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Review Article

Interdependence of tetrapyrrole metabolism, the generation of oxidative stress and the mitigative oxidative stress response

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ABSTRACT

Tetrapyrroles are involved in light harvesting and light perception, electron-transfer reactions, and as co-factors for key enzymes and sensory proteins. Under conditions in which cells exhibit stress-induced imbalances of photosynthetic reactions, or light absorption exceeds the ability of the cell to use photo-excitation energy in synthesis reactions, redox imbalance can occur in photosynthetic cells. Such conditions can lead to the generation of reactive oxygen species (ROS) associated with alterations in tetrapyrrole homeostasis. ROS accumulation can result in cellular damage and detrimental effects on organismal fitness, or ROS molecules can serve as signals to induce a protective or damage-mitigating oxidative stress signaling response in cells. Induced oxidative stress responses include tetrapyrrole-dependent and -independent mechanisms for mitigating ROS generation and/or accumulation. Thus, tetrapyrroles can be contributors to oxidative stress, but are also essential in the oxidative stress response to protect cells by contributing to detoxification of ROS. In this review, we highlight the interconnection and interdependence of tetrapyrrole metabolism with the occurrence of oxidative stress and protective oxidative stress signaling responses in photosynthetic organisms.

Contents

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Introduction

Tetrapyrroles are linear or cyclic molecules containing four pyrrole rings that are ubiquitously utilized as cofactors in all kingdoms. These molecules are involved in central metabolic processes, including respiration, methanogenesis and photosynthesis (reviewed in [1]). The most versatile tetrapyrrole cofactor is the porphyrin heme. This cyclic tetrapyrrole contains a central iron atom and is a major player in many cellular processes. Heme-bound proteins, i.e., hemoproteins, are involved in diverse functions ranging from oxygen transport to cellular signaling, energy transduction, lipid biosynthesis, and gene regulation, among others (reviewed in [1–3]). In photosynthesis, chlorophyll and the open-chain phycobilins are the most abundant and functionally important tetrapyrroles. Chlorophyll is present in the core photosystems of oxygenic photosynthetic organisms and the extended light-harvesting complexes of plants and algae (reviewed in [4–6]). Phycobilins are found in the light-harvesting phycobilisomes attached to the core photosystems of algae and cyanobacteria and phycobilins and related linear tetraypyrrole bilins serve as the chromophores of plant and bacterial photoreceptors (reviewed in [7]).

Tetrapyrrole biosynthesis has been studied in great detail and is outlined in many excellent reviews [1,8]. A central portion of tetrapyrrole synthesis yields products for chlorophyll synthesis and for production of heme and heme-derived tetrapyrroles, all of which are critical for photosynthesis and respiration. This part of tetrapyrrole synthesis includes the formation of protoporphyrin IX, a cyclic tetrapyrrole, after which the pathway bifurcates into the magnesium-dependent chlorophyll or iron-dependent heme branches (Fig. 1). The cleavage of heme and subsequent reduction of the biliverdin product yields bilins, which can act as chromophores for light-sensing photoreceptors or light-harvesting phycobiliproteins as introduced above. In this regard, tetrapyrroles are of special interest in the photosynthetic cell.

Photooxidative stress is a core part of a photosynthetic lifestyle. It can be caused by overreduction of the photosynthetic apparatus when light absorbed exceeds the needs for carbon accumulation or the capacity for electron transfer. When light is in excess, energy transfer from photoexcited chlorophyll in photosystem II to oxygen results in singlet oxygen ($^1O_2$) formation [9–11]. Other reactive oxygen species (ROS) form through distinct mechanisms, e.g., electron transfer from electron acceptors of photosystem I to oxygen instead of ferredoxin primarily leads to superoxide anion radical ($O_2^{\bullet -}$) production [12]. The relatively stable ROS hydrogen peroxide (H_2O_2) can be produced due to reduction of superoxide, and can be detoxified by catalases or peroxidases (reviewed in [13,14])(note: see Table 1 for description of these and other molecules involved in oxidative stress). However, H_2O_2 formation can also be catalyzed by metals such as iron to generate hydroxyl radical ($HO^{\bullet}$) in Fenton chemistry [15].

Besides chlorophyll, other tetrapyrroles can act as photosensitizers due to their ability to absorb light of different wavelengths. These molecules, thus, also pose a threat to the cell when they accumulate in their free form due to changes in their synthesis and utilization [16,17]. Central to cellular survival and productivity, therefore, is a need to mitigate any potential damage associated with the accumulation of free tetrapyrroles. Notably, an accumulation of tetrapyrroles in the cell, e.g., by a change in flow through biosynthetic pathways, leads to increased production and/or activity of ROS-detoxifying enzymes, including superoxide dismutase (SOD) and catalase enzymes [18]. Additionally, detoxification of redox-active heme can be achieved by heme-binding proteins through export, sequestration and/or degradation of heme (reviewed in [19]). On the contrary, some tetrapyrroles have been reported to have antioxidant properties and thus rather than causing damage to cells can support ROS scavenging [20]. These observations highlight the complex relationship between tetrapyrrole metabolism and oxidative stress. In this review, we primarily focus on the interdependence of tetrapyrroles and oxidative stress in photosynthetic organisms.

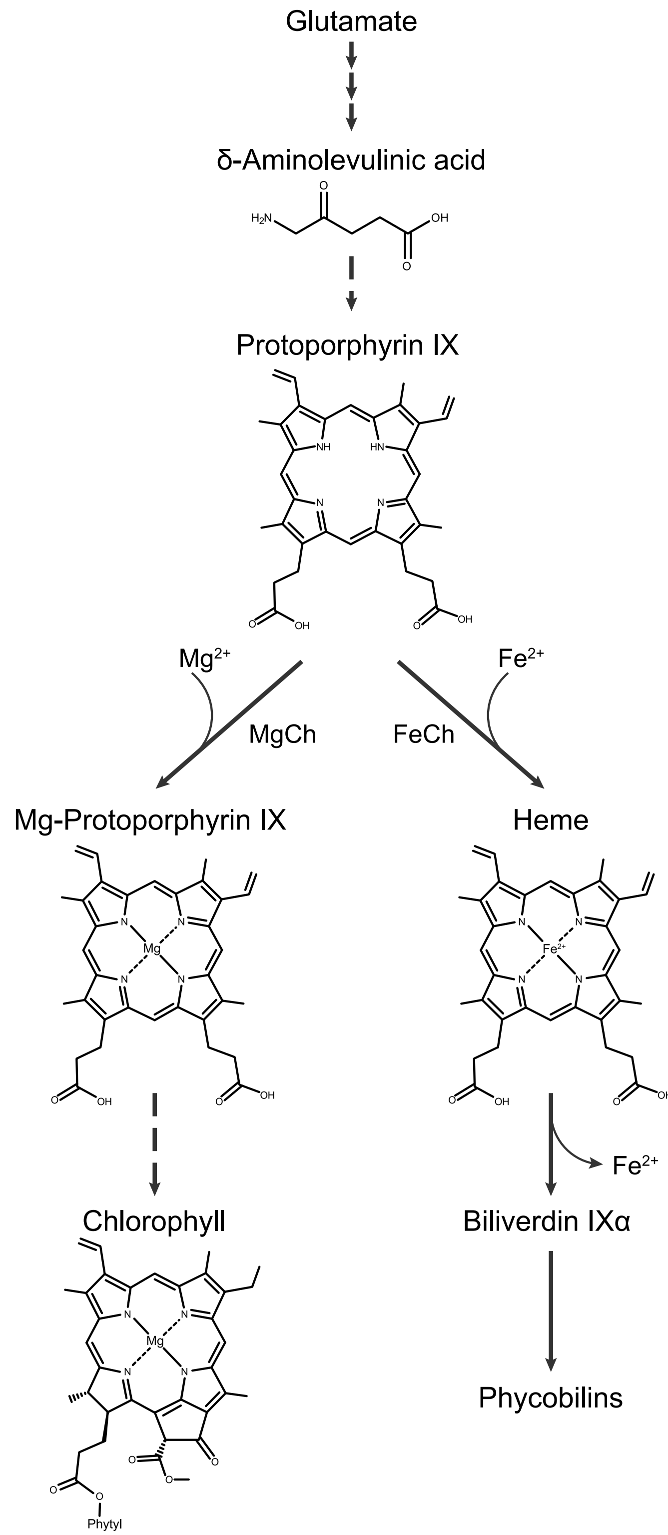

Fig. 1. Tetrapyrrole biosynthesis. Eight molecules of δ-aminolaevulinic acid (ð-ALA) form the tetrapyrrole ring. The cyclic tetrapyrrole protoporphyrin IX, a porphyrin, feeds into the magnesium-dependent (Mg^{2+}) chlorophyll or iron-dependent (Fe^{2+}) heme pathway. The chlorophylls are essential components in the photosystems, whereas the phycobilins serve in light-harvesting in the phycobilisome antennae [1].