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LETTER TO THE EDITOR

# Evolutionary and functional aspects of C-to-U editing at position 28 of tRNA$^{Cys}$(GCA) in plant mitochondria

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In plant mitochondria, editing of messenger RNA by C-to-U conversions is essential for correct gene expression as it usually improves the protein-sequence conservation between different species or sometimes affects the reading frames (for a review, see Maier et al., 1996). Editing sites have been identified in mitochondrial (mt) RNA of all major groups of land plants, including Bryophytes, Pteridophytes, Prespermaphytes, and Spermaphytes (Hiesel et al., 1994a,b; Malek et al., 1996). Editing mainly affects messenger RNA, but editing sites have also been identified in three transfer RNAs. In dicot mitochondria a C-to-U editing event corrects a C:A mismatch into a U:A base pair in the acceptor stem of tRNA$^{Phe}$(GAA) (Maréchal-Drouard et al., 1993; Binder et al., 1994). In the gymnosperm *Larix leptoeuropaea*, three C-to-U conversions restore a U:A base pair in the acceptor stem, D stem, and anticodon stem of tRNA$^{His}$(GUG), respectively (Maréchal-Drouard et al., 1996b). The third example described is the *Oenothera berteriana* mt tRNA$^{Cys}$(GCA), where a $C_{28}$:$U_{42}$ mismatch is converted into a $U_{28}$:$U_{42}$ noncanonical base pair (Binder et al., 1994). In the case of both tRNA$^{Phe}$ and tRNA$^{His}$, editing of precursors is a prerequisite for 5′ and 3′ processing to generate a mature tRNA (Marchfelder et al., 1996; Maréchal-Drouard et al., 1996a, 1996b; Kunzmann et al., 1998). The role of editing in the case of tRNA$^{Cys}$ has not been studied so far, although it has been shown that it occurs at the precursor level (Binder et al., 1994). In this letter, we report an evolutionary and functional study of mt tRNA$^{Cys}$(GCA) editing in plant mitochondria.

The cloverleaf structure of the mt tRNA$^{Cys}$(GCA) deduced from the sequence of the single *Solanum tuberosum* mt *trnC* gene (EMBL Accession Number X93575) is identical to its counterpart in *O. berteriana* and reveals a weak anticodon stem with a $U_{27}$:$G_{43}$ noncanonical interaction, and a $C_{28}$:$U_{42}$ mismatch. By analyzing RT-PCR amplified cDNAs of *S. tuberosum* mt tRNA$^{Cys}$ precursors (362 nt in length), we found that 7 out of 11 independent clones contained a T at position 28. The ratio of edited versus nonedited mature tRNA$^{Cys}$ was determined by RT-mini-sequencing. When total *S. tuberosum* mt tRNAs were used as template, only dATP was incorporated, demonstrating that the mature tRNA$^{Cys}$ is fully edited in vivo (Fig. 1B).

From an evolutionary point of view, the comparison of the *S. tuberosum* mt *trnC* gene with its counterpart in *Marchantia polymorpha* shows in particular two differences in the anticodon stem (Fig. 1A). In *M. polymorpha*, an A residue at position 43 allows a $T_{27}$:$A_{43}$ base pairing, and a T residue is present at position 28. Considering that this sequence is more closely related to the ancestral sequence, we postulated that the C-to-U editing site found in dicot mitochondria restores this ancestral sequence. To confirm this hypothesis, we first tried to determine when, during the evolution of land plants, the mt *trnC* gene acquired a C at position 28 and when the C28-to-U28 editing event occurred. To do so, the internal sequence of *trnC* (from position 25 to 52) was PCR-amplified, cloned, and sequenced in several species that belong to different groups of land plants. A single difference could be observed in this region between the different plants tested: a T residue was present at position 28 of mt *trnC* in the Pteridophyte *Pteris nephrolepis* (Filicales order) and in the

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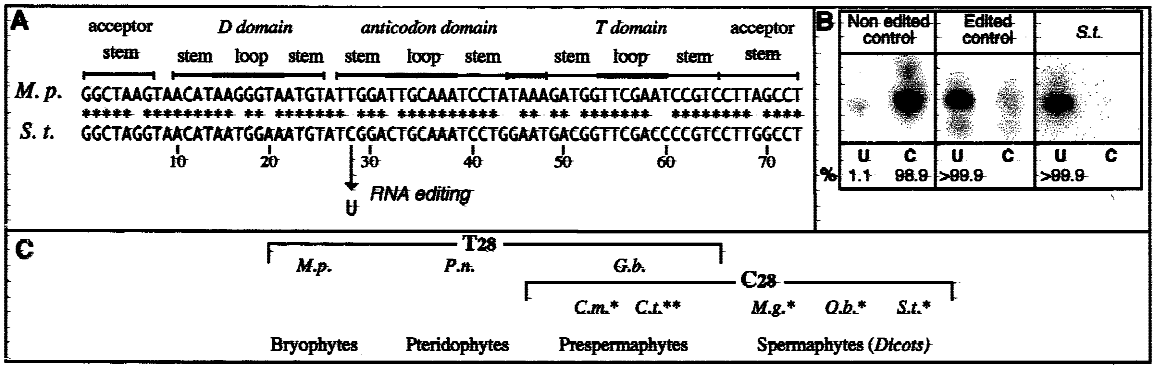


**FIGURE 1.** **A**: Alignment of the mt *trnC* sequence from *M. polymorpha* (*M.p.*) (EMBL Accession Number M68929) and *S. tuberosum* (*S.t.*). Asterisks correspond to conserved positions. **B**: RT-mini-sequencing of position 28 of *S. tuberosum* mt tRNA$^{Cys}$. In vitro-generated nonedited or edited transcripts were used in control experiments. U lanes correspond to incubations with [$\alpha$-$^{32}$P]dATP, and C lanes to incubations with [$\alpha$-$^{32}$P]dGTP. Signal intensities, quantified with the MacBas 2.2 software (Fuji), are indicated as a percentage of total signal. **C**: Nucleotide present at position 28 of mt *trnC* sequence in different plant species. *P.n.*: *P. nephrolepis*, *G.b.*: *G. biloba*, *C.m.*: *C. mexicana*, *C.t.*: *C. taiwanensis*, *M.g.*: *M. grandiflora*, *O.b.*: *O. berteriana* (EMBL Accession Number X76497). *: species where tRNA$^{Cys}$ is edited. **: species where editing was not investigated.

Prespermaphyte *Ginkgo biloba* (Ginkgoales order), whereas a C was found at the same position in the Prespermaphytes *Cycas taiwanensis* and *Ceratozamia mexicana* (Cycadales order), and in the Spermaphyte *Magnolia grandiflora* (Magnoliales order, Magnoliidae subclass) (Fig. 1C). In angiosperms, Magnoliidae represent the earliest dicot subclass from which other dicot subclasses and monocots were derived. Furthermore, our data suggest that Cycadales are more related to the Prespermaphyte ancestors of angiosperms than Ginkgoales, and that the mutation T28 to C28 was probably acquired within the group of Prespermaphytes. These data demonstrate the usefulness of molecular approaches with mt sequences to better define land-plant phylogeny (Hiesel et al., 1994b). Furthermore, using RT-mini-sequencing, a U was identified at position 28 of mt tRNA$^{Cys}$ of *M. grandiflora* (data not shown), showing that this editing event occurs in early angiosperms. Sequence analysis of cloned RT-PCR products obtained with total circularized tRNA from *C. mexicana* revealed the posttranscriptionally added 3′-CCA sequence at the circularization site and only T at position 28, demonstrating that mature tRNA$^{Cys}$ is fully edited in Cycadales. Taken together, these results show that a U28 was maintained in mt tRNA$^{Cys}$ during land-plant evolution, either at the genomic level or at the transcript level after C-to-U editing (Fig. 1C). This observation suggests that U28 is essential for the accumulation of functional tRNA$^{Cys}$.

Editing could be important for several steps of tRNA expression, including processing of precursors, base modifications, aminoacylation, and interactions with translation factors and ribosomes. In the two other examples of tRNA editing described so far in plant mitochondria, correction of C:A mismatches into classical U:A base pair is required for correct and efficient processing of tRNA precursors. Here we show that maturation of *S. tuberosum* mt tRNA$^{Cys}$ precursors into tRNA-sized molecules was obtained similarly with nonedited and edited precursors in the presence of a *S. tuberosum* mt processing extract (Fig. 2A). However, it should be noted that only partial processing of the tRNA$^{Cys}$ precursors was observed, as compared to the efficient processing of larch mt tRNA$^{His}$ precursors (Maréchal-Drouard et al., 1996b) obtained with the same processing extract (data not shown). The possible role of C28-to-U28 editing was also examined in another tRNA-processing step, posttranscriptional 3′-CCA addition. When incubated in the presence of a *S. tuberosum* mt enzymatic extract containing CCase activity, the CCA end was efficiently and correctly added to both nonedited and edited tRNA$^{Cys}$ transcripts lacking the 3′-CCA end (Fig. 2B), showing that a U at position 28 is not required for addition of 3′-CCA. As editing does not affect processing of tRNA$^{Cys}$, we looked for a possible implication of this U28 residue in the aminoacylation reaction. When aminoacylation of in vitro synthesized tRNA$^{Cys}$ transcripts containing either C28 or U28 was compared, no significant difference was observed (Fig. 2C). Furthermore, cysteinylation of nonedited tRNA$^{Cys}$ transcript with [$^{35}$S] cysteine in the presence of mixes of cold competitor *L*-amino acids in equimolar concentration did not differ significantly from the control with only cysteine (data not shown), indicating that the C28-containing form of tRNA$^{Cys}$ is not mischarged, and that editing is not necessary to prevent misaminoacylation. All together, these data suggest that the nonedited tRNA$^{Cys}$, although it was never found in vivo, could be correctly processed and recognized by the cysteinyl-tRNA synthetase with the same efficiency as the edited form. However, as their ability to interact with translation factors and ribosomes was

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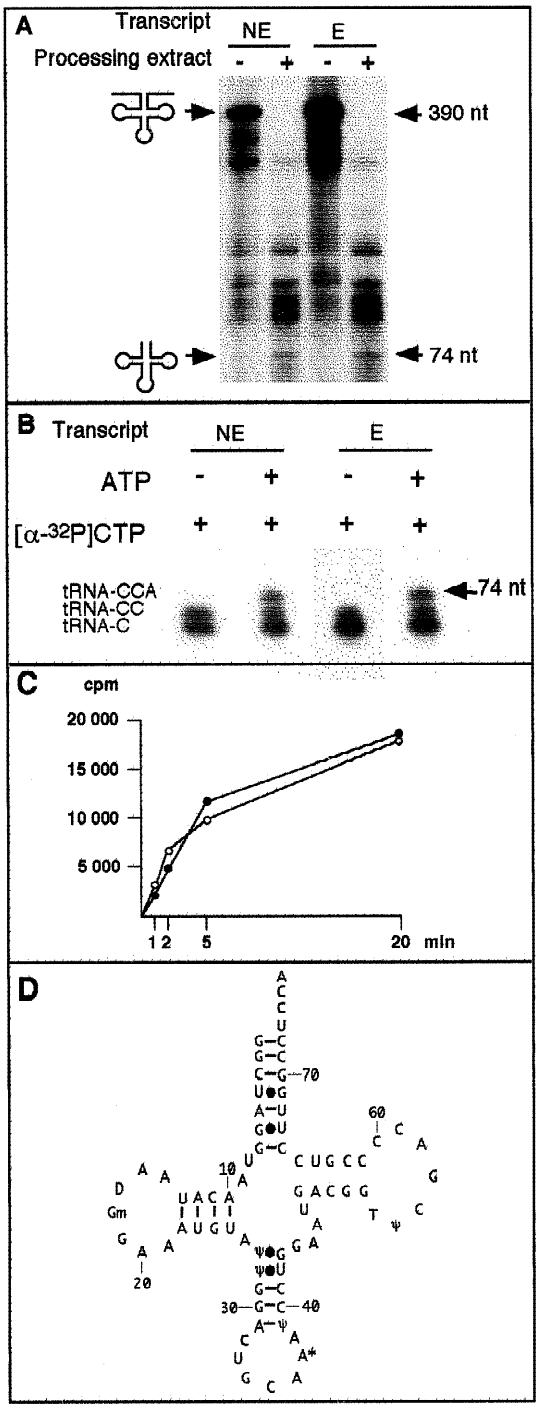


**FIGURE 2.** **A**: In vitro processing of the nonedited (NE) or the edited (E) precursor forms of *S. tuberosum* mt tRNA$^{Cys}$ in the absence (−) or presence (+) of the *S. tuberosum* mt processing extract. **B**: Addition of the CCA sequence at the 3′ end of nonedited (NE) or edited (E) forms of CCA-lacking *S. tuberosum* mt tRNA$^{Cys}$ in the absence (−) or presence (+) of cold ATP. Migration of the in vitro-synthesized mature-size *S. tuberosum* mt tRNA$^{Cys}$ (74 nt including 3′-CCA) is indicated by an arrowhead. **C**: Aminoacylation kinetics of in vitro-synthesized *S. tuberosum* nonedited (open dots) or edited (black dots) mt tRNA$^{Cys}$ in the presence of a saturating amount of an *S. tuberosum* mt enzymatic extract and in the presence of *L*-[$^{35}$S]cysteine. **D**: Secondary structure of *S. tuberosum* mt tRNA$^{Cys}$(GCA) deduced from direct tRNA sequencing (EMBL Accession Number AJ243756). Black dots correspond to noncanonical interactions. Numbering is according to Sprinzl et al. (1998). A*: N6-isopentenyladenosine or 2-methylthio-N6-isopentenyladenosine.

not investigated, we cannot exclude that in vivo the nonedited and edited tRNA$^{Cys}$ forms support protein synthesis differently. In the case of dicot mt tRNA$^{Phe}$ and larch mt tRNA$^{His}$ precursors, editing involves C:A mismatch corrections in base-paired regions and is an absolute prerequisite for recognition by tRNA processing enzymes in vitro. The editing site in tRNA$^{Cys}$ is also located in a base-paired region but, by contrast, does not correct a base pair mismatch. This change is apparently not necessary to improve the interaction with enzymes such as RNA-processing enzymes or cysteinyl-tRNA synthetase, at least in vitro.

The last hypothesis for a functional role of editing in *S. tuberosum* mt tRNA$^{Cys}$ is its possible implication in further posttranscriptional modifications. To test this possibility, the sequence of the *S. tuberosum* mt tRNA$^{Cys}$(GCA) previously purified by two-dimensional polyacrylamide gel electrophoresis (Maréchal-Drouard et al., 1990) was determined. Eight modified nucleotides were identified, including 3 Ψ residues in the anticodon stem at positions 27, 28, and 39 (Fig. 2D). These results imply that the editing event affecting this tRNA is required to generate a Ψ at position 28. C-to-U conversion via cytidine deaminase activity (Yu & Schuster, 1995) is a general phenomenon in plant mitochondria, and it has been demonstrated in different organisms that Ψ residues are formed in a posttranscriptional isomerization reaction catalyzed by multiple Ψ synthases (see, e.g., Koonin, 1996). These two activities target different atoms in the pyrimidic core: deamination occurs on the C4, whereas U-to-Ψ isomerization affects N1 and C5. Thus we propose a two-step model to explain how Ψ28 can be generated in *S. tuberosum* mt tRNA$^{Cys}$ (Fig. 3). Interestingly, a similar case has been observed in *Escherichia coli* tRNA$^{Ser}$(GGA), where the C20 residue is converted into a dihydrouridine (Motorin et al., 1996), probably by a two-step mechanism involving a C-to-U deamination (pers. comm. of H. Grosjean in Price & Gray, 1998).

The editing event occurring at position 28 of mt tRNA$^{Cys}$ allows a U to be maintained at this position during land-plant evolution. Although no obvious function can be assigned to this editing site from the in vitro

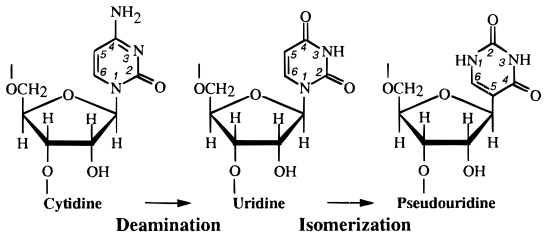


**FIGURE 3.** Two-step model proposed to generate a Ψ at position 28 in *S. tuberosum* mt tRNA$^{Cys}$(GCA). The first step involves cytidine-to-uridine editing via a deamination process, and the second step involves an isomerization reaction leading to pseudouridine formation.

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experiments, we cannot exclude that, in vivo, a U28 is essential for correct and stable folding of this tRNA. This stabilizing effect could take place at two levels. First, it has been shown by different techniques that, among the different possible mismatches, UU pairs are more stable than UC or CU pairs (Santa Lucia et al., 1991). Second, the role of the environment is also important and the geometry around a base pair is determined primarily by the immediately adjacent base pair (Masquida & Westhof, 2000). As a matter of fact, Leontis and Westhof (1999) have proposed that, in the case of the tandem motif U80•G96/G81•U95 present in the E loop of bacterial 5S rRNA, the wobble G81•U95 can be substituted quasi-isosterically by U81•U95, C81•C95, or U81•C95, but rarely by C81•U95. If we now consider that mt tRNA$^{Cys}$ contains a wobble U27•G43 pair, the wobble U28•U42 pair appears to be greatly preferable to C28•U42 and could explain why C28 is converted into U.

As C-to-U deamination appears to be a prerequisite for pseudouridylation at position 28, the requirement for this editing event could also be related to the function of Ψ28. Although Ψ residues are ubiquitous in structural RNAs of archaebacteria, eubacteria, and eukaryotes (Limbach et al., 1994; Sprinzl et al., 1998), their function in tRNA is not clear. In most cases, it is generally assumed that they permit fine scale improvement of the tRNA structure. For instance, it has been shown that Ψ residues can stabilize RNA by improving RNA stacking (Davis, 1995). Stabilization of tRNA structure by a Ψ residue at position 39 was also shown in the case of *E. coli* tRNA$^{Phe}$ (Davis & Poulter, 1991) and human tRNA$^{Lys\text{-}3}$ (Durant & Davis, 1999). More generally, these residues could be a favorable site for tRNA hydration, where a water molecule can be involved in hydrogen bonds with the phosphate backbone and with the N1 atom in the Ψ pyrimidic core (Auffinger & Westhof, 1998). So far, no study has been reported concerning the function of Ψ residues at position 27 or 28. In conclusion, it seems probable that both processes, editing and isomerization, act in synergy to stabilize tRNA$^{Cys}$ in vivo. Although Ψ:U base pairing in tRNA has been previously described (Schejter et al., 1982), a structural analysis of the *S. tuberosum* mt tRNA$^{Cys}$ will be necessary to identify the putative Ψ27:G43 and Ψ28:U42 base pairing. Further investigations will be required to assign a function to Ψ28, and explain why this editing event is necessary.

## MATERIALS AND METHODS

*M. grandiflora, C. taiwanensis*, and *C. mexicana* leaves were provided by the Strasbourg Botanical Garden. *G. biloba* leaves were harvested in a local garden. For total nucleic acid extraction, 2 gm of leaves were ground in liquid nitrogen, resuspended in 10 mL of extraction buffer (10 mm Tris-HCl, pH 7.5; 10 mm $MgCl_2$; 1% SDS), and filtered through gauze. Total nucleic acids were phenol-extracted and precipitated by ethanol. Total nucleic acids from *P. nephrolepis* were a gift from Dr. P. Guillemot. Total tmRNA and mtDNA were extracted from purified potato mitochondria according to Maréchal-Drouard et al. (1990).

Transfer RNA RT-mini-sequencing and tRNA circularization were essentially performed as described in Syvänen et al. (1991), and Yokobori and Paabo (1995), respectively. Determination of the *S. tuberosum* mt tRNA$^{Cys}$(GCA) sequence was performed using the technique of Stanley and Vassilenko (1978).

Uniformly labeled precursor tRNA transcripts were synthesized by using T7 RNA polymerase (Promega) under standard conditions. Constructs encoding the mature tRNA$^{Cys}$ were amplified by PCR with the relevant primers so that the tRNA gene sequence was directly fused to the T7 RNA polymerase promoter at the 5′ terminus and to a *Bst*NI site at the 3′ terminus (Perret et al., 1990). As the *S. tuberosum* mt *trnC* gene contains a *Bst*NI restriction site at positions 40–44 (EMBL Accession Number X93575), we used the *trnC* sequence of *Arabidopsis thaliana*, where a single nucleotide difference at position 44 in the variable loop removes this internal *Bst*NI site (EMBL Accession Number Y08501). PCR and RT-PCR amplifications, gene cloning, and sequencing were performed essentially as described in Remacle and Maréchal-Drouard (1996).

Processing assays were performed as described in Maréchal-Drouard et al. (1996a). Aminoacylations were conducted at 25 °C in the presence of 0.7 $\mu$Ci of *L*-[$^{35}$S]cysteine (1,000 Ci/mmol; NEN Life Science) under optimal conditions (Maréchal-Drouard et al., 1995). In vitro CCase assays were performed as described in Fey et al. (1999).

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