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Differential expression of uncoupling mitochondrial protein and alternative oxidase in the plant response to stress

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Abstract Different cell types, organs and tissues shape their mitochondrial proteome according to the cellular environment that is dictated by differentiation, development and metabolic status. Under each circumstance, members of multigenic families that encode mitochondrial proteins are differentially expressed to meet the mitochondrial metabolic demand. However, the mitochondrial proteome may drastically change in response to stress conditions. Examples of the changes in mitochondrial protein expression caused by stress are represented by the energy-dissipating mitochondrial uncoupling protein (UCP) and alternative oxidase (AOx). UCP and AOx belong to multigenic families in plants, and their members, which are expressed in a time/tissue specific manner, respond differentially to stress conditions. In general, UCP and AOx are not expressed at the same levels concurrently in the same tissue, and the level of each protein varies in each stress condition. In addition, under non-stress conditions, UCP is expressed at much higher levels compared with AOx. The role of their differential expression in plant growth, development and response to stress is discussed.

Keywords Plant · Mitochondria · UCP · AOx · Stress

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Introduction

Plants possess at least two energy-dissipating systems in their mitochondria: one is comprised of uncoupling proteins (UCPs), and the other is comprised of alternative oxidases (AOxs). Both systems lead to a decrease in the efficiency of oxidative phosphorylation. AOx also leads to heat production in certain tissues of thermogenic plants, whereas UCP, although it is involved in heat production in the brown adipose tissue (BAT) of mammals (Nicholls and Rial 1999), has not been associated with heat production in plants (Jarmuszkiewicz et al. 2001). UCP and AOx are present concurrently in the mitochondria of green tomato fruit, but these proteins do not work simultaneously because free fatty acids block the activity of AOx while activating UCP (Sluse and Jarmuszkiewicz 2000). Recently, investigations into the sequenced plant genomes and EST collections have allowed the identification and characterization of the gene families that encode UCP and AOx (Hourton-Cabassa et al. 2004; Borecky et al. 2006). UCP and AOx are ubiquitous in plants and could have various physiological roles including heat production and protection against oxygen free radicals (Ito-Inaba et al. 2009). UCP may also play a role in regulating the energy metabolism in mitochondria to cope with the excessive production of reactive oxygen species (Brandalise et al. 2003a; Considine et al. 2003). AOx could work as a valve in situations that lead to increases in reducing power and phosphate potential in the cell (Jarmuszkiewicz et al. 2001). Thus, the two energy-dissipating pathways seem to complement the absence of one another to meet the physiological demand of a particular cell/tissue or to respond to particular changes imposed by stress. In this review, we focus on the role of the UCP and AOx gene families in the plant response to stress.

The role of UCP and AOx in plant bioenergetics

Plant UCP has been shown to modulate mitochondrial membrane potential, ROS production and tricarboxylic acid cycle flux, thus modulating the energy balance within the mitochondria. High membrane potential leads to increased ROS production and increased UCP activation, both of which increase proton conductance and results in a reduced membrane potential that in turn reduces ROS production (Sluse et al. 2006). This situation may alleviate the thermodynamic restrictions on the tricarboxylic acid cycle flux (Smith et al., 2004).

In skunk cabbage flowers, the temperature is controlled by the activation of AOx, possibly by UCPs, and also by increased mitochondrial biogenesis (Ito-Inaba et al. 2009). In low temperature conditions, AOx and UCP are enhanced in the stamen while mitochondrial density is higher in the microspore cells, and these alterations are correlated with the metabolic rate of the female stage (Ito-Inaba et al. 2009). The increased AOx and UCP activities along with the increased mitochondria density in this thermogenic plant are believed to protect pollen maturation against low temperature damage (Onda et al. 2008). This is somewhat consistent with the processes in the brown adipose tissue (BAT) of mammals. In the BAT, increases in the number of mitochondria and UCP1 expression in polar bears and small rodents are responsible for temperature control when these animals are exposed to low temperature conditions (Nicholls and Rial 1999). In addition to the protective role of the thermogenic activity of skunk cabbage florets, the increases in temperature could also help the evaporation of volatile compounds that attract pollinators and provide a warm environment for insect pollinators (Seymour et al. 2003).

The mitochondrial energy metabolism depends on the interaction between UCP and several proteins. Conditions that lead to increased production of ROS cause an energetic imbalance that is compensated for by the up-regulation of enzymes that compete with UCP2 for the substrate (Sluse et al. 2006). The mitochondrial proteomic adaptation requires cross-talk between mitochondria and the nucleus to down- or up-regulate the expression of the genes that encode mitochondrial proteins that are involved in the stress response (Sluse et al. 2006).

An interesting point regarding the role of UCPs in plant metabolism was raised by the finding that UCP1 is involved in regulating the efficiency of photosynthesis. An Arabidopsis UCP1 knock-out mutant has shown that the protein is required to adapt to ROS poisoning of the respiratory chain during photosynthesis. UCP allows a controlled dissipation of the proton gradient that relieves the thermodynamic constraint on electron flux and allows continued photorespiration (Sweetlove et al. 2006).

Genome architecture of UCP and AOx

UCPs in eukaryotes form a separate family within the superfamily of mitochondrial anion carriers (Nogueira et al. 2005). Phylogenetic analysis of amino acid sequences from diverse organisms grouped the UCPs into five subfamilies: subfamily I comprises animal UCP1, UCP2, and UCP3; subfamilies II comprises plant UCP1 and UCP2; subfamily V comprises plant UCP4 and UCP6; subfamily III comprises mammalian UCP4 and plant UCP3 along with a C. elegans UCP; and subfamily IV comprises the mammalian brain mitochondrial UCP5 (Nogueira et al. 2005). UCPs are ubiquitously distributed in a wide range of organisms including animals, plants, fungi, and protozoan (Nogueira et al. 2005; Hourton-Cabassa et al. 2004).

Genome investigations have identified six genes that encode UCPs and five genes that encode AOx in the Arabidopsis genome (Fig. 1) (Borecky et al. 2006). The genes that encode UCP1 and UCP2 are located on chromosomes 3 and 5, respectively. These two genes contain nine exons in an almost identical configuration. UCPs 3 and 6 contain only two exons and are located on chromosomes 1 and 5, respectively, while UCP4 and AtPUMP5 are located on chromosomes 4 and 2, respectively and are intronless genes (Nogueira et al. 2005; Borecky et al. 2006). Other plants, such as rice, have genes that encode UCPs in a structural configuration similar to that of Arabidopsis, and the par wise similarities in the UCP gene structure of these plants suggest that they arose by chromosome duplications (Nogueira et al. 2005; Borecky et al. 2006). Five genes that encode UCPs were found in

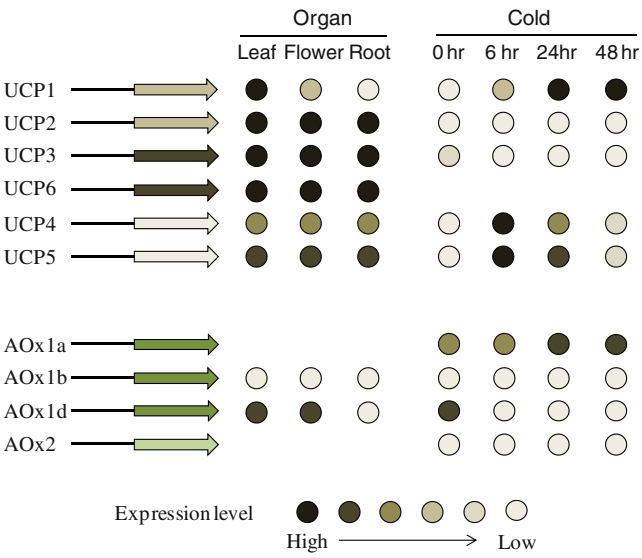

Fig. 1 Representation of the expression profile of UCP and AOx in different Arabidopsis organs in response to low temperature conditions (4°C). Data adapted from Borecky et al. 2006

sugarcane, which also possesses four AOx orthologues (Borecky et al. 2006).

Differential expression of UCP and AOx in plants under normal and stress conditions

Members of the plant UCP and AOx families have been shown to be expressed in a time/tissue/stress-dependent manner in a pattern that differs between monocots and dicots (Fig. 1). In the monocot sugarcane, it was shown that UCP2 expression in young leaves was not altered when plants were subjected to 4°C for up to 48 h (Borecky et al. 2006). UCP1 and 3 expression was not detected in young sugarcane leaves during the chilling treatment, whereas UCP4 and 5 were strongly induced (Borecky et al. 2006). Accordingly, sugarcane AOx1a expression was nearly unaffected by chilling stress, whereas AOx1c was slightly induced after 6 h at 4°C. In contrast, sugarcane AOx1b and AOx1d expression was undetectable in plantlets that were subjected to chilling stress. In the dicot Arabidopsis leaves, although UCP2, 3 and 6 expression did not appear to be altered by chilling stress, UCP1, 4 and 5 expression was strongly induced by cold treatment (Borecky et al. 2006). Accordingly, when Arabidopsis plants were subjected to 4°C, Ox1a was induced in the leaves, AOx1b, AOx1c and AOx2 were undetectable or were expressed at very low levels and AOx1d was down-regulated (Borecky et al. 2006). These findings are consistent with the observation that in soybean plants, UCP and AOx are differentially expressed in a time-dependent manner, which suggests that the two energy-dissipating systems operate at different times (Daley et al. 2003).

Compared to wild-type control plants, transgenic tobacco plants that overexpress Arabidopsis UCP1 showed a significant increase in tolerance to oxidative stress promoted by exogenous hydrogen peroxide (Brandalise et al. 2003a).

Using an Arabidopsis *aox1a* gene knock-out mutant, it was demonstrated that this isoform is mainly expressed in the leaves and are involved in plant acclimation to low temperature conditions (Watanabe et al. 2008). However, despite the absence of AOx1a, the mutant did not present visible phenotype alterations compared to the wild type. Compared to wild type controls, many proteins of the respiratory chain, including UCP1, were increased in the mutant to compensate for the absence of AOx in low temperature conditions (Watanabe et al. 2008)

UCP along with the mitochondrial potassium channel (PmitoK ATP) has been shown to be induced by hyperosmotic stress in durum wheat plants (Trono et al. 2004). It was shown that both systems were activated by reactive oxygen species and were able to control mitochondrial superoxide anion production (Trono et al. 2004).

Expression studies demonstrated that ZmPUMP is ubiquitously expressed in maize tissues, and its transcript level is not altered in the early stages of embryo germination. In contrast to known UCP genes, ZmPUMP is not responsive to cold stress. Instead, its expression is increased in response to H2O2- or menadione-induced oxidative stress (Brandalise et al. 2003b).

Concluding remarks

The existence of gene families that encode isoforms of the mitochondrial energy-dissipating proteins, UCP and AOx, clearly indicate that those proteins, which may have originated by chromosome duplication, evolved to meet the demand of mitochondrial metabolism of the diverse cell types, organs and tissues. However, these two proteins do not work alone. Instead, they participate as members of an orchestra that is comprised of proteins encoded by the nuclear and mitochondrial genomes. Clear evidence for this has been shown by studies of the mitochondrial proteome of the mice BAT and WAT, which showed that the BAT mitochondrial proteome is dramatically different from the WAT mitochondrial proteome and that cold exposure increases mitochondrial mass and respiratory potential by upregulating UCP1 and Complex I (Forner et al. 2009). The understanding of the physiological role UCP and AOx in plants would be important in determining the mitochondrial proteome of thermogenic tissues of plants that are exposed to different stress conditions.

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