Title: Is RNA editing implicated in group II-intron survival in the angiosperm mitochondrial genome?

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Abstract

Introns may be considered as optional because they are removed from mRNA molecules, but introns are fairly preserved for unknown reasons. Previously, the mitochondrial rps3 gene of sugar beet (*Beta vulgaris* L., Caryophyllales) was shown to represent a unique example of an intron loss. We have determined the distribution of the rps3 intron in 19 Caryophyllalean species. The intron was absent from the Amaranthaceae and the Achatocarpaceae. In the Caryophyllaceae, *Dianthus japonicus* rps3 was pseudogenized but the intronic sequence was retained. Intact intron-bearing rps3 copies were cloned from *Portulaca grandiflora* and *Myrtillocactus geometrizans*, members of the sister clade of the Amaranthaceae-Achatocarpaceae-Caryophyllaceae clade. Most of the C-to-U RNA-editing sites in *Portulaca* and *Myrtillocactus* rps3 transcripts were homologous in the two species as well as in the sugar beet rps3, which, unlike other 12 rps3 transcripts, lacks editing in the exonic regions around the intron. Provided that the loss of editing preceded the loss of rps3 intron, it appears conceivable that a requirement for editing could have prevented the loss of group-II introns retained in angiosperm mitochondrial genomes. This interpretation is an alternative to the conventional one that views the loss of editing as a mere trace of RNA-mediated gene conversion.

Keywords: plant mitochondria, mitochondrial genome, evolution, Caryophyllales, Amaranthaceae, group-II intron, retroprocessing
Unlike in animals, introns are prevalent in land plant mitochondrial genes (Knoop 2004; Bonen 2008). In angiosperms, there are ~25 known group I and group II mitochondrial introns that interrupt eleven genes (Kitazaki and Kubo 2010).

The distribution of introns is more or less variable among angiosperm species. A well known example is the group I intron of \textit{cox1}, whose dissemination appears to have involved horizontal transfers and/or occasional losses during angiosperm diversification. As a result, its distribution is not consistent with angiosperm taxonomy (Cusimano et al. 2008; Sanchez-Puerta et al. 2008). Compared to the \textit{cox1} intron, the group II-intron content appears to be rather conservative and intronic variation (presence or absence of the intronic sequence) is fairly well correlated with taxonomy. For example, the distribution of intron 1 of \textit{cox2} (\textit{cox2-i1}) in 30 taxa led De Benedetto et al. (1992) to conclude that the presence/absence of \textit{cox2-i1} has a potential as a phylogenetically informative character.

There is no report of a group II-intron gain in angiosperm mitochondria (Kubo et al. 2011); intronic variation therefore can be interpreted as resulting from intron loss. Currently available information suggests that the loss of group-II introns could involve retroprocessing, an RNA-mediated homologous recombination in which mRNA is reverse-transcribed into cDNA which subsequently recombines with genomic DNA (Geiss et al. 1994). Intron loss through retroprocessing not only erases intronic sequences from the genome but also reduces the necessity for RNA editing, a post-transcriptional mRNA modification of land plants that alters specific cytosine (C) residues to uracil (U). This is because a cDNA sequence that is substituted for a genomic region contains thymine (T) residues at sites that are occupied by C in the original sequence. Therefore, intron loss can be expected to accompany editing site reduction in the exonic regions around the intron (Geiss et al. 1994). In fact, comparison of intron-bearing and intron-lacking copies of three genes (\textit{cox2}, \textit{nad4} and \textit{nad7}) revealed a reduced number of RNA editing sites (Geiss et al. 1994; Itchoda et al. 2002; Sloan et al. 2010). However, while intronic variation in the \textit{cox2}, \textit{nad4} and \textit{nad7} genes appear to have occurred independently several times in different angiosperm lineages (Gass et al. 1992; Pla et al. 1995; Sloan et al. 2010), no such pronounced variability has been reported from other genes. This suggests that some introns tend to be preserved during angiosperm evolution for unknown reasons.
In this context, the rps3 gene provides a unique example: the sugar beet (Beta vulgaris L.) rps3 lacks introns, while the other angiosperm genes identified to date contain an intron (Laroche and Bousquet 1999; Kubo et al. 2000). To better understand the implications of the loss of the rps3 intron, we examined the (taxonomic) distribution of the rps3 intron among the Caryophyllales, to which sugar beet belongs.

A set of primers (P1 and P2) were designed based on the exon-1 and exon-2 sequences of angiosperm rps3 (rps3-ex1 and rps3-ex2, respectively) to target rps3-i (experimental procedures are detailed in supplementary materials). Total cellular DNAs were isolated from 11 species covering 6 families of the Caryophyllales (Table 1) and subjected to PCR using P1 and P2. As shown in Fig. 1a, six species including sugar beet gave PCR products of 170bp. These PCR products were cloned into plasmid vectors for nucleotide sequencing. The six sequences were highly homologous to the intron-less rps3 of sugar beet mitochondria (Fig. S1a). On the other hand, four other species gave PCR products of ~1.5 kbp (Fig. 1a), which were found to contain intron- and exon sequences (Fig. S1b). No PCR product was amplified from Dianthus (Fig. 1a).

The failure to amplify the rps3 sequence from Dianthus suggests the lack of the intact mitochondrial gene. To test this idea, we first amplified the rps3-ex1 and rps3-ex2 regions from petunia total cellular DNA using two primer sets (P3 and P4, and P5 and P6, respectively, designed based on DDBJ/GenBank/EMBL accession no. X67028). The amplified DNA fragments were labeled and then hybridized with a DNA blot containing Dianthus total cellular DNA. As shown in Fig. 2, the rps3-ex2 probe hybridized to a 1.1-kbp EcoRI fragment, but the rps3-ex1 probe failed to identify any bands from Dianthus. Therefore, the rps3-ex1 sequence seems to be missing or to strongly diverge in the Dianthus genome. We may ask whether the rps3-i sequence is present immediately upstream of rps3-ex2 in Dianthus. Several primers corresponding to sequences of rps3-i conserved in angiosperms were used in combination with the P2 primer for amplification trials. PCR products were obtained when we used primer P7 (Fig. 1b). Nucleotide sequencing revealed that the Dianthus amplicon contained both the rps3-ex2 and rps3-i sequences (Fig. S1b).

We examined the organization of the angiosperm mitochondrial rps3 using data in the
public databases. More than 20 complete mitochondrial sequences as well as \textit{rps3} gene sequences from 18 angiosperms are available but, \textit{rps3}-\textit{i} was absent only from the sugar beet gene (data not shown). In the mitochondrial genome of \textit{Silene latifolia} Poir., which is a member of the Caryophyllaceae as is \textit{Dianthus}, the \textit{rps3-ex1} sequence was missing but a portion of \textit{rps3}-\textit{i} and almost the entire \textit{rps3-ex2} were present (Fig. S1b). No species possessed intron-less as well as intron-bearing \textit{rps3} copies (Fig. 1 and data not shown). To summarize, intron-less \textit{rps3} copies were detected in Amaranthaceae and Achatocarpaceae, and it seems reasonable to postulate that \textit{rps3}-\textit{i} was lost in a common ancestor of the two families. This result is congruent with recent phylogenetic models that resolved Amaranthaceae and Achatocarpaceae as two closely related clades (Soltis et al. 2011), with their closest sister clade being the Caryophyllaceae.

Next we addressed the question whether the five RNA editing sites in sugar beet \textit{rps3}, which were confined to \textit{rps3-ex2} (Matsunaga et al. 2011) (Fig. 3 and Fig. S2), could be interpreted as traces of the retroprocessing that erased \textit{rps3}-\textit{i}. For this purpose, it was necessary to compare editing sites between intron-less \textit{rps3} and intron-bearing \textit{rps3} copies in Caryophyllales. Although Caryophyllaceae is the closest sister clade of Amaranthaceae-Achatocarpaceae in the phylogenetic tree (Soltis et al. 2011), the Caryophyllaceae \textit{rps3} seemed unsuitable because it appeared to be a pseudo gene as was seen in \textit{Dianthus} and \textit{Silene}. We selected \textit{Portulaca grandiflora} and \textit{Myrtillocactus geometrizans}, which belong to the sister clades of Amaranthaceae-Achatocarpaceae-Caryophyllaceae in the order Caryophyllales.

Genomic DNA fragments of \textit{Portulaca grandiflora} that hybridized with the petunia \textit{rps3} probe were cloned, sequenced and assembled into a contig, in which 74-bp \textit{rps3-ex1}, 1215-bp \textit{rps3}-\textit{i} and 1615-bp \textit{rps3-ex2} sequences were found (DDBJ/GenBank/EMBL accession no. AB666467). This sequence information was used to design a set of primers (P8 and P9) that subsequently were employed to amplify the complete \textit{rps3} gene of \textit{Myrtillocactus geometrizans}. As a result, \textit{Myrtillocactus rps3} was revealed to consist of 74-bp \textit{rps3-ex1}, 1705-bp \textit{rps3-i} and 1609-bp \textit{rps3-ex2} (DDBJ/GenBank/EMBL accession no. AB666468). DNA gel blot analysis indicated that \textit{Portulaca rps3} and \textit{Myrtillocactus rps3} are single-copy genes (Fig. 2).
To determine the RNA editing sites, reverse transcription (RT) PCR was performed using leaf (*Portulaca*) or stem (*Myrtillocactus*) total RNA as templates with two sets of primers (P8 and P10, and P11 and P9). Nucleotide sequencing of ten independent clones from amplicons of each RT-PCR revealed three and five C-to-U RNA editing sites in *Portulaca* and *Myrtillocactus*, respectively (Fig S2). All but one editing event (depicted as e8 in Fig. S2) improved the similarity of the amino acid sequence with homologues from other species (data not shown). One editing event (e8) in *Myrtillocactus* did not alter the amino-acid specificity of the codon (i.e. silent editing). Three editing sites identified in *Portulaca rps3* transcripts were found also at homologous positions in sugar beet (e22, e27 and e28 in Fig S2). Two editing sites (e14 and e19) that were edited in sugar beet but not in *Portulaca* corresponded to adenosine (A) and T residues in the *Portulaca* genome, respectively. In *Myrtillocactus*, four out of the five editing sites matched with sites in sugar beet (Fig S2). The silent editing in *Myrtillocactus* (e8) was not detected in sugar beet and *Portulaca*. One of the five editings in sugar beet (e19) appeared to be unnecessary in *Myrtillocactus* because a T residue was present at the corresponding site (Fig. S2).

We complemented our own data with the publicly available data regarding *rps3* transcript editing from 12 different plant species (Fig. S2). RNA-editing sites that were experimentally identified or predicted using a computer program (sources are summarized in Table S1) numbered 37 (e1 to e37) in total. This analysis revealed that *rps3* transcripts of sugar beet, *Portulaca* and *Myrtillocactus* are devoid of editing events in their 5' (e1 to e7) and 3' (e29 to e37) regions (Fig. 3 and Fig. S2), and that the number (3 to 5) of RNA editing sites in these three *rps3* transcripts is clearly smaller than that (7-17) in other *rps3* transcripts. We placed *rps3-i* loss and loss or gain of e1 to e7 and e29 to e37 editings at positions on the phylogenetic tree that maximized parsimony (Fig. 3). This analysis favored the loss of the 16 editing sites prior to the evolutionary separation of sugar beet, *Myrtillocactus* and *Portulaca*, although another possibilities cannot be excluded.

There have been some reports suggesting a possible association between RNA editing and group-II intron. For example, the editing frequency at the e4 site of rice *rps3* was lower in unspliced RNA than in spliced RNA (Kurihara-Yonemoto and Kubo 2011). Similar
observations of differential editing status between unspliced and spliced RNA have been reported from petunia cox2, maize cox2, wheat cox2, wheat nad4 and wheat nad7 (Sutton et al. 1991; Yang and Mulligan 1991; Li-Pook-Than et al. 2007). Furthermore, mRNAs transcribed from modified mitochondrial genes whose group-II introns had been removed were less frequently edited compared to mRNAs transcribed from the original intron-bearing genes (Castandet et al. 2010). The possible association between RNA editing and the presence of a group-II intron suggested by these reports allows us to speculate that the loss of rps3-i from the genome might affect certain RNA editing events. Modification of the editing sites by genomic C-to-T substitution (or cDNA-mediated gene conversion that does not affect intron content but reduces editing sites) would weaken the significance of rps3-i for rps3 expression. Consequently, the loss of rps3-i could have become inconsequential in the Caryophyllales lineage leading to sugar beet, Myrtillocactus and Portulaca. This hypothesis calls for further evaluation in future studies.

Acknowledgements

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References


Table 1  Plant materials used in this study and presence/absence of rps3-i

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\(^a\) Absence, \(^b\) Presence
Figure legends

**Fig. 1** PCR amplification of *rps3-i* from the 11 species listed in Table 1.  

a  PCR amplification with primers P1 and P2. Size markers are shown on the right (bp).  

b  PCR amplification with primers P7 and P2 using *Dianthus japonicus, Basella alba, Mirabilis jalapa, Myrtillocactus geometrizans* and *Portulaca grandiflora* total DNAs as templates. Size markers are shown on the right (bp).

**Fig. 2** DNA gel blot analysis using 5 µg of total cellular DNA digested with *EcoRI*.  

Petunia *rps3-ex1* and *rps3-ex2* sequences were used as probes. The sample was electrophoresed in a 1% agarose gel. Sugar beet (Beta), *Myrtillocactus geometrizans* (Myrtillocactus), *Dianthus japonicus* (Dianthus) and *Portulaca grandiflora* (Portulaca) were subjected to this experiment. Size markers are shown on the left (kbp).

**Fig. 3** Phylogenetic relationship among 15 plant species including sugar beet (Beet), *Portulaca grandiflora* (Portulaca), *Myrtillocactus geometrizans* (Myrtillocactus), grapevine (Grape), *Arabidopsis thaliana* (Arabidopsis), rapeseed, *Oenothera berteriana* (Oenothera), sunflower, watermelon, zucchini, petunia, tobacco, papaya, *Magnolia x soulangeana* (Magnolia) and rice, based on Soltis et al. (2011) and the Angiosperm Phylogeny Website (http://www.mobot.org/mobot/research/apweb/). Branch length does not indicate phylogenetic distance. Arrows pointing to top indicate loss of editings and intron, while arrows pointing downwards highlight gain of editings. *rps3* organization and its editing status (for e1-e7 and e29-e37 only) is shown on the right (for details, see Fig. S2). Boxes with numbers following the letter ‘e’ indicate specific residues depicted in Fig. S2. Filled, gray and open boxes represent experimentally confirmed editing, editing predicted *in silico*, and no editing, respectively. Horizontal lines between the boxes indicate *rps3-i*. 
Experimental details

1. Isolation of nucleic acids

Total cellular DNA was isolated according to Doyle and Doyle (‘Isolation of plant DNA from fresh tissue’. Focus 12:13-15, 1990). Total RNA was isolated by using RNeasy Plant Mini Kit (Qiagen, Valencia, CA). Isolated RNA samples were further purified by incubation with RNase-free DNase I (Takara Bio, Ohtsu, Japan) according to the manufacturer’s instructions.

2. Molecular cloning

PCR was done using BlendTaq (Toyobo Life Science, Osaka, Japan). Reverse transcription (RT) PCR was performed according to Singer-Sam et al. (‘Measurement by quantitative PCR of changes in HPRT, PGK-1, PGK-2, APRT, MTase and Zfy gene transcripts during mouse spermatogenesis.’ Nucleic Acids Research 18: 1255-1259, 1991). PCR products were cloned into the pBluescript vector (Stratagene, La Jolla, CA). Nucleotide sequences were determined using Li-COR4200L (Li-COR, Lincoln, NE) or ABI3130 (Applied Biosystems, Foster City, CA).

3. Hybridization

Genomic DNA was transferred onto Hybond N+ membrane (GE Healthcare UK, Amersham Place, England) after gel electrophoresis. DNA fragments of interest were labeled with alkaline phosphatase using the AlkPhos Direct DNA labeling system (GE
Healthcare UK). Hybridization was done according to the manufacturer's instruction.

4. Nucleotide sequences of oligonucleotide primers

P1, 5'-TTTCGGTAAGGCTGAATCGTAGTTC-3'
P2, 5'-GGAAAGCCAAAGGTAAGTCTCCTCGT-3'
P3, 5'-AGTAAAGTCTAAGCGCATAT-3'
P4, 5'-CTGGGAGAACTAAAGACTG-3'
P5, 5'-GACTCTATTTATTATTTGGT-3'
P6, 5'-CGTTCAAATAATAGTTGTACCCTACGG-3'
P7, 5'-CATCTCAAGTATAGGCGAAAGGA-3'
P8, 5'-ATATATGGCAGAAAAGGAAATCC-3'
P9, 5'-TTTTCAATTTCGACTATAAGAAATCC-3'
P10, 5'-GTATTGAATAAGTATTGCAT-3'
P11, 5'-AGACCTCCTCTCAATTATTTGG-3'
a. Beta, Chenopodium, Celosia, Gomphrena, Spinacia, Achatocarpus, Dianthus, Basella, Mirabilis, Myrtillocactus, Porturaca

b. 300
Fig. S1 Sequence comparison of portions of rps3.  

**a.** Part of the nucleotide sequences of PCR products shown in Fig. 1a. The boundary between rps3-ex1 and rps3-ex2 is shown by a vertical line.

**b.** Part of the nucleotide sequences of PCR products shown in Fig. 1b. Sequence data of *Silene latifolia* rps3 (HM562727) is included. Dashes are included for maximum matching. The boundary between rps3-i and rps3-ex2 is indicated by a vertical line.
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Tobacco

Sunflower

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Papaya

Oenothera

Watermelon

Zucchini

Grape

Rice

Magnolia
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1533
Papaya
AAAGGCGCA-------------------GAAATAGCGAGAACTGAATGCGGAAAGTATGGAAAAGTCTCT
1563
Oenothera
AAAGGTGCA-------------------GAAATAGCTAGAACTGAATGCGGAAAGTATGGAAAAACATCT
1560
Watermelon
AAAGGTGCA-------------------GAAATAGCTAGAACTGAATGCGGAAAGTATGGAAAAACATCT
1560
Zucchini
AAAGGTGCA-------------------GAAATAGCTAGAACTGAATGCGGAAAGTATGGAAAAACATCT
1554
Grape
AAAGGTGCA-------------------GAAATAGCTAGAACTGAATGCGGAAAGTATGGAAAAACATCT
1563
Rice
GGGGGTGCG-------------------GAAATAGCTAGAACTGAATGCGGAAAGTATGGAAAAACATCT
1560
Magnolia
GGGGGTGCG-------------------GAAATAGCTAGAACTGAATGCGGAAAGTATGGAAAAACATCT
1473
Fig. S2 Nucleotide sequence alignment of rps3-coding regions of sugar beet (Beet), Portulaca grandiflora (Portulaca), Myrtillocactus geometrizans (Myrtillocactus), grapevine (Grape), Arabidopsis thaliana (Arabidopsis), rapeseed, Oenothera berteriana (Oenothera), sunflower, watermelon, zucchini, petunia, tobacco, papaya, Magnolia x soulangeana (Magnolia) and rice.
Nucleotide residues are numbered from the first base of the initiation codon. Exon/intron boundaries are indicated by vertical lines. Intronic sequences are not considered. Dashes are included for maximum matching. Editing sites are highlighted in black (experimentally confirmed) or gray (predicted), and numbered from e1 to e37. Sources of the data are Matsunaga et al. (Plant Cell Reports, 2011 30: 231-238) and others shown in Table S1.