Nº PROYECTO : 1141197
TÍTULO PROYECTO : MITOCHONDRIAL BIOGENESIS AND FUNCTION IN PLANTS: INSIGHTS INTO THE ROLE OF RESPIRATORY COMPLEX II, SIRTUINS AND PENTATRICOPEPTIDE REPEAT PROTEINS
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INVESTIGADOR(A) RESPONSABLE : XAVIER SERGIO JORDANA DE BUEN
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MODIFICACIONES ACADÉMICAS

El informe no presenta modificaciones académicas.
PROJECT RESULTS:

Describe the results of your research in reference to its original and/or modified Project objectives.

The maximum extension of this section is 5 pages (Arial or Verdana font, size 10).

The general goal of our research has been to understand mitochondrial biogenesis and function in plants, using *Arabidopsis thaliana* as a model, and mutants in Complex II, sirtuins and pentatricopeptide repeat (PPR) proteins as tools.

Note: In Arabidopsis italic capital letters denote nuclear genes (e.g. *SDH2*), italic low case letters mutants (e.g. *sdh2*), and normal capital proteins proteins (e.g. *SDH2*). For mitochondrial genes, low case italics letters are used for wild type genes (e.g. *cox3, nad4, tatC*).

**Project Goal 1: To gain insight into the role of complex II in embryo development and germination, and in seedling establishment.**

Results are included in the paper by Restovic et al. published in Frontiers in Plant Science (see products section, Front. Plant. Sci. 8:277, 2017).

Complex II (succinate dehydrogenase, SDH) is an essential mitochondrial enzyme involved in both the tricarboxylic acid (TCA) cycle and the respiratory chain. Complex II subunits are all nuclear-encoded in Arabidopsis and somewhat surprisingly, several subunits are encoded by more than one gene. For instance three genes, *SDH2.1, SDH2.2* and *SDH2.3* encode the iron-sulfur subunit, which transfer the electrons from the flavoprotein (SDH1) containing the succinate binding and oxidation site, to the ubiquinone in the internal membrane (binding site in the subunits SDH3 and SDH4 which anchor the complex to the membrane). Considering that in most organisms there is a single *SDH2* gene, the presence of multiple genes raises questions about their role in growth and development.

Work we performed before this project showed that *SDH2.1* and *SDH2.2* genes likely arose from a recent duplication and are redundant since both have similar exon-intron structures, encode nearly identical proteins, are similarly expressed and the individual knockout mutants do not have any phenotype. Moreover, we have been unable to obtain double *sdh2.1/sdh2.2* homozygous mutants in spite of the large number of analyzed seedlings from the offspring of double heterozygous plants (*SDH2.1/sdh2.1;SDH2.2/sdh2.2*), strengthening the conclusion that they are redundant and that the presence of at least one functional allele (out of 4) is essential for plant viability.

*SDH2.3* exon-intron structure is different, the encoded protein has only 67% identity with *SDH2.1/2.2*, and *SDH2.3* is specifically expressed in the embryo during seed maturation: its mRNA accumulates in maturing embryos, is abundant in dry seeds, and declines during germination and early post-germinative growth. In contrast, *SDH2.1* is expressed at a very low level and *SDH2.2* is not expressed during seed maturation and in dry seeds, and their expression is induced during germination. Thus, expression data suggest that a complex II with *SDH2.3* may have a role during maturation and/or during germination and early post-germinative growth, and this hypothesis has been addressed in this project.

A result not included in the paper is the observation that *SDH2.3* promoter has higher activity in the embryo protodermis (Figure 1 Anexo), which may suggest a role in this cell layer for instance in providing energy for transport of precursors during storage product synthesis. However, as reported in the “Informe de avance”, we have been unable to uncover a role of complex II during seed maturation, since neither single mutants (*sdh2.3, sdh2.1*) nor double mutants (*sdh2.1/sdh2.3*) showed significant differences in seed weight, seed protein and lipid content (main storage products synthesized during maturation) and seed iron distribution, when compared to wild type seeds.

Despite these results we have been able, by using the protein synthesis inhibitor cycloheximide, *sdh2* mutants and an in situ assay for SDH activity, to conclusively shown that complex II (and not only subunit mRNAs) is already present in mature embryos before imbibition, and contains mainly *SDH2.3* as iron-sulfur subunit (~90% *SDH2.3*, 10% *SDH2.1*) (Figure 4 in the paper, Restovic et al., 2017).

In contrast, complex II plays an important but not essential role in providing energy through succinate oxidation during seed germination, since germination is delayed in seeds lacking *SDH2.3* and in wild type seeds treated with TTFA, a complex II inhibitor (Figure 5 in the
Furthermore, complex II inhibitors (TTFA, carboxin, malonate, i.e. competitive and non-competitive) completely block greening and seedling establishment, highlighting an essential role of this complex (and by extension of the respiratory chain and the mitochondrion) in the acquisition of photosynthetic competence and the transition from heterotrophy to autotrophy (Figures 5 to 7 in the paper). Higher sensitivity of the sdh2 mutants to the inhibitors showed that their effects are mediated by complex II inhibition.

**SDH2.3** specific expression during embryo maturation also raises interesting questions about its regulation (it is the only described TCA cycle and electron transport chain gene to have such specific embryo expression). During this project we have extended previous work and have defined: a) the promoter region possessing all the cis-elements necessary and sufficient for high expression in seeds (Figure 1 paper by Restovic et al., 2017). This region contains three ABRE (ABA-responsive elements) and one RY element which are necessary but not sufficient for high seed expression; b) the promoter is regulated by heterodimers of bZIP transcription factors (bZIP53/bZIP10) acting through the ABRE elements (Figures 2A and 3); and c) expression is regulated by the hormone ABA (abscisic acid) in seeds (Figure 2B). These data complemented previous work demonstrating that **SDH2.3** transcription is also regulated by seed maturation master transcription factors of the B3 domain transcription factor family (ABI3, FUS3, LEC2).

**It is very important to point out that the presence of two types of SDH2 proteins (SDH2.1/2.2-like and SDH2.3-like) appears to be a general feature in angiosperms and that in monocots (maize and rice) **SDH2.3** expression is also seed-specific (our unpublished results). Thus, the results obtained in Arabidopsis can be extrapolated, and an embryo specific iron-sulfur subunit may have evolved to deal with the stressful conditions encountered during desiccation (iron-sulfur centres are for instance very sensitive to oxidative stress).**

**Project Goal 2: To gain insight into the role of sirtuins in plant development and metabolism.**

Sirtuins are a conserved family of NAD⁺-dependent deacetylases and ADP-ribosyltransferases. Yeast Sir2, the founding member, is a histone deacetylase (HDAC) involved in chromatin silencing at the mating-type loci, rDNA and telomeres. Yeast Sir2 and its orthologs in worms and flies have been associated with an increased life-span, although this issue is still controversial. In mammals there are seven sirtuins (SIRT1-7), SIRT1 (closest to yeast Sir2), SIRT6 and SIRT 7 are nuclear, SIRT2 is primarily cytosolic, and SIRT3, SIRT4 and SIRT5 are found in mitochondria. Both nuclear (through the regulation of genes encoding mitochondrial proteins) and mitochondrial sirtuins influence mitochondrial function in mammals. Through its NAD⁺ dependence, sirtuin activity is directly linked to cellular metabolic and energetic status, and in turn regulates multiple metabolic pathways, including energy metabolism.

**Angiosperms possess only two sirtuin genes**

The presence of two sirtuin genes in Arabidopsis, tomato, rice and poplar, and of one sirtuin gene in maize, barrel medic and wheat has been reported. As many more plant genome sequences are currently available, we sought to know how conserved are the sirtuins in plants. We identified 111 plant sirtuins from 54 species and aligned their conserved sir2 deacetylase domain to construct an unrooted phylogenetic tree, which includes the sequences of seven human sirtuins (hsSIRT1-7), two sirtuins from Archeae and the *E. coli* CobB sirtuin (Figure 2 Anexo). Sirtuins are divided into five clades corresponding to classes I to IV and U. Our phylogenetic analysis clearly shows that all angiosperms including the basal species *Amborella trichopoda* and *Nelumbo nucifera* possess only two sirtuins belonging to classes II and IV. SRT2 (class II) proteins cluster with mitochondrial human sirtuin 4 (hsSIRT4), and SRT1 (class IV) proteins cluster with nuclear human sirtuin 6 (hsSRT6, a histone deacetylase). Algae, the lycophyte *S. moellendorffii* and the moss *P. patens* possess additional sirtuins, suggesting that higher plants have lost sirtuin genes during evolution.

**Arabidopsis SRT1 is a nuclear protein and SRT2 isoforms, which arise from alternative splicing, are mitochondrial**

SRT1 and SRT2 exon-intron structures are conserved in land plants (not shown), including mosses and lycophytes (but not algae), and both are expressed at low levels (data from Affymetrix microarrays). SRT1-GFP fusion protein confirmed nuclear localization (Figure 3 Anexo). SRT2 pre-mRNA is alternatively spliced: two forms (SRT2.1 and 2.2) differ only in the 5'UTR and encode the same polypeptide, one form (SRT2.5) encodes a protein with a shorter mitochondrial targeting peptide. These three mRNAs represent around 70-75% of transcripts and
encode putative functional proteins, and both the protein encoded by SRT2.1/2.2 and SRT2.5 direct GFP to mitochondria (Figure 4 Anexo). Interestingly, in around 25-30% of transcripts alternative splicing incorporates premature stop codons (PTC) through retention of intron sequences. The most frequent (~22-25% of the transcripts) event is retention of the first 11 nt from intron 5 in exon 5. Using RNAseq data from wild type and non sense mediated decay (NMD) mutants we showed that these mRNAs with PTC are degraded through NMD, and thus this is a mechanism of regulation of SRT2 expression (see “Informe de avance” for more details). Furthermore, analysis of RNAseq data in NMD mutants shows that steady state SRT2 expression is higher (3-4 times) due to an increase of the PTC isoforms which represent 75% of the total, suggesting that in wild type plants only about 25% of the pre-mRNAs are correctly processed to be translational proteins. The other 75% would include the PTC and is actively degraded, giving the 25% of transcripts with PTC in the steady-state mature mRNA population (see “Informe de avance”). One may ask why a so high proportion of transcripts are synthesized to be degraded, and a possible regulation of this process deserves further research.

SRT1 is an essential gene and is important for gametophyte development

To explore SRT1 and SRT2 function in Arabidopsis, we obtained two homozygous knockout srt2 mutants (T-DNA insertions in exon 3 and intron 7) and one line heterozygous for a T-DNA insertion in intron 5 of SRT1 (Figure 5 Anexo). No visible phenotypic alterations were observed in the srt2 mutants under standard growth conditions (long day, 16h light) or in short day conditions (8h light). No differences were found when compared to wild type plants for hypocotyl elongation in the dark, primary root length, number of lateral roots, establishment after 4-5 days in the dark, and germination at 5°C.

In the srt1 mutant allele, insertion will interrupt the SIR2 domain and is thus expected to result in a null mutation. When more than 150 herbicide resistant plants from the progeny of selfed heterozygous plants were genotyped, no homozygous mutant seedlings were identified, suggesting that SRT1 is an essential gene and that either embryo and/or gametophyte development are altered. SRT1 transcript levels were evaluated by qRT-PCR and shown to be lower in heterozygous SRT1/srt1 plants compared to wild type plants (about 40-60%).

To analyze reproductive development, we evaluated seed set: the average number of seeds per silique in heterozygous mutant plants was 56% that of wild type plants (Figure 6A Anexo). Closer examination of siliques collected before desiccation revealed the presence of small, white corpuscles that may correspond to unfertilized ovules or seeds aborted at an early developmental stage (Figure 6B Anexo). Quantification confirmed the presence of 50-60% normal seeds and 40-45% unfertilized ovules/aborted seeds in SRT1/srt1 siliques (Figure 6C Anexo). These results showing less than 75% normal seeds and the presence of likely unfertilized ovules in the SRT1/srt1 siliques suggest that, in addition to embryo lethality, there are defects in female gametophytes carrying the srt1 allele.

Female and male gametophytes were examined. Nomarski optics was employed to observe female gametophytes allowed to progress to the terminal developmental stage, in the absence of fertilization. In SRT1/srt1 pistils, in addition to embryo sacs with a wild type phenotype (Figure 7B Anexo), many embryo sacs with an abnormal phenotype in which polar nuclei fail to fuse to form the 2n central cell nucleus, were present (Figure 7C Anexo). Microscopic analysis of mature pollen grains stained by the method of Alexander showed that in SRT1/srt1 anthers a significant proportion of male gametophytes aborted (Figure 7D Anexo). Non viable pollen grains occurred with a frequency of 29 to 36% (Table 1 Anexo). Consistent with roughly 60% of the pollen grains carrying the mutant srt1 allele (30% of total pollen grains) being unviable. Altogether, these results showed that both embryo sac and pollen development are compromised in SRT1/srt1 plants and strongly suggest that the srt1 mutation is gametophytic.

Further support was obtained by genetic analysis of the srt1 allele (T-DNA codes for Basta resistance). The segregation ratio of herbicide resistance in the progeny of selfed heterozygous mutant plants was 1.34 (Table 2 Anexo), far below from the 3:1 segregation (75% resistant) expected for a dominant trait and also below from a 2:1 segregation (67% resistance) of a mutant allele causing only embryo lethality. Female and male transmission efficiencies (TE) of the srt1 allele were evaluated by carrying out reciprocal test crosses between heterozygous SRT1/srt1 and wild type plants (Table 3 Anexo). When heterozygous SRT1/srt1 plants were used as the female parent, a female TE of 72% was scored, and when SRT1/srt1 plants were used as the male parent, a TE of 43% was measured. In other words, 28% of the ovules and 57% of the pollen grains carrying the mutated allele were unable to transmit it.

Thus, our results confirm that the srt1 mutation is gametophytic, and that SRT1 is
important for both pollen and embryo sac development. However, given that the srt1 mutation is only partially penetrant in both gametophytes the absence of homozygous srt1/srt1 mutant plants in more than 150 analyzed seedlings from the progeny of selfed SRT1/srt1 plants indicates srt1/srt1 embryo lethality. This is also consistent with the observed reduction in seed set (Figure 6 Anexo).

SRT1 regulates flowering

Heterozygous SRT1/srt1 plants were phenotypically indistinguishable from wild type plants during vegetative development. However, we noticed a difference between heterozygous mutant and wild type plants in flowering time, with SRT1/srt1 plants flowering early than wild type plants (Figure 8A and B Anexo). Furthermore, we obtained transgenic lines over-expressing SRT1 and analysis of two representative lines showed that they have the opposite phenotype, flowering late than wild type plants (Figure 8A and B).

A second important parameter used to analyze flowering is the number of rosette leaves at flowering: its evaluation allows us to determine if early or late flowering is due to accelerated (or retarded) plant development. Our results show that this is not the case, since SRT1/srt1 plants have less and over-expressing plants more rosette leaves at flowering time (Figure 8C Anexo).

Consistent with these results, when we evaluated the expression of the floral integrators FLC and FT, we found that in the SRT1/srt1 plants expression of the floral inducer FT increased and expression of the floral repressor FLC decreased, and the opposite is observed in plants over-expressing SRT1 (Figure 9 Anexo). In contrast, no changes occurred in the expression of another floral integrator, SOC1.

Project Goal 3: To characterize the role of PPR proteins in mitochondrial RNA editing

Results are included in two papers by Arenas-M et al., published in Mitochondrion (see products section, Mitochondrion 19, 126-134, 2014) and Plant and Cell Physiology (Plant Cell Physiol 59 (2) 355-365, 2018, doi:10.1093/pcp/pcx190, see products section).

RNA editing post-transcriptionally changes the nucleotide sequence of transcripts. In flowering plants, this change involves the deamination of more than 400 specific cytidines to uridines in mitochondrial transcripts (and 30-40 in chloroplast transcripts). Most changes occur in mRNA coding regions, almost always modify their coding potential, correcting codons to encode conserved amino acids, and are necessary for the synthesis of functional proteins. Experiments with in organello or in vitro editing systems showed that a cis-region in the RNA between -20 or -25 and +6 nucleotides relative to the target site is generally necessary and sufficient for editing. The regions upstream of the edited C in these cis-elements are recognized and bound by specificity factors, the Pentatricopeptide Repeat (PPR) proteins, which constitute the largest family of proteins in angiosperms (>400). PPR proteins are characterized by degenerate motifs of 35 amino acids arranged as tandem repeats. Some PPR proteins (PLS subfamily, half of the PPR proteins) contain repeats shorter (S) or longer (L) than the canonical (P) 35 amino acid repeat, and one or two additional domains in the C-terminal region: the E-domain and the DYW-domain. All the known PPR proteins required for editing at specific sites are of the PLS subfamily, and contain the E or the E and DYW domains. DYW domains seem to form the primary component of cytidine deaminase, and may act in trans.

We have undertaken some years ago the search of specific trans-factors involved in RNA editing of plant mitochondrial transcripts, by selecting PPR candidate genes based on four criteria: i) PPR genes with ESTs or cDNA sequences in public databases; ii) Mitochondrial destination predicted by different subcellular sorting algorithms (Predotar, TargetP, iPSORT, Mitoprot2); iii) Members of the PLS subfamily with E or E and DYW motifs; iv) Low sequence similarity with other Arabidopsis PPR proteins (to avoid gene redundancy). This procedure ended with a list of candidates. The first characterized PPR gene selected in this way (At3g25060, MEF25 for Mitochondrial Editing Factor) encodes an E-PPR protein and was shown to be essential for RNA editing at the nad1-308 site in Arabidopsis mitochondria (Arenas-M et al., 2013, FEBS Lett. 587, 887-891).

During this project we have thoroughly characterized two additional mitochondrial PPR proteins, MEF26 and MEF31, as editing specificity factors.

MEF26 is a PPR protein (with 20 PPR motifs) of the DYW subclass and its N-terminus is able to target GFP to mitochondria and not to chloroplasts (Figure 1 in the Mitochondrion paper). We isolated two mutants (mef26-1 and mef26-2, Figure 2A in the paper) and examined the RNA editing status of 434 mitochondrial sites and all chloroplast sites. In the mutants, no editing
defects were found in chloroplasts, and two sites were affected in two mitochondrial transcripts, confirming the localization results. In the transcript encoding subunit III of cytochrome c oxidase (respiratory complex IV), editing at site 311 (cox3-311) is abolished in the absence of MEF26 (Figure 2B and C). In contrast, editing at site nad4-166, in the transcript encoding subunit 4 of NADH dehydrogenase (respiratory complex I), is only partially affected, with a reduction of 40-45% (Figure 2B in the paper). Wild type editing is restored at both sites in complemented plants (mutant mef26-2 transformed with the wild type MEF26 gene), demonstrating that MEF26 is indeed necessary for editing at both sites. Interestingly, the nearby sites located three nucleotides downstream (cox3-314) and two nucleotides upstream (nad4-164) are normally edited in the mutant plants and thus should be recognized by other PPR proteins.

In wild type plants cox3-311 and nad4-166 sites are fully edited, changing codon identities from Ser (UCU) to Phe (UUU) and Arg (CGG) to Trp (UGG), respectively. These amino acids are highly conserved (Figure 3 in the paper), and thus the lack of editing at cox3-311 would generate a COX3 polypeptide with a Ser104 instead of a Phe104, and editing reduction at nad4-166 would generate a mixture of NAD4 with Arg56 and Trp56. However, no phenotypic alterations were observed, at least under standard growth conditions, suggesting that these changes are tolerated by mitochondria.

PPR proteins bind to specific RNA sequences through a recently proposed recognition code between PPR motifs and the nucleotides in the RNA. In the case of RNA editing, PPR motifs are aligned to the RNA cis sequence such that the C-terminal S motif is in contact with the nucleotide at the -4 position (relative to the C to be edited). According to this code, the PPR motifs of MEF26 clearly match the upstream sequence (-23 to -4) of both cox3-311 and nad4-166, which are ranked at 1st and 2nd positions of the most probable targets, respectively (Figure 4 in the paper). Thus, our results support the proposed recognition code for PPR protein-RNA interactions, and direct recognition of sites cox3-311 and nad4-166 by MEF26.

MEF31 is a PPR protein of the E subclass and possesses 14 PPR motifs and the E domain (Figure 2A in the Plant and Cell Physiology paper). Its amino-terminal amino acid sequence directs GFP to mitochondria and not to chloroplasts (Figure 1 in the paper). We obtained two mutants (Supplementary Figure 1) and used them to evaluate editing at 269 sites, including all chloroplastic sites. MEF31 is only involved in editing at two mitochondrial sites in the same transcript encoding subunit C of the twin-arginine translocation (tat) pathway (Figure 2B and Table 1 in the paper), confirming mitochondrial localization. MEF31 is essential for editing at site tatC-581 and application of the amino acid code for RNA recognition by PPR motifs supports the view that MEF31 directly targets this site by recognizing its cis-sequence (Figure 4 in the paper).

In contrast, editing at site tatC-586 five nucleotides downstream is only partially affected in plants lacking MEF31, being restored to wild type levels (as editing at site tatC-581 in complemented plants (Figure 2B and Table 1 in the paper). Application of the amino acid code (Figure 4) and analysis of individual RNA molecules for editing at sites 581 and 586 (Figure 3) suggest that MEF31 does not directly target site tatC-586, and only indirectly influences editing at this site. Results clearly show that editing at site 581 is not absolutely required for editing at site 586 however it may increase editing efficiency at site 586. Interestingly, site tatC-587 is efficiently edited in both wild type plants and plants lacking MEF31 (Figure 2, Table 1) and is thus independent of this PPR protein. The most straightforward explanation for an indirect effect of MEF31 on editing at site 586 is that U at position 581 (-5 relative to the C to be edited) would improve recognition of the tatC-586 cis sequence by a second unknown PPR protein. A model accounting for this hypothesis was presented in the paper (Figure 6). Furthermore, a third PPR protein would target site 587, and in this case its binding would not be influenced by the pyrimidine at site 581 (C or U). Identification of a PPR protein required for editing at site tatC-586 and able to discriminate between C or U at -5 would support our hypothesis.

The tatC subunit is part of the tat pathway which in bacteria is involved in the export of folded proteins (role unknown in plants, although its involvement in complex III biogenesis has been proposed). In wild type Arabidopsis plants editing at site tatC-581 changes the codon identity from proline (CCA) to leucine (CUA). This editing event is conserved in angiosperms (Figure 5A and Table 2 in the paper) and the encoded Leu194 is conserved in plants (Figure 5B). Thus the absence of editing at this site in the mutants would generate a protein with a proline at this otherwise conserved leucine; however no phenotypic alterations were visible, at least under standard growth conditions. In contrast, editing at site tatC-586 has no effect on protein sequence (silent editing), and this site is also partially edited (and silent) in rice and canola and is not edited in other angiosperms (Figure 5A and Table 2).
Para trabajos en Prensa/ Aceptados/Enviados adjunte copia de carta de aceptación o de recepción.

N°: 1
Nombre Completo de la Revista: Mitochondrion
Título (Idioma original): The pentatricopeptide repeat protein MEF26 participates in RNA editing in mitochondrial cox3 and nad 4 transcripts
Indexación: WoS
ISSN:
Año: 2014
Vol.: 19
N°:
Páginas: 126-134
Estado de la publicación a la fecha: Publicada
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N°: 2
Autor (a)(es/as): Restovic, F.; Espinoza-Corral, R.; Gómez, I.; Vicente-Carbajosa, J; Jordana, X.
Nombre Completo de la Revista: Frontiers in Plant Science
Título (Idioma original): An active mitochondrial complex II present in mature seeds contains an embryo-specific iron-sulfur subunit regulated by ABA and bZIP53 and is involved in germination and seedling establishment
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Archivo(s) Asociado(s) al artículo:
fpls_08_00277_publicado.pdf
The pentatricopeptide repeat protein MEF31 is required for editing at site 581 of the mitochondrial tatC transcript and indirectly influences editing at site 586 of the same transcript

Otras Fuentes de financiamiento, si las hay:
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Otras Publicaciones / Productos

Sin información ingresada.

Congresos

Nº: 1
Título (Idioma original): MEF31 is a PPR protein necessary for editing of the orfX mitochondrial transcript in Arabidopsis thaliana
Nombre del Congreso: 38 Reunión Anual de la Sociedad de Bioquímica y Biología Molecular de Chile
País: CHILE
Ciudad: Puerto Varas
Fecha Inicio: 22/09/2015
Fecha Término: 25/09/2015
Nombre Publicación: libro de resúmenes
Año: 2015
Vol.: 
Nº: 
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Envía documento en papel: no
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<td>The nuclear-encoded plant pentatricopeptide protein MEF31 is involved in RNA editing at two near sites in the mitochondrial transcript encoding subunit C of the twin-arginine translocation pathway</td>
<td>Nombre del Congreso:</td>
<td>42nd FEBS Congress, from molecules to cells and back</td>
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**Autores:** Vargas-Pérez, J.; Gómez, M.I.; Jordana, X.; Roschütztardtz, H.

**Título (Idioma original):** Evaluation of the importance of putative mitochondrial iron transporters in reproductive development of Arabidopsis thaliana

**Nombre del Congreso:** XL Reunión Anual de la Sociedad de Bioquímica y Biología Molecular de Chile

**País:** CHILE

**Ciudad:** Puerto Varas

**Fecha Inicio:** 26/09/2017

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**Nombre Publicación:** Libro de Resúmenes

**Año:** 2017

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**Nº:** 

**Páginas:** 233

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**TESIS/MEMORIAS**

**Nº:** 1

**Título de Tesis:** MEF26 es una proteína PPR necesaria para la edición eficiente de dos sitios en dos transcritos mitocondriales de Arabidopsis thaliana

**Nombre y Apellidos del (de la) Alumno(a):** Sebastián Moreno Ramírez

**Nombre y Apellidos del (de la) Tutor(a):** Xavier Jordana de Buen

**Título Grado:** Pregrado

**Institución:** P Universidad Católica de Chile

**País:** CHILE

**Ciudad:** Santiago

**Estado de Tesis:** Terminada

**Fecha Inicio:** 01/08/2012

**Fecha Término:** 11/06/2014

**Envió documento en papel:** no

**Archivo Asociado:** tesis_s_morenol.pdf


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**Nº:** 2

**Título de Tesis:** Análisis de la regulación transcripcional del gen SDH2-3 de Arabidopsis thaliana y de la presencia del polipéptido SDH2-3 en semillas

**Nombre y Apellidos del (de la) Alumno(a):** Roberto Espinoza Corral
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**ANEXOS**

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A continuación se detallan los anexos físicos/papel que no se incluyen en el informe en formato PDF.