High Affinity Amino Acid Transporters Specifically Expressed in Xylem Parenchyma and Developing Seeds of Arabidopsis*

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Arabidopsis amino acid transporters (AAPs) show individual temporal and spatial expression patterns. A new amino acid transporter, AAP8 was isolated by reverse transcriptase-PCR. Growth and transport assays in comparison to AAP1–5 characterize AAP8 and AAP6 as high affinity amino acid transport systems from Arabidopsis. Histochemical promoter-β-glucuronidase (GUS) studies identified AAP6 expression in xylem parenchyma, cells requiring high affinity transport due to the low amino acid concentration in xylem sap. AAP6 may thus function in uptake of amino acids from xylem. Histochemical analysis of AAP8 revealed stage-dependent expression in siliques and developing seeds. Thus AAP8 is probably responsible for import of organic nitrogen into developing seeds. The only missing transporter of the family AAP7 was nonfunctional in yeast. AAP8 and AAP6 in some cases specific, e.g. in lupins where especially asparagine and glutamine contribute to the N enrichment in the phloem (8). The transfer activities lead to changes in the composition of the phloem sap on its way to the developing seeds (9).

The import of amino acids into seeds that occurs mainly via the phloem requires efficient exchange mechanisms between xylem and phloem (10). As a last step, the seeds have to be able to take up the amino acids arriving through the phloem. High affinity transport of all available amino acids is an essential prerequisite for seed development since the accumulation of storage proteins must be preceded by an import of amino acids. It could be shown that the expression of the amino acid transporter in seeds precedes the expression of the storage protein AtS1 in Arabidopsis (11). A similar increase in the expression of a legume amino acid transporter has been shown recently in Vicia faba (12). In pea it has been demonstrated that PsAAP1 is expressed in the transfer cell layer of cotyledons and might be responsible for taking up amino acids released from the seed coat (13). Among the different transporter genes identified in Arabidopsis so far, AAP1 and AAP2 were most highly expressed in immature siliques of Arabidopsis, indicating a role in supplying developing seeds with organic nitrogen. Biochemical properties of these transporters characterize them as low affinity transport systems (14). In analogy to sucrose transport-

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1 The abbreviations used are: RT, reverse transcription; GUS, β-glucuronidase; AuxRE, auxin response elements.
2 W. N. Fischer and W. B. Frommer, unpublished data.
3 T. Martin, unpublished result.

Plant Material, Growth, Transformation, and Analysis—Arabidopsis thaliana L. ecotype Col-0 was grown either in axenic culture on MS medium (30) supplemented with 2% sucrose or cultured in soil in the greenhouse. Arabidopsis plants were transformed using Agrobacterium tumefaciens pGV2260 under vacuum infiltration as described in Ref. 31.

MATERIALS AND METHODS

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ers, one may also expect that multiple transporters with differing kinetic characteristics are responsible for import into seeds. This would allow the growing seed to adapt to varying N-supply and alteration in amino acids available.

In Arabidopsis glutamate, aspartate, glutamine, and asparagine are the major transport forms of amino acids distributed through phloem and xylem (7). Concentration and composition of amino acids in phloem and mesophyll cytosol are similar, whereas a concentration gradient can be found between the apoplast and the phloem sap (15). This gradient indicates that active transport systems are involved in uptake of amino acids from the apoplast into the phloem. Complex kinetics and phase transitions in uptake depending on the amino acid concentrations have been described for barley roots (16). In sugar beet vesicles uptake studies revealed multiphasic kinetics as well as pH dependence for amino acid uptake (17, 18). In agreement with the complex physiology and uptake studies, multiple amino acid transporter genes have been isolated from Arabidopsis by complementation of yeast transport mutants with plant cDNAs (19–23). These genes can be classified into different families (24, 25). The ATF1 superfamily (amino acid transporter family 1) consists of several subfamilies: the AAPs (amino acid permeases), the LHTs (lysine histidine transporters), the ProTs (proline and compatible solutes transporters), the AUXs (putative auxin transporter) and several new subfamilies (25). One transporter, ANT1, of this new subfamily has been characterized recently as a transporter for neutral and acidic amino acids (26). The CAT subfamily (cationic amino acid transporters) is a member of the second plant amino acid transporter family, namely the APC-superfamily (24, 27).

Within the complete Arabidopsis genome, eight related sequences belonging to the AAP family can be identified. Six of these eight genes have been characterized as functional transporters so far. AAP1–5 were shown to mediate transport of a broad spectrum of amino acids with low selectivity by a proton-dependent mechanism (14, 22, 28, 29). For glutamine, glutamate, and asparagine as major transport forms of organic nitrogen, these transporters have $K_m$ values that are in a physiological range with respect to the concentrations of these amino acids found in the phloem and xylem. Aspartate is transported by most AAPs with an extremely low affinity and efficiency. Only AAP6 has a $K_m$ value for aspartate that is in a physiological range (14). The described properties of AAPs thus match the activities expected for transport proteins involved in moving a wide spectrum of amino acids into the phloem sap and into the xylem sap consistent with the properties described for uptake kinetics measured in plasma membrane vesicles of leaves (17). Despite the well described biochemical properties, information about tissue- and cell-specific expression of these genes is not well established.

A third member of the AAP family expressed in young seeds and veins of the siliques was isolated and functionally characterized. Although most closely related to AAP1 on a protein sequence level and found in duplicated regions on chromosome I, it is the high affinity of AAP8 toward aspartate that characterizes this protein as a high affinity transporter for acidic amino acids. This transporter expressed in young seeds and veins of siliques shows a fine-tuned expression pattern. With its biochemical properties it can complete the needs to adapt to various substrates during seed development. AAP6 as a high affinity transporter was localized to the xylem parenchyma cells, fulfilling both expression pattern and biochemical properties of the described physiological predictions for xylem-to-phloem transfer of amino acids.

Transport Measurements—Plant cells were pre-grown to logarithmic phase harvested at $A_{600nm}$ = 0.5, washed, and resuspended in ice cold buffer (50 mM NaPO4, pH 4.5, 0.6 mM sorbitol) to a final $A_{600nm}$ = 5. Cells were preincubated with 10 μM of 1 μM glucose (30°C, 5 min). Then 110 μL of buffer, labeled with [3H]leucine (7.4 GBq/mmol, Amersham Biosciences), and unlabelled aspartate of the desired concentration was added to the transporter systems at 4°C. Samples were removed after 20, 60, 120, and 240 s, transferred to 4 mL of ice-cold buffer, filtered on glass fiber filters, and washed twice with 4 mL of buffer. Radioactivity was determined by liquid scintillation spectrometry. Endogenous uptake activity of yeast transformed with empty vector pFL61 was subtracted as background activity. Transport measurements were performed on media lacking uracil supplemented with 0.5 g/liter ammonium sulfate. Growth assays were performed on media without uracil supplemented with 0.5 g/liter ammonium sulfate. Growth assays were performed on media lacking uracil supplemented with 0.5 g/liter ammonium sulfate. Growth assays were performed on media lacking uracil supplemented with 0.5 g/liter ammonium sulfate. Growth assays were performed on media lacking uracil supplemented with 0.5 g/liter ammonium sulfate. Growth assays were performed on media lacking uracil supplemented with 0.5 g/liter ammonium sulfate. Growth assays were performed on media lacking uracil supplemented with 0.5 g/liter ammonium sulfate.
mments were repeated independently and represent the mean of six experiments. Competition experiments were performed with a concentration of 450 μM aspartate and a 10-fold excess of respective amino acids according to Fischer et al. (22).

RESULTS

Cloning of AAP7 and -8—Data base searches revealed that the Arabidopsis genome contains eight members of the AAP family. To obtain the full complement of all eight genes from Arabidopsis, the remaining two cDNAs of AAP7 and AAP8 were cloned by RT-PCR. The identity of the PCR fragments was verified by sequencing and database comparison with the annotated sequence (accession numbers AtAAP8, AAC34329; AtAAP7, BAB10054). The cDNAs code for proteins with 476 (AAP8) and 467 amino acids (AAP7), with a molecular mass of 52 kDa and 51.7 kDa, respectively. The closest homologs of AAP8 are AAP1 with 75% identity and AAP6 with about 70% identity on protein level, whereas AAP7 is the most distant member in this group (Table I, Fig. 1). AAP1, -6 and -8 form one of the three branches in the phylogenetic tree of the eight AAPs (Fig. 1). Using transmembrane prediction programs (THMM; www.CBS.dk) the proteins are likely to have 9–10 transmembrane domains with the N terminus predicted to be cytosolic and the C terminus predicted to be outside (Fig. 2D, AAP8).

The overall predicted structure is in agreement with the biochemical characterization of the topology of AAP1/NAT2 (37) and predictions for other AAPs (25). The genomic sequence of AAP8 contains six exons and five introns, an exon-intron structure very similar to that of AAP1 (Fig. 2A). AAP6 also contains five introns in the coding sequence, but the location of the introns is different to AAP1 and AAP8. AAP7 contains seven exons and six introns and is located on chromosome 5. AAP1 and AAP8 are both located on chromosome I in duplicated regions (Fig. 2C). To analyze whether potential duplication of AAP1 and AAP8 points to a redundant function, biochemical properties and expression pattern of AAP7 and AAP8 were analyzed and compared with related proteins.

Functional Characterization of AAP7 and -8 in Comparison to Related Transporters—The yeast mutant 22Δ8AA lacking eight amino acid transport systems was transformed with the cDNAs of AAP7 and -8 subcloned in the yeast expression vector pFL61 (32). Yeast transformed with empty vector (C1) was used as control. 22Δ8AA is unable to utilize arginine, aspartate, citrulline, γ-aminobutyric acid, glutamate, or proline as sole nitrogen sources. AAP1 and AAP6 in pFL61 were used for comparison since they are most closely related to AAP8 on protein level. AAP5 was included due to the higher affinity toward basic amino acids (14). On media containing 1 and 3 mM aspartate, citrulline, glutamate, or proline as sole nitrogen sources, AAP1 and AAP6 were able to grow, except AAP7 (Fig. 3). Cells transformed with the control plasmids (C1) grew only on 6 mM aspartate, glutamate, and arginine containing media. AAP7 was nonfunctional, whereas yeast cells expressing AAP8 mediated high capacity transport of the respective amino acids. On media with aspartate as a sole nitrogen source only yeast transformed with AAP8 and AAP6 showed significant growth. Within 4 days, neither of the AAPs mediated sufficient aspartate transport to enable growth on 1 mM aspartate; however, after 4 days, AAP8-expressing cells formed small colonies. After 7 days of growth on 1 mM aspartate, cells transformed with AAP6 also formed small colonies, whereas on 3 mM aspartate only cells expressing AAP8 and -6 could grow.

Direct L-[14C] aspartate uptake was determined at a 10-fold excess of all proteinogenic amino acids. Strongest competitors for aspartate uptake were proline, alanine, and methionine.

| TABLE I |
| Positives (%) and identities (%) and positives (%) based on BLOSUM62 matrix (55) on protein level between the eight members of the Arabidopsis AAP family |
| AAP1 | AAP2 | AAP3 | AAP4 | AAP5 | AAP6 | AAP7 | AAP8 |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Identity (%) | 72 | 70 | 70 | 70 | 70 | 70 | 70 |
| Positives (%) | 65 | 65 | 65 | 65 | 65 | 65 | 65 |

FIG. 1. Computer-aided analysis of the homologies between AAPs. Maximum parsimony analyses were performed using PAUP 4.0b10 (54) with all DNA characters unweighted and gaps scored as missing characters. Heuristic tree searches were executed using 100 random sequence additions and the tree bisection-reconnection branch-swapping algorithm with random sequence analysis. The complete alignment was based on 389 sites; 180 were phylogenetically informative. Percentage bootstrap values of 1000 replicates are given at each branch point. Branch lengths (drawn in the horizontal dimension only) are proportional to phylogenetic distance. The length of vertical lines has no meaning and was adjusted arbitrarily for ease of terminus labeling. The AAP homologs can be divided in three different clusters (shadowed areas). Sequences of AAP1–8 (19, 21, 22, AAP8: AAC34329, AtAAP7: BAB10054). The putative auxin carrier AUX1 (20) was used as an out-group.
In principal most amino acids were good competitors with the exception of the basic amino acids arginine, histidine, and lysine. The selectivity of the competition experiments is in agreement with previous studies showing that the basic amino acids are recognized only by AAP3 and AAP5 in in vivo competition experiments (14). Thus AAP8 can be classified as a general amino acid permease and, when expressed in yeast, mediates a higher transport capacity for aspartate as compared with the other AAPs.

AAP7 is the most distantly related member of the AAP family, a group of well characterized amino acid transporters within the ATF1 superfamily (25). However AAP7 did not mediate growth on aspartate, glutamate, proline, arginine, or citrulline (Fig. 3). The inability to complement any of the mutant phenotypes may be due to poor targeting to the yeast plasma membrane, an altered substrate spectrum as in the case of the related putative auxin transporter AUX1 (38), or lost functionality. In addition expression was not detectable on

Fig. 2. In silico analysis of AAP8, -7, -6, and -1. A, comparison of the exon-intron structure of AAP1, AAP6, AAP7, and AAP8 (exons black, introns white). Number below the sequence indicate the start of the intron, numbers above the length of the intron. B, promoter analysis of the 2.5-kb promoter from AAP8 used for GUS fusion. ARF-1 Motif tgtctc, SEF1 atattta, CAT repeat CATCAATACATCAT, napin motif TACACAT; not depicted are two ABI5 embryo-specific binding sites at –145 and –122: ACANNGC. C, relative position of AAP1, -6, -7, and -8 on the chromosomes. The duplicated region on chromosome I harbors the sequence of AAP1 and AAP8. D, prediction of the transmembrane domains of AAP8 using prediction programs (www.cbs.dtu.dk/services/TMHMM)
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Fig. 3. Complementation of yeast mutants by new AAPs. Comparison of the growth of the mutant strain 22Δ8AA mediated by AAP8 and -7 on different amino acids and citrulline as sole nitrogen sources compared with characterized AAPs (1, 5, and 6). Yeast transformed with the empty vector (C1) served as control. Concentrations were varied from 1 to 6 mM. The most striking difference was the growth of AAP6 on 1 mM aspartate observed after 6 days. Yeast transformed with AAP6 started to form small colonies. On 3 mM aspartate only AAP6 and AAP 8 mediated growth. 6 mM asp, glu, and arg as nitrogen source were not selective since the controls could grow. Growth on citrulline was in general slower than on other N sources and therefore documented after 9 days.

RNA gel blots and with promoter GUS studies so far.

Comparison of the Aspartate Transport Capabilities of AAP1, -6, and -8—So far AAP6 was the transporter with the highest Vmax value for aspartate. Screenings for a transporter specific for acidic amino acids by heterologous complementation of a glutamate- and aspartate-deficient yeast strain with an expression cDNA library from Arabidopsis resulted only in the identification of AAP6 (14). For direct comparability, the kinetic properties of AAP1, AAP6, and AAP8 were determined in uptake experiments (Fig. 5). The Km value of AAP 8 for aspartate was 444 μM, for AAP1 774 μM, and for AAP6 248 μM. The Vmax of AAP8 was 1.7 nmol of asp−1 · mg of protein−1 and about 6-fold higher than the value obtained for AAP6 (0.342 nmol of asp−1 · mg of protein−1). Among the previously analyzed AAPs, AAP6 had the highest affinity for aspartate when determined in oocytes (1.6 mM) (14) which is consistent with the yeast uptake experiments. The Km values obtained from the yeast uptake experiments differ form the values obtained in oocytes (14). Electrophysiological data showed that apparent affinities for amino acids were sensitive to pH changes and the net charge of the substrate. Nevertheless AAP8 has a Ks value for aspartate in between AAP6 and AAP1 and the highest Vmax when compared in the same heterologous system. The better growth in the yeast experiments can be explained by the higher transport capacity. AAP1, the closest homologue to AAP8, had the lowest affinity for aspartate with a Ks value of 774 μM in agreement with the yeast growth assays.

Promoter Analysis and Expression Pattern of AAP8—The genomic sequence corresponding to 2.5 kb upstream of the ATG of AAP8 was analyzed in silico for cis-acting regulatory elements using the PLACE data base (plant cis-acting regulatory elements) (39). Two potential TATA boxes were identified 106 and 164 bases upstream of the ATG (Fig 2B). A motif (napin motif TACACAT) responsible for specific binding of a protein extracted from developing Brassica napus seeds was found at position −218 (40). Repeated CAT elements were found around −480 bp, and a SEF1 element (Soybean embryo factor 1) is located around −790 bp. SEF1 is a binding motif found in soybean 7S globulin storage protein at position −640 and −765 (41). Using the same data base, napin and SEF1 motifs were also found in the promoter of AAP1 (napin motif 301 bp upstream ATG, SEF1 607 bp upstream ATG), but not in promoter regions of other AAPs. This finding is consistent with the AAP1 promoter activity in developing seeds of Arabidopsis (11). Motifs involved in binding the bZIP transcription factor ABI5 (ACAAAG, −145 and ACATCG, −122) are also present in the 5′-region. ABI5 is a transcription factor involved in ABA response and embryogenesis (42, 43). A single core motif found in several AuxRE (auxin response elements) binding sites (TGTCCT) was found at position −918 (44). Altogether the promoter carries regulatory elements that may be indicative for expression in developing seeds.

Expression of AAP8 in Seeds and Veins of Siliques—Using RNA gel blot analysis with RNA from all organs no expression of AAP8 was detectable (data not shown), although the cDNA of AAP8 had been isolated from root material. Since promoter GUS analysis is much more sensitive and gives additional information of tissue specificity, the 2.5-kb region upstream of the ATG was isolated, and a translational fusion to the uidA gene was created. Young transgenic seedlings were subjected to different N sources, N-starvation, high light, low light, drought stress, salt stress, and wounding. Under none of these conditions was expression of GUS visible in seedlings. Therefore plants were analyzed systematically, and all organs of various
developmental stages were screened for GUS activity. First positive results were obtained from flower buds (Fig. 6A) and young seeds 2–4 days after pollination. At heart stage of embryo development only seeds were stained in the silique (Fig. 6B; stages according to Ref. 45). Higher magnification showed that also funiculi were stained (Fig. 6C). In older siliques staining was visible in vascular tissue, whereas seeds were no longer stained (Fig. 6D–E). At the same stage (7–9 days after pollination) also the vascular tissue of stems showed staining (Fig. 6F). In old siliques (>10 days after pollination) GUS activity was no longer detectable (Fig. 6G). In a few lines very week staining of the root was also visible (data not shown). Intensive staining was visible at the base of flowers and at early stages of siliques development, indicating transport, potentially for amino acid cycling.

In tobacco plants transformed with the promoter uidA construct GUS activity was strictly limited to the reproductive organs. Expression was found in ovules and ovary (Fig. 7, A and B).

Expression of AAP6 in Xylem Parenchyma and Root Branching Areas—AAP6 is the only transporter with low \( K_m \) values for most acidic and neutral amino acids and is regarded as a general high affinity transporter (14). Therefore AAP6 would be a good candidate for expression at sites with low amino acid concentrations. Using RNA gel blot analysis expression of AAP6 was found mainly in roots, sink leaves, and cauline leaves, and to a lower extent in stem, flower, and source leaves (23). Leaf expression is inversely regulated during sink source transition as compared with AAP4 and sucrose transporter SUT1 (22, 46). To localize the cell types that express AAP6, promoter GUS studies were performed. In seedlings, GUS staining was detected in the vasculature of leaves, including

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**Fig. 5.** Determination of the \( K_m \) values of AAP1, AAP6, and AAP8 for aspartate in yeast. Linear uptake rates of radioactive aspartate were determined in six repeats with concentrations from 1 \( \mu \)M to 10 mM. The calculated \( K_m \) value of AAP1 is about 774 \( \mu \)M, for AAP8 444 \( \mu \)M, and for AAP 6 248 \( \mu \)M. \( V_{max} \) is 1.7 nmol asp · mg of prot\(^{-1} \) for AAP8, 0.6 for AAP1, and 0.342 for AAP6.

**Fig. 6.** GUS expression pattern under control of the AAP8 promoter in buds, developing seeds, and siliques of Arabidopsis. A, GUS-staining in the veins of young flowers and peduncle. B, staining of seeds 2–4 days after pollination. C, higher magnification of the seeds from B. D, GUS expression in the veins of siliques 7–9 days after pollination. E, siliques were opened to assure that seeds were not stained. F, stem of siliques from picture G. Overview of the expression in the various stages from buds to siliques. In siliques 10 days after pollination no more staining was detectable.
minor veins and around hydathodes (Fig. 8, A and F). In roots staining was preferentially in areas around lateral root initiation (Fig. 8B). Cross-sections of petioles showed intensive staining around the xylem, but no staining in the phloem (Fig. 8C). Higher resolution revealed that only cells directly neighboring the xylem vessels, i.e. xylem parenchyma, were stained (Fig. 8D). Since all AAPs are described as proton symporters AAP6 must be involved in the uptake of amino acids diffusing out of the xylem tracheids into the xylem parenchyma. Expression was also found in veins of sepals. The staining in leaves was found in 40 transformed of 44 plants, and six lines stained for root GUS activity were all positive.
DISCUSSION

Specific Expression of AAPs—The Arabidopsis genome contains in excess of 53 different putative amino acid transporter genes with eight members in the AAP family alone (25, 47). All AAPs display a low selectivity regarding amino acid side chains (14, 22). This raised the question why so many transporters are present in the plant and whether transporters are redundant. Bioinformatic analysis showed that AAP1 and AAP8 are both located in a duplicated region, potentially suggesting redundancy. The similarity of the exon-intron structures of AAP1 and AAP8 further supported the hypothesis of gene duplication during evolution. However redundancy does not seem very probable, considering that the intron sequences are not conserved, whereas the coding regions share 70% similarity. An alternative explanation might therefore be that the proteins are required for specific functions and thus have different properties. Differential regulation in specific cell types would be necessary for this specificity. RNA gel blot analysis had shown that six of the AAPs display different organ specificity (22, 23). However according to this crude analysis, expression patterns were overlapping in several cases, e.g. AAP1 and -2 are both highly expressed in siliques. Siliques are composed of multiple cell types comprising maternal and filial tissues and especially the seeds with endosperm and embryo. Promoter GUS analysis showed that AAP2 expression is restricted to the vascular system of the siliques, whereas AAP1 expression was exclusively found in the seeds. In addition AAP2 is expressed in major veins of leaves and the veins of stems of mature plants. AAP8 completes with its properties the spectrum of amino acids not transported by the other AAPs expressed in seeds and siliques.

As the AAPs have been characterized as proton symporters, energization by H+/ATPases is required (28, 29). The expression of AAP1, AAP2, and AAP8 correlates with the expression pattern of two H+/ATPase genes AHA10 and AHA3, which are expressed in seeds and in vascular tissue respectively (51, 52). Under the assumption that the AAPs do not work in the reverse direction, effectors have to be proposed that have yet to be identified. These proteins might represent a different class of proteins potentially belonging to the ABC transporter family (53). Strong GUS staining at the peduncle was also found for the other amino acid transporters expressed in siliques (11) and it would be interesting to examine whether this specific area marks a control point for the supply of amino acids to the siliques.

Taken together, specificity and timing of the expression of AAP8 indicates a role in supplying seeds with organic nitrogen. AAP8 has significant different biochemical properties and expression profile compared with other AAPs. AAP6 was localized to xylem parenchyma cells, being the first amino acid expressed in this cell type. With such biochemical properties and expression pattern, this transporter supports the hypothesis of a xylem to phloem transfer of amino acids. The number of transported substrates and the complexity of development explains the number of related transport genes found in the Arabidopsis genome. The variations in affinities towards substrates and individual expression patterns like AAP8 and APP6 within the AAP family rather points to a finely tuned network of collaborating genes rather than to simple redundancy or duplication.

REFERENCES

1. Jeschke, W. D., Wolf, O., and Patz, J. S. (1990) in Recent Advances in Phloem Transport and Assimilate Compartmentation (Bonnemain, J. L., Delrot, S., Lucas, W. J., and Dainty, J., eds) Ouest Editions, Nantes, France
2. Schobert, C., and Komor, E. (1990) Planta 181, 85–90
3. McNeil, D. L., Atkins, C. A., and Patz, J. S. (1979) Plant Physiol. 63, 1076–1081
4. Van Bel, A. J. E., and van der Schoot, C. (1980) Plant Sci. Lett. 19, 101–107
5. Patz, J. S., Sharkey, P. J., and Lewis, O. A. M. (1975) Planta 114, 11–26
6. Maathuis, F. J., Ishida, A. M., Sanders, D., and Schroeder, J. J. (1997) Plant Physiol. 114, 1141–1149
7. Lam, H. M., Coschigano, K., Schultz, C., Melo-Oliveira, B., Tijaden, G., Oliver, I., Ngai, N., Hsieh, M. H., and Coruzzi, G. (1995) Plant Cell 7, 887–898
8. Atkins, C. A. (1999) Aust. J. Plant Physiol. 27, 531–537
9. Hayashi, H., Okada, Y., Mano, H., Kume, R., Matsuhashi, S., Ishioka, N. S., Uchida, H., and Chino, M. (1997) Plant Sci. 122, 11–26
10. Patz, J. S., Sharkey, P. J., and Atkins, C. A. (1975) Planta 114, 1076–1077
11. Hirner, B., Fischer, W. N., Rentzsch, D., Kwart, M., and Fronner, W. B. (1998) Plant J. 14, 535–544
12. Miranda, M., Borisjuk, L., Tewea, A., Heim, U., Sauer, N., Wobus, U., and...
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