FEBS Letters 583 (2009) 2249–2254

FEBS Letters

journal homepage: www.FEBSLetters.org

Subcellular localization of rice histone deacetylases in organelles

Pil Joong Chung, Youn Shic Kim, Su-Hyun Park, Baek Hie Nahm, Ju-Kon Kim *

School of Biotechnology and Environmental Engineering, Myongji University, Yongin 449-728, Republic of Korea

ARTICLE INFO

Article history:
Received 12 May 2009
Revised 1 June 2009
Accepted 2 June 2009
Available online 6 June 2009

Edited by Ulf-Ingo Flügge

Keywords:
Rice histone deacetylase
Chloroplast
Mitochondria
OsHDAC6
OsHDAC10
OsSIR2b

ABSTRACT

Histone deacetylases (HDACs) are known to function in the nucleus. Here, we report on the organellar localization of three rice HDACs, OsSIR2b, OsHDAC6, and OsHDAC10. The *35S:OsSIR2b-GFP* and *35S:OsHDAC10-GFP* constructs were introduced into tobacco BY2 cells. Co-localization analysis of the green fluorescent protein and MitoTracker fluorescent signals in the transformed BY2 cells indicated that OsSIR2b and OsHDAC10 are localized in the mitochondria. Transgenic Arabidopsis lines harboring *35S:OsHDAC6-GFP* and *35S:OsHDAC10-GFP* constructs were similarly analyzed, revealing that OsHDAC6-GFP is localized exclusively in chloroplasts, whereas OsHDAC10-GFP is localized in both mitochondria and chloroplasts. The presence of OsHDAC6-GFP and OsHDAC10-GFP in chloroplasts was verified by immunodetection.

1. Introduction

The acetylation/deacetylation of histones that are catalyzed by histone acetyltransferases (HATs) and histone deacetylases (HDACs) is an important protein modification involved in the regulation of many biological processes [1]. Although most of the seminal experiments in this area focused on the role of histone acetylation in transcriptional control in the nucleus, recent findings have suggested that the deacetylase activity of HDACs is neither restricted to histone proteins nor always localized in the nucleus [2]. Indeed, some HDACs are partially cytoplasmic and some HDACs are known to act on non-histone substrates including the cytoskeletal protein tubulin and the transcription factor p53 [3,4]. In addition, Schwer et al. [5] previously demonstrated that hSIRT3, a human ortholog of yeast sirtuin2 (SIR2), is an exclusive mitochondrial NAD-dependent deacetylase. Acetyl-CoA synthetase 2 is the first example of a mitochondrial protein being deacetylated by hSIRT3 [6].

Since the identification of HDAC RPD3 in yeast [7], a number of eukaryotic HDACs have been characterized and grouped into distinct classes based on their sequence homology to three yeast HDACs. These include Reduced Potassium Dependency3 (RPD3, class I), Histone DeAcetylase1 (HDA1, class II), and SIR2 (class III) [8,9]. Plants have an additional class of HDACs, the HD2 class [10]. HDACs are also found in prokaryotes, but very little is known about their function. The prokaryotic enzymes acetoin utilization protein (AcuC) and acetylpolyamine amidohydrolase (APAH) are similar in amino acid sequence to the classes I and II HDACs of eukaryotes, respectively [11]. More recently, a new member of the HDAC family, human HDAC11, has been identified [12] and classified as a novel class IV and member of these enzymes [13,14] are more similar in sequence to prokaryotic HDACs.

2. Materials and methods

2.1. Bioinformatic analysis of subcellular localization

BLAST searches and alignments were performed using the National Center for Biotechnology Information (http://ncbi.nlm.nih.gov) and ClustalW (http://clustalw.genome.ad.jp) websites, respectively. A phylogenic tree was made from the protein alignment via ClustalW and then visualized using FigTree version 2.1 (http://tree.bio.ed.ac.uk/software/figtree). Predictions of subcellular localization were made using iPSORT prediction (http://hc.ims.u-tokyo.ac.jp/iPSORT/index.html), TargetP prediction (http://www.cbs.dtu.dk/services/TargetP) and MitoProt (http://ihg2.helmholtz-muenchen.de/ihg/mitoprot.html).

Abbreviations: HDAC, histone deacetylase; GFP, green fluorescent protein; RT-PCR, reverse transcription-polymerase chain reaction; SIR2, sirtuin2.

* Corresponding author. Fax: +82 31 335 8249.
E-mail address: jukon306@gmail.com (J.-K. Kim).

0014-5793/$36.00
doi:10.1016/j.febslet.2009.06.003

2.2. Reverse transcription-polymerase chain reaction (RT-PCR) assay

Gene expression was analyzed by semi-quantitative RT-PCR. Total RNAs were extracted from tissues using Tri reagent (MRC Inc., Cincinnati, OH) according to the method previously described [15]. Oligo(dT) primed reverse transcription of first-strand cDNA synthesis was carried out with 5 μg total RNA using Superscript™ III First-strand synthesis System (Invitrogen, Carlsbad, CA). To ensure exponential amplification, equal volumes of each first strand reaction were amplified with gene-specific primer pairs (Table S2). Thermocycling conditions were 94 °C for 5 min followed by 35 cycles of 94 °C for 1 min, 55–60 °C for 30 s, and 68 °C for 30 s.

2.3. Plant transformation

All constructs for BY2 and Arabidopsis transformation were prepared using the vector pGWB5, which carries a kanamycin- and a hygromycin-selective marker. The plasmid pGWB5 was kindly provided by Prof. Yang Do Choi at Seoul National University, Korea. The PCR products containing the coding sequences for *OsHDAC1*, *6*, *10*, and *OsSIR2b* were cloned into pGWB5 via Gateway Technology (Invitrogen, Carlsbad, CA) to produce full-length OsHDAC proteins fused with green fluorescent protein (GFP) at their C-termini. The recombinant *35S:OsHDAC-GFP* plasmids were introduced into the *Agrobacterium tumefaciens* AGL1 strains through electroporation, and the resulting *Agrobacterium* strains were then used to transform tobacco BY2 (*Nicotiana tabacum* cv Bright Yellow 2) cells and *Arabidopsis thaliana* Columbia.

2.4. Subcellular localization

To stain mitochondria, calli were immersed in 0.2 μM MitoTracker Orange CMTMRos (Molecular Probes, M7510, Eugene, OR) for 15 min, and then mounted on slides with half-strength MS liquid for imaging. The Arabidopsis seedlings were then grown at 22 °C in 16-h-light/8-h-dark conditions. For RT-PCR, leaf tissues were harvested from plants grown for 4 weeks. For staining of nuclei with DAPI (4′,6-diamidino-2-phenylindole; Sigma, St. Louis, MO), roots were extracted from 10 d-old seedlings grown on Murashige and Skoog medium, pH 5.7, containing 0.5% sucrose and 0.8% bacto-agar. The Arabidopsis roots were fixed in 3% glutaraldehyde (Sigma) and stained with 1% DAPI for 4 h. GFP expression in transformed tobacco BY2 cells and Arabidopsis leaves was observed by confocal laser scanning microscopy (LSM510 Meta; Zeiss).

2.5. Protein extractions and immunoblot analysis

To prepare chloroplast fractions, fresh leaves from transgenic and control Arabidopsis plants were homogenized in extraction buffer (50 mM HEPES–KOH, pH 7.5, 330 mM sorbitol, 1 mM $MgCl_2$, 2 mM EDTA, pH 8.0, 0.25% BSA, and 0.1% sodium ascorbate). Intact chloroplasts were then enriched by centrifugation of cell lysates through a Percoll density gradient (40–80%), essentially as described previously [16]. Nuclear-enriched fractions were prepared from Arabidopsis leaves also as described previously [17]. Protein extracts were then separated on 17.5% SDS–polyacrylamide gels and blotted onto a polyvinylidene difluoride (PVDF) membrane (Immobilon-P, Millipore Corporation, Billerica, MA) using a semi-dry transfer apparatus (Bio-Rad). The immunoreactive proteins were detected using primary antibodies against histone H4 (#07-108, Upstate Biotechnology, Lake Placid, NY), GFP (0436324; Nacalai Tesque Inc., Japan) and Lhcb1 (AS01 004; Agrisera, Sweden), and detected by chemiluminescence with Pierce Super Signal Substrate (Pierce, Rockford, IL) in accordance with the manufacturer's protocol.

3. Results

3.1. Prediction of subcellular localization of rice HDACs and their expression

Previously, the rice genome was predicted to contain 16 HDAC genes [9]. Although a histone deacetylating function of OsHDAC proteins can be anticipated due to the levels of homology with their yeast counterparts, very little is known about the biological activities and subcellular localization of these enzymes in rice. In our current study, we have analyzed the organellar localization of three rice HDACs, OsSIR2b, OsHDAC6, and OsHDAC10. Phylogenic analysis of the 123 HDACs identified thus far in eukaryotic and prokaryotic organisms [8] has revealed the presence of five classes of these enzymes (Fig. S1 and Table S1). Of the 123 known HDACs, three in human, hSIRT3, 4, and 5 that belong to the class III group (SIR2), have been reported to be targeted to mitochondrial compartments (Table 1) [5,18]. We predicted the subcellular localization of the 123 HDACs in silico using the software, TargetP, iPSORT, and MitoProt, identifying a total of eight HDACs that appeared to localize in the chloroplasts and/or mitochondria (Table 1). This group included three HDACs from rice, one from Arabidopsis and one from Drosophila, in addition to the three human HDACs previously reported. Among the three rice HDACs, OsHDAC6 was predicted to be localized exclusively to chloroplasts, whereas OsHDAC10 and OsSIR2b to either mitochondria and/or chloroplasts. We found that there was a higher probability that OsHDAC10 targeted to the chloroplasts than to mitochondria, with the opposite holding true for OsSIR2b. This is because the probability values for targeting to mitochondria obtained using MitoProt were 0.084 for OsHDAC10 and 0.918 for OsSIR2b.

The levels of *OsHDAC6*, *OsHDAC10*, and *OsSIR2b* transcripts were analyzed by RT-PCR using total RNAs from various rice plant tissues at different developmental stages (Fig. 1A). *OsHDAC10* and *OsSIR2b* transcripts were detectable in coleoptiles, roots, leaves, flag leaves, and flowers, whereas *OsHDAC6* transcripts were detectable in leaves and flowers, but not in young roots and coleoptiles (Fig. 1B).

3.2. Subcellular localization of OsHDAC6, OsHDAC10, and OsSir2b

To investigate whether the three rice HDACs truly localized at the organelles predicted experimentally, full-length cDNAs for the corresponding genes were isolated, fused to a GFP at their C-terminus, and linked to the 35S promoter to enable constitutive expression. For targeting to mitochondria, *35S:OsSIR2b-GFP*, *35S:OsHDAC10-GFP*, and *35S:OsHDAC6-GFP* were introduced into tobacco BY2 cells. GFP fluorescent signals were then detected using confocal laser scanning microscopy. OsSIR2b and OsHDAC10 were indeed found to be targeted to the mitochondria, as evidenced by the co-localization of GFP and MitoTracker, a mitochondrial-specific dye, and this was not the case with the OsHDAC6 (Fig. 2). OsSIR2b-GFP was observed to be targeted exclusively to mitochondria, i.e. the GFP signals were completely co-localized with those of MitoTracker. In contrast, OsHDAC10-GFP appeared to be targeted to other organelles in addition to mitochondria, because some of the detectable GFP fluorescence was not co-localized with MitoTracker (Fig. 2).

These observations prompted us to transform Arabidopsis with *35S:OsHDAC10-GFP* and *35S:OsHDAC6-GFP* together with *35S:OsHDAC1-GFP* as a control for nuclear localization (Fig. S2) [19]. These three constructs were introduced into *Arabidopsis thaliana* Columbia using the *Agrobacterium*-mediated transformation method [20]. Transgenic lines derived from the *35S:OsHDAC1-GFP*, *35S:OsHDAC6-GFP*, and *35S:OsHDAC10-GFP* transformants were selected

Table 1
Predicted subcellular localization of rice histone deacetylases.

Name	Class	Protein ID[a]	Organism	Program			Reference
				TargetP[b]	iPSORT[c]	MitoProt[d]	
OsHDAC6	IV	NP 001057914	*Oryza sativa*	C[e]	C	0.043	This paper
OsHDAC10	II	ABA95964	*Oryza sativa*	M[f]	C	0.084	This paper
OsSIR2b	III	ABA95936	*Oryza sativa*	C	M	0.918	This paper
AtHDA9	I	CAB72470	*Arabidopsis thaliana*	–	C	0.045	–
DmSRT407	III	AAF46055	*Drosophila melanogaster*	M	M	0.782	–
hSIRT3	III	AAD40851	*Homo sapiens*	M	–	0.746	Schwer et al. [5]
hSIRT4	III	AAD40852	*Homo sapiens*	M	M	0.904	Michishita et al. [18]
hSIRT5	III	AAD40853	*Homo sapiens*	M	M	0.805	Michishita et al. [18]

[a] Genebank accession numbers.
[b] TargetP (http://www.cbs.dtu.dk/services/TargetP/).
[c] iPSORT (http://hc.ims.u-tokyo.ac.jp/iPSORT/index.html).
[d] MitoProt (http://ihg2.helmholtz-muenchen.de/ihg/mitoprot.html).
[e] Chloroplasts.
[f] Mitochondria.

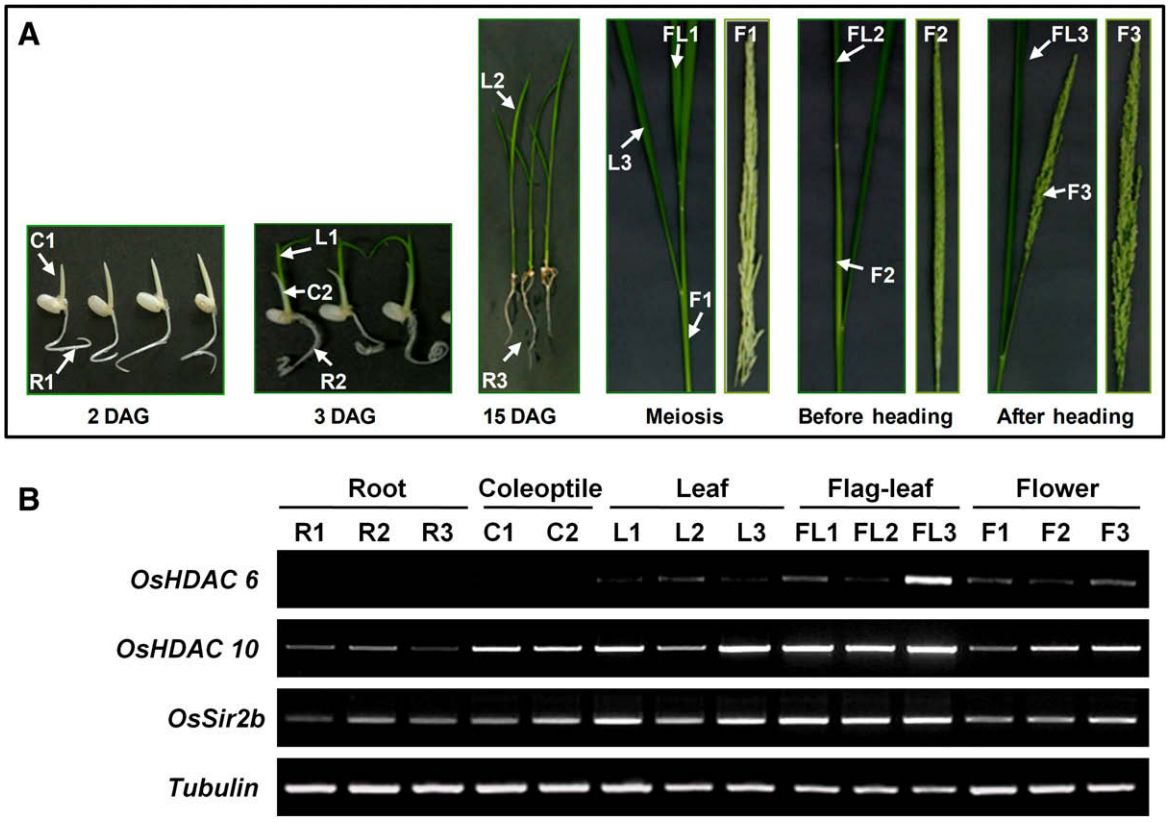

Fig. 1. Expression analysis of *OsHDAC6*, *10*, and *OsSIR2b* in various plant tissues at different developmental stages. (A) Rice seeds were germinated and grown on Murashige and Skoog agar medium in the dark for 2 d (2 DAG) and then in the light for 1 d at 28 °C (3 DAG). Seedlings were then transplanted into soil pots, and grown in the greenhouse for 12 d (15 DAG) until meiosis (meiosis), just prior to heading (before heading) and also right after heading (after heading). (B) RT-PCR analyses of rice HDACs in the indicated tissues and developmental stages. Rice tubulin was used as an internal control. C, coleoptiles; R, roots; L, leaves; FL, flag leaves; F, flowers (panicles).

and transgene expression was assayed by RT-PCR using total RNAs extracted from the leaf tissues of 30 d-old plants (Fig. 3A). *OsHDAC1-GFP*, *OsHDAC6-GFP*, and *OsHDAC10-GFP* transcripts were clearly detectable in the corresponding transgenic lines but not in the non-transgenic (NT) controls. Confocal image analysis of the leaf tissues of *35S:OsHDAC6-GFP* Arabidopsis revealed that OsHDAC6-GFP is targeted exclusively to chloroplasts as the GFP fluorescence was completely superimposed with the autofluorescence signals of the chlorophylls (Fig. 3B). In leaf tissues of *35S:OsHDAC10-GFP* Arabidopsis, in contrast, most of the OsHDAC10-GFP expression appeared to be localized at the chloroplasts (Fig. 3B). These results are again consistent with our observations in BY2 cells. Overall, our current data demonstrate that OsSIR2b and OsHDAC6 are localized exclusively in mitochondria and chloroplasts, respectively, and that OsHDAC10 is localized in both of these organelles.

3.3. Immunolocalization of OsHDAC6 and OsHDAC10 in chloroplasts

To verify the presence of OsHDAC6-GFP and OsHDAC10-GFP proteins in chloroplasts, we prepared both chloroplast- and nuclear-enriched fractions together with cytoplasmic fractions from the transgenic leaves of the *35S:OsHDAC6-GFP* and *35S:OsHDAC10-GFP* Arabidopsis lines. Immunoblotting experiments using anti-GFP

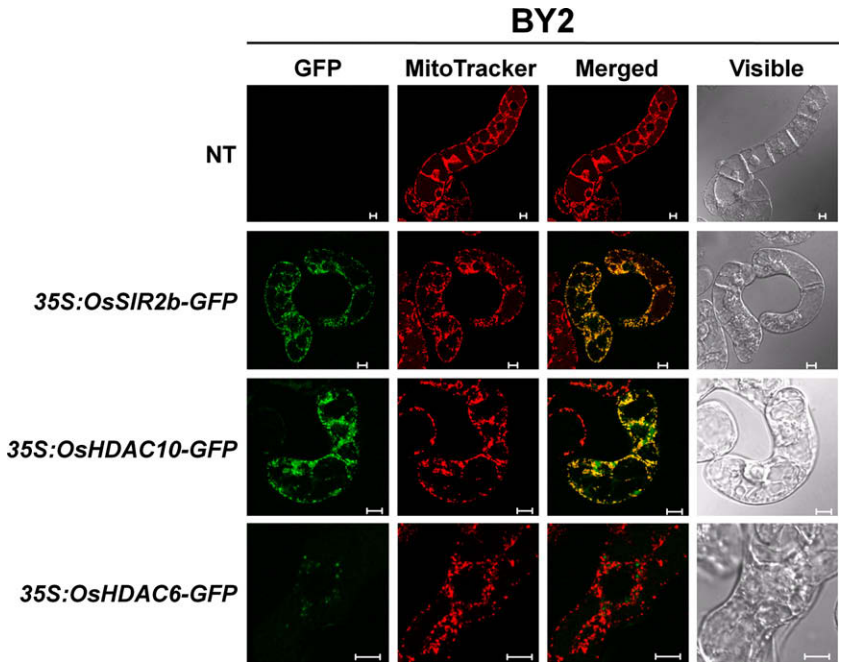

Fig. 2. Subcellular localization of OsSIR2b, OsHDAC10, and OsHDAC6 in tobacco BY2. The *35S:OsSIR2b-GFP*, *35S:OsHDAC10-GFP*, and *35S:OsHDAC6-GFP* constructs were transformed into tobacco BY2 cells. GFP and MitoTracker signals in the transformed tobacco BY2 cells was separately observed by confocal laser scanning microscopy and then resulting images were merged. Visible denotes light microscopic images. Scale bars, 10 μm.

antibodies revealed that OsHDAC6-GFP was predominant in the chloroplast-enriched fractions with some expression in the nuclear-enriched fractions. These analyses also revealed that OsHDAC10-GFP proteins were present in the chloroplast-enriched fractions, but not in the cytoplasmic nor nuclear-enriched fractions (Fig. 3C). The light-harvesting chlorophyll protein complex (Lhcb1), a protein that is specifically localized in chloroplasts, was detected only in chloroplast-enriched fractions (Fig. 3C), suggesting that OsHDAC6-GFP and OsHDAC10-GFP localize predominantly in chloroplasts in the transgenic Arabidopsis plants. In addition, the OsHDAC6-GFP proteins appeared to reside also in the nucleus with a slightly higher molecular weight compared with chloroplasts. The OsHDAC1-GFP protein, a nuclear-specific control, was detected only in nuclear-enriched fractions (Fig. 3C).

4. Discussion

In the current study, we found that some eukaryotic (human, rice, Arabidopsis, and Drosophila) HDACs may be targeted to mitochondria and/or chloroplasts using the prediction programs. Earlier studies have shown that human SIRT3 is a mitochondrial protein with NAD-dependent deacetylase activity and that it activates the Acetyl-CoA synthetase 2, an AMP-forming enzyme [6]. As such, hSIRT3 is involved in controlling central metabolic processes by reversibly acetylating Lys, an invariant residue of a conserved motif in the family of AMP-forming enzymes [21]. OsSIR2b shares a 39% amino acid homology with hSIRT3 in the conserved domain, and was also found to be localized to the mitochondria of tobacco BY2 cells in our current experiments, suggesting that OsSIR2b and hSIRT3 have similar functions.

Previously, it was reported that the prokaryotic protein AcuC (acetoin utilization protein) and the proteobacterium Apah (acetylpolyamine amidohydrolase) may have diverged from a common ancestor and subsequently evolved to give rise to the eukaryotic classes I and II HDACs, respectively [22]. A new group of HDACs, the class IV group, has been distinguished from the class I group containing HDACs that are similar to AcuC [12,14]. The class IV HDACs include OsHDAC6 which is more closely related to the prokaryotic AcuC protein than to other classes of HDACs (Fig. S1). The sequence similarity between OsHDAC6 and AcuC, together with our observation that OsHDAC6-GFP is localized to chloroplasts in transgenic leaves, suggests their common function for eukaryotic organelles and prokaryotic cells. Interestingly, Scher et al. [23] have reported that hSIRT3 not only localizes to the mitochondria, but also to the nucleus. The hSIRT3 protein is transported from the nucleus to the mitochondria upon the onset of cellular stresses such as DNA damage induced by UV-irradiation or overexpression of hSIRT3 itself. Similarly, the OsHDAC6 protein analyzed in our current experiments may be transported from the nucleus to the chloroplast upon overexpression of OsHDAC6-GFP, leaving some proteins still in the nucleus.

Earlier studies have shown the subcellular localization of plant HDACs, ZmRpd3 in maize [24] and OsSRT1 in rice [25]. The maize ZmRpd3 was localized in both nucleus and cytoplasm, probably through the nucleus-cytoplasmic shuttling. Of the four classes of eukaryotic SIR2-like proteins [26], plant proteins are found only in classes II and IV. The rice OsSRT1, a member of the class IV, was shown to be localized in the nucleus by using transient expression in onion cells [25]; whereas, our OsSIR2b, a member of the class II, was shown to be localized in mitochondria of tobacco BY2 cells (in this study). Seven human SIRT proteins were reported to be different in their subcellular locations [18], i.e. hSIRT1, 6, and 7 in nucleus, hSIRT2 in cytoplasm, and hSIRT3, 4, and 5 in mitochondria. Recently, using five different softwares, Arabidopsis HDACs were predicted to be localized in nucleus, mitochondria and chloroplasts [27]. Arabidopsis orthologs of OsHDAC6, OsHDAC10, and OsSir2b proteins appear to be atHDA2 (Genbank accession number AAD40129), atHDA14 (Genbank accession number CAB38805), and atSRT2 (Genbank accession number CAC05449), respectively. The orthologs share 65–71% of protein sequence homology with being highly conserved in the HDAC domain. It will be interesting to see whether the Arabidopsis orthologs are also targeted to organelles. The fact that OsHDACs are localized in chloroplasts and/or mitochondria in plants implies roles in central met-

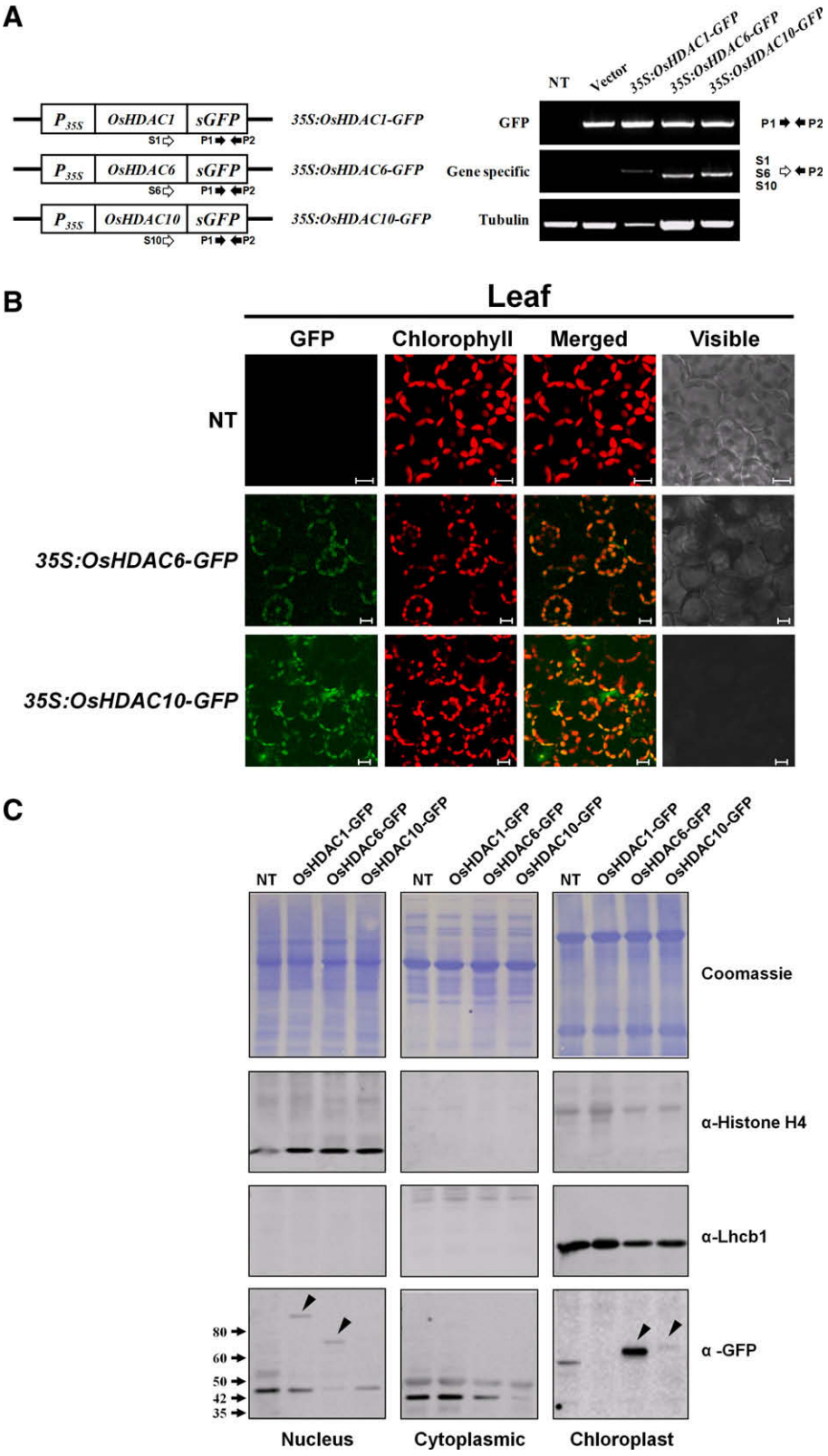

Fig. 3. Subcellular localization of OsHDAC6 and OsHDAC10 in transgenic *Arabidopsis*. (A) cDNAs for *OsHDAC1*, *6*, and *10* were fused to GFP at their C-termini, and placed under the control of the cauliflower mosaic virus 35S promoter. The resultant constructs were then transformed into Arabidopsis and RT-PCR was performed using GFP primers (P1 and P2) and gene-specific primers (S1, 6, or 10 vs P2). (B) Expression of the OsHDAC6-GFP and OsHDAC10-GFP proteins in leaves of transgenic Arabidopsis was observed by confocal laser scanning microscopy, these fluorescence images were merged with those of the chlorophylls in the leaves. Visible denotes light microscope images. Scale bars, 10 μm. (C) Immunodetection of OsHDAC6-GFP and OsHDAC10-GFP proteins in chloroplast-enriched fractions. Nucleus-enriched (Nucleus), cytoplasmic, and chloroplast-enriched (Chloroplast) fractions were prepared from the *35S:OsHDAC1-GFP*, *35S:OsHDAC6-GFP*, and *35S:OsHDAC10-GFP* Arabidopsis plants. About 30 μg of proteins were separated by 17.5% SDS–PAGE and transferred to a PVDF membrane. The immunoreactive proteins were detected using primary antibodies against GFP, histone H4, and the light-harvesting chlorophyll protein complex (Lhcb1) that is specifically localized in chloroplasts.

abolic pathways including photosynthesis. The underlying mechanisms by which the organellar OsHDACs exert their roles in plants remain to be elucidated.

Acknowledgements

This work was supported by the Ministry of Education, Science and Technology of Korea, through the Crop Functional Genomics Center (CG2111 to J.-K.K.) and by Rural Development Administration through the Biogreen21 Program (grant to J.-K.K.).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.febslet.2009.06.003.

References

[1] Strahl, B.D. and Allis, C.D. (2000) The language of covalent histone modifications. Nature 403, 41–45.
[2] Glozak, M.A., Sengupta, N., Zhang, X. and Seto, E. (2005) Acetylation and deacetylation of non-histone proteins. Gene 363, 15–23.
[3] Hubbert, C., Guardiola, A., Shao, R., Kawaguchi, Y., Ito, A., Nixon, A., Yoshida, M., Wang, X.F. and Yao, T.P. (2002) HDA6 is a microtubule-associated deacetylase. Nature 417, 455–458.
[4] Ito, A., Kawaguchi, Y., Lai, C.F., Kovacs, J.J., Higashimoto, Y., Appella, E. and Yao, T.P. (2002) MDM-HDAC1-mediated deacetylation of p53 is required for its degradation. EMBO J. 21, 6236–6245.
[5] Schwer, B., North, B.J., Frye, R.A., Ott, M. and Verdin, E. (2002) The human silent information regulator 2 homologue SIRT3 is a mitochondrial nicotinamide adenine dinucleotide-dependent deacetylase. J. Cell Biol. 158, 647–657.
[6] Schwer, B., Bunkenborg, J., Verdin, R.O., Andersen, J.S. and Verdin, E. (2006) Reversible lysine acetylation controls the activity of the mitochondrial enzyme acetyl-CoA synthetase 2. Proc. Natl. Acad. Sci. USA 103, 10224–10229.
[7] Taunton, J., Hassig, C.A. and Schreiber, S.L. (1996) A mammalian histone deacetylase related to the yeast transcriptional regulator Rpd3p. Science 272, 408–411.
[8] Pandey, R., Muller, A., Napoli, C.A., Selinger, D.A., Pikaard, C.S., Richards, E.J., Bender, J., Mount, D.W. and Jorgensen, R.A. (2002) Analysis of histone acetyltransferase and histone deacetylase families of *Arabidopsis thaliana* suggests functional diversification of chromatin modification among multicellular eukaryotes. Nucleic Acids Res. 30, 5036–5055.
[9] Fu, W., Wu, K. and Duan, J. (2007) Sequence and expression analysis of histone deacetylases in rice. Biochem. Biophys. Res. Commun. 356, 843–850.
[10] Lusser, A., Brosch, G., Loidl, A., Haas, H. and Loidl, P. (1997) Identification of maize histone deacetylase HD2 as an acidic nucleolar phosphoprotein. Science 277, 88–91.
[11] Leipe, D.D. and Landsman, D. (1997) Histone deacetylases, acetoin utilization proteins and acetylpolyamine amidohydrolases are members of an ancient protein superfamily. Nucleic Acids Res. 18, 3693–3697.
[12] Gao, L., Cueto, M.A., Asselbergs, F. and Atadja, P. (2002) Cloning and functional characterization of HDAC11, a novel member of the human histone deacetylase family. J. Biol. Chem. 277, 25748–25755.
[13] Gregoretti, I.V., Lee, Y.M. and Goodson, H.V. (2004) Molecular evolution of the histone deacetylase family: functional implication of phylogenetic analysis. J. Mol. Biol. 338, 17–31.
[14] Ledent, V. and Vervoort, M. (2006) Comparative genomics of the class 4 histone deacetylase family indicates a complex evolutionary history. BMC Biol. 4, 1–10.
[15] Oh, S.J., Kim, S.J., Kim, Y.S., Park, S.H., Ha, S.H. and Kim, J.K. (2008) Arabidopsis cyclin D2 expressed in rice forms a functional cyclin-dependent kinase complex that enhances seedling growth. Plant Biotechnol. Rep. 2, 227–231.
[16] Weigel, D. and Glazebrook, J. (2002) Arabidopsis: A Laboratory Manual, Cold Spring Harbor Laboratory Press, New York. pp. 217–219.
[17] Chung, P.J., Kim, Y.S., Jeong, J.S., Park, S.H., Nahm, H.B. and Kim, J.K. (2009) The histone deacetylase OsHDAC1 epigenetically regulates the OsNAC6 gene that controls seedling root growth of rice. Plant J. doi:10.1111/j.1365-313X.2009.03908.x (accepted article online 28.04.2009).
[18] Michishita, E., Park, J.Y., Burneskis, J.M., Barrett, J.C. and Horikawa, I. (2005) Evolutionarily conserved and nonconserved cellular localizations and functions of human SIRT proteins. Mol. Biol. Cell 16, 4623–4635.
[19] Jang, I.C., Pahk, Y.M., Song, S.I., Kwon, H.J., Nahm, B.H. and Kim, J.K. (2003) Structure and expression of the rice class-I type histone deacetylase genes OsHDAC1-3:OsHDAC1 overexpression in transgenic plants leads to increased growth rate and altered architecture. Plant J. 33, 531–541.
[20] Criqui, M., Parmentier, Y., Derevier, A., Shen, W., Dong, A. and Genschik, P. (2000) Cell cycle-dependent proteolysis and ectopic overexpression of cyclin B1 in tobacco BY2 cells. Plant J. 24, 763–773.
[21] Starai, V.J., Celic, I., Cole, R.N., Boeke, J.D. and Escalante-Semerena, J.C. (2002) Sir2-dependent activation of acetyl-CoA synthetase by deacetylation of active lysine. Science 298, 2390–2392.
[22] Grozinger, C.M., Hassig, C.M. and Schreiber, S.L. (1999) Three proteins define a class of human histone deacetylase related to yeast Hda1p. Proc. Natl. Acad. Sci. USA 96, 4868–4873.
[23] Scher, M.B., Vaquero, A. and Reinberg, D. (2007) SirT3 is a nuclear NAD^+-dependent histone deacetylase that translocates to the mitochondria upon cellular stress. Genes Dev. 21, 920–928.
[24] Varotto, S., Locatelli, S., Canova, S., Pipal, A., Motto, M. and Rossi, V. (2003) Expression profile and cellular localization of maize Rpd3-type histone deacetylases during plant development. Plant Physiol. 133, 1–12.
[25] Huang, L., Sun, Q., Qin, F., Li, C., Zhao, Y. and Zhou, D. (2007) Down-regulation of a SILENT INFORMATION REGULATOR2-related histone deacetylase gene, OsSIRT1, induces DNA fragmentation and cell death in rice. Plant Physiol. 144, 1508–1519.
[26] Frey, R.A. (2000) Phylogenetic classification of prokaryotic and eukaryotic Sir2-like proteins. Biochem. Biophys. Res. Commun. 273, 793–798.
[27] Alinsug, M.V., Yu, C.W. and Wu, K. (2009) Phylogenetic analysis, subcellular localization, and expression patterns of RPD3/HDA1 family histone deacetylases in plants. BMC Plant Biol. 9, 1–15.