Identification, Cloning, and Properties of Cytosolic d-Ribulose-5-phosphate 3-Epimerase from Higher Plants*

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Stanislav Kopriva‡, Anna Koprivova§, and Karl-Heinz Süß¶

From the Institute of Plant Physiology, Altenbergrain 21, 3013 Bern, Switzerland and the ¶ Institute of Plant Genetics and Crop Plant Research, Corrensstrasse 3, 06466 Gatersleben, Germany

Plant cells contain a complete oxidative pentose phosphate pathway in the chloroplasts, but an incomplete pathway was proposed to be present in the cytosol, with cytosolic (cyt) isoforms of ribulose-5-phosphate 3-epimerase (RPEase) and other non-oxidative branch enzymes being undetectable. Here we present for the first time the identification, cloning, and properties of a cyt-RPEase in rice (Oryza sativa) and presence of its homologues in other plant species. Recombinant cyt-RPEase is a homodimer of 24.3-kDa subunits such as in the case of the animal and yeast enzymes, whereas the chloroplast (chl) RPEase is a hexamer. Cytosolic and chloroplasmatic RPEases cannot be separated by anion exchange chromatography. Since plant cyt-RPEase is more closely related in its primary structure to homologous enzymes in animal and yeast cells than to the chloroplast RPEase, the plant nuclear genes coding for cytosolic and chloroplast RPEases were most likely derived from eubacteria and cyanobacteria, respectively. Accumulation of cyt-RPEase-mRNA and protein is high in root cells, lacking chl-RPEase, and lower in green tissue. These and other observations support the view that green and non-green plant cells possess a complete oxidative pentose phosphate pathway in the cytosol.

The oxidative pentose phosphate pathway (OPPP) fulfills an essential role in intermediate carbohydrate metabolism of prokaryotic and eukaryotic cells. Through breakdown of sugars in its oxidative branch, the OPPP generates reductant (NADPH) for fatty acid and amino acid synthesis. Enzymes of the reversible, non-oxidative branch of this pathway provide erythrose 4-phosphate for the shikimate pathway, the products of which are used for the synthesis of aromatic amino acids, flavonoids, and lignin, and ribose 5-phosphate for nucleic acid synthesis. The OPPP in the cytosol of yeast cells is vital for oxidative stress defense through supply of NADPH for the glutathione reductase (1, 2). The chloroplast (chl) OPPP enzymebiculate-5-phosphate 3-epimerase (RPEase, EC 5.1.3.1) was found to be critically involved in the early development of nematode feeding plant cells (3).

Since OPPP enzymes in animal and yeast cells are located exclusively in the cytosol, some textbooks propose an analogous location of this pathway in plant cells (4–6). Reportedly, however, several essential OPPP enzymes could not be detected in the cytosol of plant leaf cells (7, 8). On the other hand, chloroplasts and chromoplasts contain the components for a complete OPPP (9, 10). Recently, nuclear-encoded genes for chloroplast enzymes with dual (amphibolic) function in the OPPP and reductive pentose phosphate cycle (Calvin cycle) have been cloned and characterized including transketolase (11–13), ribose-5-phosphate isomerase (14), and RPEase (13, 15–17).

Relatively little is known about the occurrence, structure, and biochemistry of plant cytosolic (cyt) OPPP enzymes. Although cytosolic glucose-6-phosphate dehydrogenase and 6-phosphogluconate dehydrogenase have been isolated from green and non-green plant tissue (6, 18), cytosolic isoforms of the non-oxidative branch OPPP enzymes transketolase, ribose-5-phosphate isomerase, and RPEase were undetectable in plant cell extracts by combined cell fractionation and enzyme chromatography experiments (7, 8). Disregarding the possibility that cytosolic enzymes may have escaped from detection due to chromatographic properties similar to the chloroplast homologues, it has been proposed that spinach leaf cells contain a complete and incomplete OPPP in their chloroplasts and cytosol, respectively (8).

To further address the important biochemical problem whether plant cells contain complete OPPP both inside and outside of their chloroplasts, we have attempted to identify and characterize non-chloroplastic enzymes of the non-oxidative branch of the OPPP. Cloning of chloroplast RPEase genes from potato and spinach (15, 16) opened up the way to search enzyme homologues. Here we report on the identification and cloning of a cyt-RPEase from rice, its heterologous and tissue-specific expression, properties, presence of homologues in other plant species, and its possible evolutionary origin.

EXPERIMENTAL PROCEDURES

Materials—The cDNA clones encoding chloroplast RPEase-related proteins in rice were obtained from the MAFF DNA Bank, Tsukuba, Japan. Materials and vendors were as follows: transketolase, triosephosphate isomerase, glycerophosphate dehydrogenase, d-ribose 5-phosphate, d-ribulose 5-phosphate, phenylmethylsulfonyl fluoride, lactate dehydrogenase, ATP, and NADH, Sigma; Bio-Spin columns, Bio-Rad; EcoRI, HindIII, and SacI restriction endonucleases, Roche Molecular Biochemicals. Oligonucleotide primers for polymerase chain reaction were synthetized by Microsynth GmbH, Balgach, Switzerland. The antisera against recombinant cytosolic RPEase were produced in Inselspital, Bern, Switzerland.

Identification and Analysis of RPEase Sequences—The GenBank and
EMBL sequence data bases were screened with the BLAST software for sequences related to the chloroplast RPEase from potato (15). The sequences found were further analyzed by the PCGENE package (Intelligenetics). The cDNA clone encoding a putative cytotic RPEase in rice, corresponding to GenBank accession number D41947, has been obtained from the MAFF DNA Bank, Tsukuba, Japan, and completely sequenced on both strands. The phylogenetic analysis of gene sequences was performed with the Treecon program (19). A RPEase tree was constructed by the neighbor-joining method (20) using the Dayhoff matrix and the statistical significance of the branches has been tested by bootstrap analysis with 100 replicates (21).

DNA and RNA Analysis—RNA was isolated from leaves, roots, and seedlings of rice by phenol extraction and LiCl precipitation. DNA was isolated from young leaves by phenol extraction and ethanol precipitation. Southern analysis of genomic DNA from Arabidopsis thaliana, Zea mays, and Oryza sativa and Northern blotting of the RNA isolated from rice tissues was performed as described (22). The blots were hybridized either with 32P-labeled total cDNA of rice cyt-RPEase or chloroplast RPEase from Solanum tuberosum (15).

Cloning and Heterologous Expression of Rice Cytotoxic and Chloroplast RPEase—The two RPEase isoforms were expressed in Escherichia coli using the pET expression system (Novagen). The rice cyt-RPEase and potato chl-RPEase (15) coding regions were cloned into pET3a and pET14b plasmids, the latter ensuring the addition of a 6-histidine tag at the N-terminus of the expressed protein. To determine the extent of heterologous expression of recombinant RPEases in bacteria, RPEase activity measurements in extracts of bacteria carrying different expression constructs were performed. Cell-free extracts were prepared from overnight cultures of bacteria by sonication in phosphate-buffered saline prior to centrifugation at 20,000 × g for 10 min.

Purification of Recombinant Cytotic and Chloroplast RPEase—Enzyme purification was performed at 4 °C, and all buffers were at pH 7.5. Cell paste (20 g) from 10 liters of culture was resuspended in 200 ml of a buffer containing 25 mM Tricine-NaOH, pH 7.5, 1 mM EDTA, 10 mM NaCl, 0.01 mM phenylmethylsulfonyl fluoride, 10% glycerol, and 10 mM L-arginine. The slurry was sonicated for 20 min with intervals and ultracentrifuged at 20,000 × g for 20 min. The supernatant was fractionated by addition of ammonium sulfate. The cyt-RPEase precipitated between 40 and 60% saturation of ammonium sulfate, whereas the chl-RPEase precipitated between 50 and 80% saturation of the salt. Protein was collected by centrifugation, desalted, and concentrated (Centricle-30, Amicon). Protein solution was applied to a Mono-Q column (5/10) adapted to a fast protein liquid chromatography unit (Amersham Pharmacia Biotech) which was pre-equilibrated with the column (5/10) adapted to a fast protein liquid chromatography unit (Centriprep-30, Amicon). Protein was only 40% identical in its primary structure with the rice and potato chl-RPEase, but possessed 52% identical residues with the cyt-RPEases from yeast (24) and human (reconstructed from EST sequences R82828, R53190, AA455653, AA373190, and AA380177) (Fig. 1). Notably, human cyt-RPEase and rice chl-RPEase share only 36% identical residues. Moreover, there are only 27–35% identical amino acid positions in the primary structure of the novel rice RPEase and three homologous enzymes in E. coli (25, 26). The novel RPEase isoform from rice lacked a chloroplast targeting sequence indicating its localization in the cytosol.

The EMBL data base was further searched for EST entries with high similarity to the novel rice RPEase. EST sequences from A. thaliana (T75815), poplar, and pine were retrieved that were 64 and 77% identical in their nucleotide and deduced amino acid sequence to the novel rice RPEase, respectively. The same sequences, however, shared only 49 and 36% identical nucleotide and amino acid residues with the chl-RPEases from rice, potato, and A. thaliana. Remarkably, the 5′-nontranslated region of the poplar EST clone (A061P33U) consists of 67 base pairs and possesses an in-frame stop codon upstream of the initial ATG codon indicating that it encodes a cytotic rather than chloroplast enzyme. Accordingly, the homologous cDNA clones from rice, A. thaliana, and pine appear to code for non-chloroplast RPEases as well.

Southern blot analysis was performed to determine the number of genes coding for the novel RPEase in rice, maize, and A. thaliana (Figs. 2, A and B). The analysis revealed 1–2 genes encoding this enzyme in the nuclear genome of these species, while only a single copy gene coding for chl-RPEase was detected in rice (Fig. 2A). The latter finding corresponds with a previous report indicating that the spinach and Arabidopsis nuclear genomes contain a single copy gene for chl-RPEase (3, 16). These results indicate an ubiquitous distribution of the gene coding for putative cyt-RPEase in higher plants.

Phylogenetic Relationship of Plant RPEases—A phylogenetic analysis was performed to investigate the evolutionary relationships between the known RPEase genes. RPEase se-
quences from 22 organisms were available at the time of this work. Three different RPEase related genes were found in *E. coli*. However, since disruption of the *rpe* gene in the *dam* operon led to an impaired growth on minimal media, only the *rpe* gene was considered to be functional (25). Therefore the other *E. coli* RPEase-related genes were used as outgroups in the phylogenetic analysis. The analysis clearly revealed the existence of two different groups of RPEase genes in plants (Fig. 3). Chloroplast RPEase of rice and other plant species are clustered and closely related to the cyanobacterial homologue from *Synechocystis*. Therefore, the nuclear gene encoding chl-RPEase was most likely acquired from the chloroplast ancestor and allocated to the plant nuclear genome through endosymbiotic gene transfer such as other genes coding for Calvin cycle enzymes (29). The other group of plant RPEases, however, is more closely related to the cytosolic enzyme homologues in yeast and animal cells than it is to any chl-RPEase. In striking analogy to the eubacterial origin of plant nuclear glyceraldehyde-3-phosphate dehydrogenase genes (30), this finding suggests that cyt-RPEase genes in the chimeric nuclear genomes originate from eubacteria and are not replaced by cyanobacterial homologues in the course of plant cell evolution. We predict, therefore, that algae also possess this RPEase gene.

Heterologous Expression and Properties of Cytosolic and Chloroplast RPEases—To compare the properties of the two types of plant RPEases, the cDNA clones coding for the cytosolic RPEase from rice was compared with the sequences of chloroplastic RPEase from spinach (*Spinach. Chl*), *Synechocystis* (*Synechoc.*), *E. coli*, yeast, and human. *Stars* and *dots* indicate identical and homologous amino acid residues, respectively. Amino acid residues identical in all 25 available RPEase sequences are marked with *double crosses*. The *arrow* indicates the cleavage site of the chloroplast targeting peptide of the spinach chl-RPEase precursor.

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2 Sources of RPEases compared in the phylogenetic analysis and GenBank accession numbers for their sequences are as follows: *Mus musculus*, AA162165, C88722; *Homo sapiens*, reconstructed from R98280, R53130, AA458563, AA373190, and AA380177; *Drosophila melanogaster*, U23145; *Caenorhabditis elegans*, U67515; and *Methanocaldococcus jannaschii*, U67515; and *Helicobacter pylori*, AA01566.

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**Fig. 1. Comparison of amino acid sequences of RPEases.** The amino acid sequence of cytosolic (*Rice Cyt.*) and chloroplastic (*Rice Chl.*) RPEase from rice was compared with the sequences of chloroplastic RPEase from spinach (*Spin. Chl.*), *Synechocystis* (*Synechoc.*), *E. coli*, yeast, and human. *Stars* and *dots* indicate identical and homologous amino acid residues, respectively. Amino acid residues identical in all 25 available RPEase sequences are marked with *double crosses*. The *arrow* indicates the cleavage site of the chloroplast targeting peptide of the spinach chl-RPEase precursor.

**Fig. 2. Southern blot analysis of genomic DNA.** *A*, the DNA from *rice* was cut with *EcoRI* (1 and 3) and *HindIII* (2 and 4) and hybridized with total cDNAs coding for plastidic (1 and 2) and cytosolic (3 and 4) RPEase. *B*, DNA from *Z. mays* (1–3) and *A. thaliana* (4–6) was cut with *EcoRI* (1 and 4), *HindIII* (2 and 5), and *SacI* (3 and 6) and hybridized with total cDNA encoding cytosolic RPEase from rice.

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**Fig. 2.** Southern blot analysis of genomic DNA. *A*, the DNA from rice was cut with *EcoRI* (1 and 3) and *HindIII* (2 and 4) and hybridized with total cDNAs coding for plastidic (1 and 2) and cytosolic (3 and 4) RPEase. *B*, DNA from *Z. mays* (1–3) and *A. thaliana* (4–6) was cut with *EcoRI* (1 and 4), *HindIII* (2 and 5), and *SacI* (3 and 6) and hybridized with total cDNA encoding cytosolic RPEase from rice.
solic enzyme in rice and chloroplast isofrom in potato (15) were overexpressed in E. coli with and without a N-terminal His-tag extension. Extracts of the E. coli transformed with the cDNA-containing vectors showed an about 6-fold higher RPEase activity than those from bacteria that had been transformed with pET14b alone (Table I). Cytosolic and chloroplast RPEases carrying the His-tag extensions were purified to homogeneity by affinity chromatography on Ni²⁺ columns and, alternatively, giving a higher yield, by fast protein liquid chromatography (8). A striking difference between both enzyme isoforms was the tendency of the cytosolic enzyme to rapidly form aggregates in the course of purification. However, enzyme aggregation could be efficiently prevented in the presence of L-arginine which also enabled growth of enzyme crystals suitable for high resolution x-ray crystallography (9). The His-tag extension apparently did not affect the activity of both types of RPEases in presence of L-arginine. No substantial differences were detected in the specific activity between freshly prepared recombinant cytosolic and chloroplast RPEases. At pH 8.0 and 25 °C, a Vmax for cytosolic and chloroplast RPEase of 16,000 and 16,500 units mg⁻¹, respectively, was determined. A similar activity value was reported for recombinant chloroplast RPEase from spinach (31). Gel permeation chromatography on a Sephadryl S-200 column in the presence of 0.2 M NaCl, in parallel with appropriate protein standards, yielded a Mr of 55,000 for the cyt-RPEase, indicating a homodimeric subunit structure. In contrast, the recombinant potato chloroplast enzyme had a Mr of 180,000 (17). X-ray crystallography demonstrated, however, that the potato chloroplast RPEase is actually a homohexamer of 148,696 Da rather than an octamer (17).  

**Tissue-specific Expression of Cytosolic and Chloroplast RPEases—**Northern blot analysis of RNA prepared from rice tissues was performed to investigate, whether cytosolic and plastidic RPEase forms are expressed in a tissue-specific manner. These experiments showed that cyt-RPEase transcript is predominantly accumulated in roots and seedlings, whereas only a small amount of mRNA was detectable in leaves (Fig. 4). In contrast, chloroplast RPEase transcript was mainly expressed in leaves, and present only in minute quantities in seedlings and roots. The same pattern of transcript expression has been previously observed in potato organs (15) and is consistent with the low accumulation of chloroplast RPEase transcript in roots of Arabidopsis thaliana (3). Western blotting of proteins prepared from the same rice tissues corroborated the results of RNA analysis for cyt-RPEase (Fig. 5), showing presence of this enzyme in all plant organs with maximum accumulation in root cells. Similar to the results of Teige et al. (15), chloroplast RPEase protein could not be detected in root tissue at all, although a low level of transcript was observed there. We also noted accumulation of a small amount of chloroplast RPEase in dark-grown seedlings even though the mRNA was hardly detectable by Northern blotting. This observation suggests that a post-transcriptional mechanism, but not light, is responsible for the tissue-specific accumulation of chloroplast RPEase. The reason why chloroplast transketolase, but not chloroplast RPEase, is accumulated at similar levels in roots and leaf mesophyll tissue (15), albeit carbon flux was observed to occur through the non-oxidative branch of OPPP in root proplastids (32), still remains to be elucidated.

**Subcellular Localization of RPEases—**Although the lack of a plastid-targeting sequence, a homodimeric subunit structure, and a higher sequence similarity with homologous cytosolic enzymes in animals and yeast as compared with chloroplast epimerase suggested the location of the novel plant RPEase in the cytosol, cell fractionation experiments combined with Western blotting were conducted to prove that conjecture.
The subcellular distribution of cyt-RPEase was investigated in root and leaf cells of which the subcellular fractions were obtained by differential centrifugation. Maize chloroplast and cyt-RPEases could be distinguished by Western blotting, because these enzymes are specifically cross-reacting with antibodies raised against the recombinant potato chl-RPEase and rice cyt-RPEase, respectively. Fig. 5 shows that cyt-RPEase was exclusively present in the cytosol fraction of both root and leaf cells. As expected, chl-RPEase was undetectable in the subcellular fractions of root cells. However, in leaf cells, chl-RPEase was detected both in the isolated chloroplasts and the cytosol fraction. The latter enzyme fraction most probably originated from the stroma of osmotically broken chloroplasts contaminating the cytosol. These results thus support the conclusion that the novel plant RPEase isoform is a cytosolic rather than chloroplast enzyme.

**DISCUSSION**

It has been proposed from combined cell fractionation and enzyme chromatography experiments that plant cells contain only an incomplete OPPP in the cytosol, because cytosolic isoforms of RPEase and other non-oxidative OPPP enzymes could not be detected (8). This work provides evidence for the presence of both cytosolic and chloroplast isoform of RPEase in rice and other plant species. The nuclear RPEase genes in rice could be divided into two groups due to their sequence similarity with chl-RPEase from potato and spinach. The rice chl-RPEase encoded by a single nuclear gene, as determined by Southern blotting, is 85% identical in the primary structure with homologous chloroplast enzymes from potato and spinach. The N-terminal amino acid residues 40–61 of the rice chl-RPEase precursor and the sequence determined from spinach chl-RPEase by N-terminal protein sequencing (13) are identical, thus indicating that the first 39 N-terminal amino acids encoded by the rice gene represent a chloroplast targeting peptide. The second group of identical ESTs in rice also codes for a RPEase, because the cDNA expressed in *E. coli* led to the formation of a single enzyme that catalyzed the conversion of ribulose 5-phosphate to xylulose 5-phosphate. That this RPEase isoform most probably represents a cytosolic enzyme is indicated by different observations: (i) the equivalent enzyme in maize is present in the cytosol of leaf and root cells, (ii) the primary structure of the enzyme is more similar to cyt-RPEases from animals and yeast cells as compared with chloroplast enzyme homologues, (iii) the novel rice RPEase gene does not encode a chloroplast-targeting peptide, and (iv) the recombinant rice RPEase expressed in *E. coli* is a homodimer such as cyt-RPEase from yeast and human cell (23, 33), whereas the chl-RPEases are homohexamers (17).

Hence, the function of amino acid residues from a high-resolution crystal structure of the wild-type and mutant chl-RPEases (17) as well as by site-directed mutagenesis (17, 34), it was interesting to analyze the conservation of these residues in the cytosolic and other RPEases. Only 17 amino acid residues are strictly conserved in all RPEases (Fig. 1), i.e. 7% of the 235 residues in spinach chl-RPEase. Among the invariant residues are Asp-43 and Asp-185 (sequence positions in mature spinach chl-RPEase), the two essential electrophiles catalyzing de- and reprotonation during pentose phosphate epimerization (17, 34), His-41, His-74, His-98, Asp-72, and Glu-100, which form two hydrogen bonding networks to enable de- and reprotonation of the catalytic aspartyl carboxylates, and Met-45, Met-76, and Met-147 positioned in the mobile loop at the top of the catalytic center (17). The evolutionary conservation of functionally essential residues not only indicates that all RPEases use the same mechanism of substrate conversion, but also indicates that the different genes coding for RPEases may be derived from the same ancestral gene. However, while the chloroplast enzyme is a hexamer, plant cyt-RPEase and homologue enzymes in animal and yeast cells (23, 33) have a dimeric subunit structure. This conclusion is supported by a crystal structure analysis of the cytosolic enzyme at high resolution. However, the reason for the different subunit structure of chloroplast and cytosolic RPEases in plants is not obvious at present, one explanation may be that networking of metabolic pathways by complementary binding interactions between sequential enzymes requires more complex RPEase structures in chloroplast than in the cytosol of heterotrophic prokaryotes and eukaryotes. The location of the dual functional (amphibolic) chloroplast enzymes RPEase and transketolase and Calvin cycle enzymes adjacent to thylakoid membranes (13, 35, 36) indicates that these catalysts are closely neighbored and may even form enzyme supercomplexes *in vivo* capable of catalyzing the oxidative and reductive pentose phosphate pathway. An analogous situation of OPPP enzymes, albeit interacting with enzyme systems other than in plastids, might exist in the cytosol of plant cells.

These results indicate that leaf mesophyll cells contain RPEase both in the cytosol and chloroplasts, whereas root cells apparently possess only cyt-RPEase, an enzyme active in the metabolically important non-oxidative branch of the OPPP. The gene coding for cyt-RPEase appears to be ubiquitously distributed in higher plants. Therefore, these observations cast doubts to a previous proposal (8) that leaf cells contain a complete OPPP in their chloroplasts and only an incomplete pathway in the cytosol due to the presence of glucose-6-phosphate dehydrogenase and 6-phosphogluconate dehydrogenase, but absence of enzymes active in the non-oxidative branch of this pathway. Although cyt-RPEase is not as abundant as its chloroplast counterpart in leaf cells, this does not disprove its potential metabolic importance. Although a search of DNA data bases did not provide evidence for cytosolic forms of transaldolase and ribose-5-phosphate isomerase, most likely due to the small number of data base entries, plants appear to possess cytosolic transketolase forms. A sequence comparison of the multiple transketolase genes in *Craterostigma plantagineum* (37) with the potato chloroplast enzyme (11) indicated that the cDNA clone tkt3 encodes a chloroplast enzyme form, whereas the clones tkt7 and tkt10 most likely coded for cyt-RPEases. It seems likely, therefore, that a complete OPPP operates both in chloroplasts and the cytosol of green plant cells as well as in the cytosol of non-green plant cells. The latter pathway is especially important biochemically, because root proplastids appear not to accumulate chloroplast RPEase, but root cells depend essentially on the use of sucrose supplied by leaf cells for the synthesis of proteins, nucleic acids, vitamins, and cell wall compounds.

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4 S. Jelakovic and K.-H. Süß, unpublished results.

5 S. Kopriva, unpublished results.
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