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The multiplicity of dehydrogenases in the electron transport chain of plant mitochondria

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Abstract

The electron transport chain in mitochondria of different organisms contains a mixture of common and specialised components. The specialised enzymes form branches to the universal electron path, especially at the level of ubiquinone, and allow the chain to adjust to different cellular and metabolic requirements. In plants, specialised components have been known for a long time. However, recently, the known number of plant respiratory chain dehydrogenases has increased, including both components specific to plants and those with mammalian counterparts. This review will highlight the novel branches and their consequences for the understanding of electron transport and redundancy of electron paths.

Keywords: Carbon metabolism; Electron transport chain; NADH; NADPH; Plant mitochondria; Ubiquinone

1. Introduction

The electron transport chain (ETC) in the mitochondrial inner membrane of most eukaryotes consists of four large protein complexes, complex I–IV. The electron transport activity of complex I, III and IV is coupled to extrusion of protons across the inner mitochondrial membrane. The electrochemical proton gradient that is formed and maintained in the process is used by the ATP synthase (also called complex V although it is not part of the ETC) to make ATP. The plant ETC, however, is highly branched. It has been known for decades that the plant oxidative phosphorylation system has several alternative pathways of electron transport, now known to be catalysed by type II NAD(P)H dehydrogenases and by the alternative oxidase (AOX). These proteins mediate bypasses around the proton-translocating multi-protein complexes (I–IV). Type II NAD(P)H dehydrogenases bypass complex I and AOX bypasses complexes III and IV (Finnegan et al., 2004; Millenaar and Lambers, 2003; Møller, 1997, 2001; Møller et al., 1993; Rasmusson et al., 2004; Siedow and Umbach, 1995; Vanlerberghe and McIntosh, 1997). The type II NAD(P)H dehydrogenases and the AOX transport electrons without pumping protons. Thus, they will not directly contribute to respiratory ATP production, nor be directly controlled by cellular adenylate status. Depending on the substrate used for respiration, AOX and type II NADH dehydrogenases are theoretically able to decrease respiratory ATP output by roughly 60 and 30%, respectively. Downstream of the ETC, the uncoupling protein, which is well-characterised in animal mitochondria where it acts as a proton channel, is also found in plants (Fernie et al., 2004; Vercesi et al., 2006). This protein allows proton flow that bypasses the ATP synthase. Thus, with regard to plant energy-balance adjustments, the uncoupling protein

Abbreviations: AOX, alternative oxidase; ETC, electron transport chain; ETF, electron transfer flavoprotein; ETFQ-OR, electron transfer flavoprotein: quinone oxidoreductase; G3P, glycerol-3-phosphate; GalL, L-galactono-1,4-lactone; UQ, ubiquinone.

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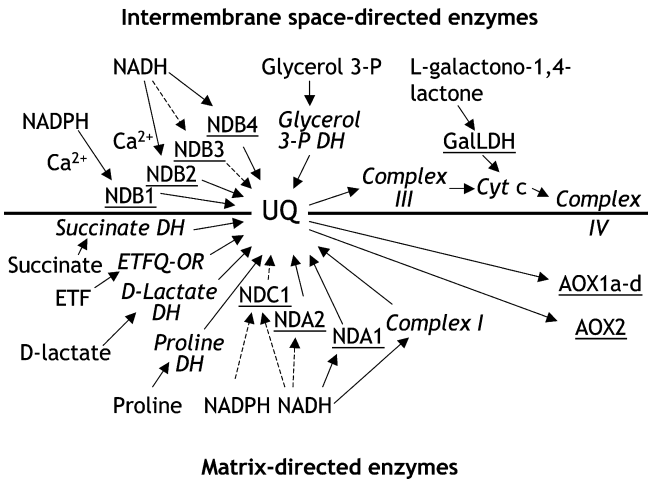

Fig. 1. The ETC in plants. Names of enzymes present in both plants and animals are italisised, whereas names of enzymes absent in animals are underlined. Most of these have homologues also in fungi and/or protists. Enzymes are denoted according to the location, matrix or intermembrane space, for their active site for hydrophilic substrates. Arrows denote transfer of reducing equivalents, *i.e.* electrons. Hypothetical paths are marked by dashed arrows. DH, dehydrogenase.

may have overlapping functions with the energy-bypass proteins in the ETC.

Apart from being energy conservation bypasses, the type II NAD(P)H dehydrogenases also provide a more diverse spectrum of entry points for electrons into the respiratory chain. Recently, our knowledge about the individual NAD(P)H dehydrogenases has increased considerably. At the same time, several additional ETC electron entry points have been characterised in plants, for example electron transfer flavoprotein: quinone oxidoreductase (ETFQ-OR), L-galactono-1,4-lactone (GalL) dehydrogenase and glycerol-3-phosphate (G3P) dehydrogenase. This has substantially increased the number of branches and thus the complexity of mitochondrial electron transport (Fig. 1). This review will give an overview of the latest developments regarding electron input branches in the plant ETC, and discuss issues relating to the coordination of the different enzymes.

2. Paths of NAD(P)H delivery to the electron transport chain

NADH and NADPH destined for respiratory oxidation will, depending on cell type and conditions, be produced by different carbon pathways inside the mitochondrion, in the cytosol, or even in the chloroplast. It may then be oxidised directly by NAD(P)H dehydrogenases with active sites facing the compartment of NAD(P)H production. Alternatively, the reducing equivalents may be shuttled to their site of entry into the mitochondrial ETC.

2.1. NAD(P)H dehydrogenases in plant mitochondria

Two types of respiratory NAD(P)H dehydrogenases (NAD(P)H:quinone oxidoreductases) exist in mitochondria, and plants contain both types. These are complex I, which is homologous to bacterial type I NADH dehydrogenases, and type II NAD(P)H dehydrogenases.

2.1.1. Complex I

Complex I in plant mitochondria is a transmembrane proton-pumping protein complex, composed of at least 40 subunits (Braun and Zabaleta, 2007; Cardol et al., 2004; Heazlewood et al., 2003; Rasmusson et al., 1998). In inside-out vesicles that expose the matrix side of the mitochondrial membrane, potato complex I reduces ubiquinone (UQ) while oxidising NADH and deamino-NADH, and with a low affinity also NADPH (Rasmusson and Møller, 1991b). The oxidation is sensitive to inhibitors like rotenone and diphenylene iodonium (Agius et al., 1998; Melo et al., 1996). In these respects, complex I in plants is similar to that of other eukaryotes. However, in peptide-permeabilised potato mitochondria, complex I has a different substrate specificity, showing lower relative rates of deamino-NADH oxidation and virtually no oxidation of NADPH (Johansson et al., 2004). Thus, complex I may be affected by the surrounding matrix proteins, which are lost upon isolation of membrane vesicles. It remains to be investigated if this effect is general for mitochondrial complex I in other eukaryotes, though it is consistent with the observation of a direct substrate transfer from malate dehydrogenase to the complex I homologue in *Escherichia coli* (Amarneh and Vik, 2005). An intramitochondrial malate shuttle involving malate dehydrogenase in proximity to complex I has also been suggested for pea leaf mitochondria (Wiskich et al., 1990). For complex I, 31 widely conserved subunits have been identified, but the complex in plants and algae contains at least 10 additional subunits (Cardol et al., 2004), which carry additional enzymatic functions. The complex contains a GalL dehydrogenase involved in ascorbate synthesis (Heazlewood et al., 2003; Millar et al., 2003) and a gamma-carbonic anhydrase domain (Braun and Zabaleta, 2007). However, unlike the complex in mammals and *Neurospora crassa*, the plant complex I appears not to contain an acyl carrier protein subunit integrated into the complex (Meyer et al., 2007; Runswick et al., 1991; Sackmann et al., 1991). It is not known whether the additional enzymatic functions of plant complex I directly influence its NADH:UQ oxidoreductase activity, but the GalLDH will contribute to electron transport downstream of UQ.

2.1.2. Type II NAD(P)H dehydrogenases

Type II NAD(P)H dehydrogenases are present in plants, fungi, protists and many bacteria, but not in animals (Friedrich et al., 1995; Joseph-Horne et al., 2001; Kerscher, 2000; Melo et al., 2004; Rasmusson et al., 2004). The genes code for polypeptides of 50–60 kDa. The enzymes usually contain one non-covalently bound FAD, except in hyperthermophilic archea where FAD is replaced by FMN (Melo et al., 2004). In eukaryotes, *Saccharomyces cerevisiae* mitochondria stand out by lacking complex I. They contain