是整合膜蛋白,有 10~12 个跨膜 α -螺旋, His337 是影响 AAP1/NAT2 结构和功能的关键氨基酸残基,其改变将影响该转运子对氨基酸的运转^[42]。进一步研究发现,拟南芥质膜 NAT2 有 11 个跨膜区域, N 末端处于细胞质内, C 末端面向细胞外, 11 个跨膜拓扑结构也是拟南芥 AAP 家族特有^[43]。已知 AAP 家族至少由 5 个基因控制, AAP 成员间至少有 54% 的氨基酸序列是一致的^[44]。AAP1 和 AAP2 倾向于正在发育的长果和子叶的维管组织中表达,可能参与种子发育和氮再转移, AAP3 主要在源叶中表达,可能参与韧皮部氨基酸的装载,在其它器官中 AAP4、AAP5 也有不同的表达水平^[44]。拟南芥的两个脯氨酸转运子基因 ProT1、ProT2 已被分离, ProT1 在所有器官中表达,尤其是根、茎、花中表达量大, ProT2 则遍布整个植株,水或盐胁迫能诱导 ProT2 强烈表达,说明在胁迫条件下 ProT2 在氮分配方面起重要作用^[38]。从拟南芥克隆得的赖氨酸、组氨酸转运子基因 LHT1 的 cDNA 长 1.7 kb, 具一个开放阅读框架,编码的蛋白有 446 个氨基酸残基,为整膜蛋白,分子量为 50.5 kD, LHT1 在所有组织中均表达,尤其在幼苗的根表、幼叶、花、花粉以及长果中表达量大,说明 LHT1 参与将赖氨酸转运到异养组织中^[37]。

已从蓖麻分离得几个氨基酸转运子基因。Bick 等获得蓖麻两个氨基酸转运子基因 RcAAP1、RcAAP2, 这两个基因在叶片和根中表达量大,进一步研究发现 RcAAP1 主要在根中表达,其转录物分布于根尖多种类型细胞中,包括表皮、皮层,中柱细胞中也有较多的表达量,表明这两个转运子可能参与种子发芽

和从土壤中吸收氨基酸,还可能参与侧根发生或木质部的氨基酸运输^[45]。从蓖麻中获得的 RcAAP3 氨基酸转运子 cDNA 长 1.7 kb,有一开放阅读框,编码的蛋白质分子量为 51 kD,有 9 ~ 11 个跨膜区域, RcAAP3 在源和库组织中均表达,可参与积累氨基酸供蛋白质合成^[46]。

6 结束语

近年来,不仅发现植物可以吸收有机 N,而且发现有一些植物嗜氨基酸。植物主要通过载体主动吸收外源氨基酸。目前,一些植物的氨基酸转运子基因已被克隆和鉴定,某些缺失氨基酸载体的突变体也已被发现。因此,传统的植物矿质营养学说似有再认识的必要。高等植物对有机 N 吸收和利用的深入研究,必将进一步丰富植物的营养理论,促进有机废弃物的合理利用,保护环境,推动农业生产的可持续发展。

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