



Mini-review

Plant mitochondria under a variety of temperature stress conditions



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ABSTRACT

The biogenesis of plant mitochondria is a multistep process that depends on a concerted expression of mitochondrial and nuclear genes. The balance between different steps of this process, embracing various fluctuations in mitochondrial transcriptome and proteome, may be affected by diverse temperature treatments. A plethora of genes with altered expression during the acting of these stimuli were identified and their expression characterized, including those encoding for classical components of energy dissipating system. Selected aspects of current interest, regarding the functioning of plant mitochondria under cold and heat stresses, are highlighted.

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1. Introduction

Abiotic stresses, including excessive cold or heat, cause a failure in the cultivation of many plant species, including major crops (Bray et al., 2000). Diverse stress conditions often produce similar effects in

cellular damage and cellular compartments. Mitochondria are dynamically involved in the stress response (Millar et al., 2005; Taylor et al., 2009), which implies the necessity of coordinated interorganellar communication. Despite their structural variability, plant mitochondrial genomes encode for a limited amount of proteins as numerous mitochondrial genes were shifted to the nuclear genome in the course of evolution (Alverson et al., 2011). Thus, a complicated and multistep biogenesis of plant mitochondria, depending on the concerted expression of mitochondrial and nuclear genes, is indispensable for the correct assembly of protein complexes (Cs) and supercomplexes (SCs); this balance may be affected by environmental stimuli.

The adaptation of metabolism to stress in plant mitochondria has been elucidated in its various aspects; nevertheless, the relative importance of that process – at the cellular and physiological levels – may not always be understood properly. Excellent reviews have been published

Abbreviations: AOX, alternative oxidase; C(s), complex(es); CSP, cold shock protein; dlps, dehydrin-like proteins; GDC, glycine decarboxylase; COR, cold-regulated; HSPs, heat shock proteins; nat-siRNA, natural antisense transcript-derived small interfering RNA; NDA, internal NAD(P)H dehydrogenases (NDA1 and NDA2); P5CDH, δ -pyrroline-5-carboxylate dehydrogenase; PPRs, pentatricopeptide repeat-containing proteins; Pro, proline; ProDH, proline dehydrogenase; PUMP, plant uncoupling mitochondrial protein; SC(s), supercomplex(es); SHMT, serine hydroxymethyltransferase; sHSP(s), small heat shock protein(s); SOD, superoxide dismutase; UCP(s), uncoupling protein(s).

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regarding the functioning of plant mitochondria under selected abiotic stress conditions (Jacoby et al., 2012; Taylor et al., 2009); however, recent data broaden our understanding of plant mitochondrial biogenesis also under temperature stress. The aim of this mini-review is to provide a comprehensive view of selected aspects of mitochondrial functioning and response under cold and heat treatments.

2. Transcriptomic responses

During retrograde and anterograde signaling pathways under abiotic stress conditions, the expression of many genes coding for mitochondrial proteins is altered. The heat-associated retrograde response was discovered first in *Arabidopsis* plants exhibiting increased thermotolerance and super-induced endogenous heat shock protein genes (*HSP*; reviewed in Rhoads and Subbaiah, 2007).

Energy-dissipating components have been postulated to play a key role in the intramitochondrial stress response (Rasmusson et al., 2004) and in active modulation of signaling pathways from mitochondria that could control the cellular stress response (Vanlerberghe et al., 2009). Regulation of diverse *AOX* (alternative oxidase) genes varies between monocots and dicots. For instance, *AOX1a* isoform in *Arabidopsis* is induced under cold and heat stresses (with almost 2-fold change; Elhafez et al., 2006); however, in sugarcane (*Saccharum* sp.) – during longer chilling – *AOX1c* is more upregulated (Borecký et al., 2006). Clifton et al. (2005) suggested that the *AOX2* isoform plays a role in interorganellar signaling as its transcripts were repressed in stress. Although *AOX1* transcripts are generally sensitive to different stress conditions and *AOX2* mRNAs are often constitutively synthesized, *AOX1d* is downregulated during exposure of *Arabidopsis* plantlets to 4 °C (Borecký and Vercesi, 2005). Interestingly, in *Citrus aurantium* cold and heat lower *AOX* mRNA abundance and also strongly suppress the accumulation of internal NAD(P)H dehydrogenase transcripts (Ziogas et al., 2013). Temperature stress alters the amount of mRNAs encoded for uncoupling proteins (*UCP1* and *UCP2*) as well as for most of the investigated alternative NAD(P)H dehydrogenases in *Arabidopsis* plants; interestingly, *NDA1* and *NDA2* transcripts encoding for internal NAD(P)H dehydrogenases are reciprocally regulated under cold and heat stresses (Elhafez et al., 2006).

The transcriptomic changes inside mitochondria (related to the mRNA turnover and steady-state abundance) are often more evident than proteomic ones (Giegé et al., 2005; Van Aken et al., 2009). Moreover, mRNA levels may not accurately reflect protein abundance, for instance in the case of some *HSP* genes (Taylor et al., 2009; Van Aken et al., 2009). This implies stress-driven dynamic regulation of the mRNA pool, which is accessible for the synthesis of mitochondrial proteins. Although mitochondrial mRNAs are generally not polyadenylated, the level of poly(A)⁺ transcripts of mitochondrial origin for mitochondrial genes co-expressed with the heat shock transcription factor At2g26150 is elevated in heat and could be reversed in heat recovery (Adamo et al., 2008).

Naydenov et al. (2010), using microarray analysis and real-time RT-PCR, showed cold-specific alterations of many mitochondrial transcripts in wheat (*Triticum aestivum*) embryos. It resulted in down- or upregulations in mRNAs of 13 mitochondrial genes. Most of them were downregulated at the initial stage of cold stress, but some (*nad*, *atp* and *cob*) showed a very evident upregulation after 2 or 3 days of cold stress. The levels of some nuclear transcripts (for Mn containing superoxide dismutase [Mn-SOD] and *AOX1a*) increased. Thus, in wheat embryos the response of mitochondrial transcription during cold stress is very quick in order to postpone embryo development before stress cessation and the occurrence of possible cellular damage.

The regulation of *Arabidopsis* mitochondrial respiratory chain components under temperature stress was also assayed in detail at RNA level by Gonzalez et al. (2007), who noticed a coordinated, tissue- and developmentally-dependent response of mitochondrial Cs components encoded by the nuclear genome. The chilling of *Arabidopsis* seedlings

resulted in major (>1.5-fold change) downregulations not only in alternative components of the respiratory chain, but – interestingly – also in γ -carbonic anhydrase isoform and CI and CII subunits. At least 1.5-fold change upregulations were more frequent and comprised 40 alterations, including 25 changes for structural subunits of CI–CIV and ATP synthase. The responses in cold-treated *Arabidopsis* dry seeds were similar; however, 69 upregulations (>1.5-fold change) included almost 46 for structural respiratory chain components.

3. Alterations in the mitochondrial proteome and protein import

The plant mitochondrial proteome, estimated to comprise at least 1500 proteins (Taylor et al., 2011), is a dynamic structure that responds to genetic, environmental and developmental signals (Millar et al., 2005). Although the amount of low-abundant mitochondrial proteins involved in cold and heat responses is still underestimated (Huang et al., 2011; Taylor et al., 2009), a list of 75 cold- and 51 heat-regulated non-redundant proteins, based on the prominent experimental data, is presented (Supplementary Table 1). However, only a limited number of studies have directly focused on the analysis of the mitochondrial proteome under temperature stress (Qin et al., 2009; Tan et al., 2012; Taylor et al., 2005; Yin et al., 2009). Selected effects of cold and heat stresses on the plant mitochondrial proteome are discussed below.

Chilling causes more pronounced breakdown of plant mitochondrial proteins than other stress conditions, like drought, even though drought induces oxidative stress more effectively (Taylor et al., 2005). However, the amount of damaged and modified (for instance oxidized or S-nitrosylated) proteins may increase under cold and – especially – heat stresses. Respiratory chain components are part of such regulation (Ziogas et al., 2013). Diverse effects on mitochondrial protein oxidation under various temperature stress conditions have been reported, even though plastids and peroxisomes in green tissues are the major ROS sources. Mitochondrially-targeted redox-sensitive GFP was significantly oxidized in severe heat. Strikingly, cold impedes perturbations in the mitochondrial redox balance (Schwarzländer et al., 2009). However, the reproducibility of such effects should be validated under field conditions. Diverse dehydrin-like proteins (dlps; 28, 52–63 kDa) were found in the mitochondria of some cereals in cold and frost responses (Borovskii et al., 2002). This study was considerably extended by Rurek (2010), who identified a few novel dlps candidates in yellow lupin (*Lupinus luteus*), cauliflower (*Brassica oleracea* var. *botrytis*) and *Arabidopsis* mitochondria also under heat stress and heat recovery conditions and specified their submitochondrial localization and topology.

Apart from classical heat shock proteins, elevated temperature also stimulates the synthesis of small heat shock proteins (sHSPs; 15–30 kDa) in plant mitochondria (Banzet et al., 1998; Lenne and Douce, 1994; Lund et al., 1998). They protect some respiratory Cs (especially CI – as the most heat-sensitive component of the respiratory chain) from degradation and proteolysis (Downs and Heckathorn, 1998; Lenne and Douce, 1994). In addition, during thermal recovery, proline (Pro) is an important nitrogen or energy resource, a compatible osmolyte and an important ROS scavenger. For its degradation, Pro is imported into mitochondria and converted to glutamate in the Pro/P5C cycle by proline dehydrogenase (ProDH) and $^1\Delta$ -pyrroline-5-carboxylate dehydrogenase (P5CDH). Enzymes of the Pro/P5C cycle are frequently expressed in a reciprocal manner under some stress conditions (Peng et al., 1996). *Arabidopsis* ProDH loss-of-function mutants are sensitive to external proline supply and heat stress (Funck et al., 2010). Free Pro is accumulated in the leaves of cold-treated wild-type cauliflower (*B. oleracea* var. *botrytis*) and mutant plants with enhanced frost resistance, selected in hydroxyPro-containing medium (Hadi et al., 2011). The level of mRNA expressed P5CDH significantly decreased in *Arabidopsis* plants expressing ectopically P5C synthetase 1 under heat stress; Pro accumulation impeded *Arabidopsis* seedlings growth, which suggests that at least under particular conditions Pro may not serve as an osmolyte (Lv et al., 2011).

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