Ageing Research Reviews 9 (2010) 117–130

Contents lists available at ScienceDirect

Ageing Research Reviews

journal homepage: www.elsevier.com/locate/arr

Review

Role of chloroplasts and other plastids in ageing and death of plants and animals: A tale of Vishnu and Shiva

Wouter G. van Doorn[a,*], Kohki Yoshimoto[b]

[a] Mann Laboratory, Department of Plant Sciences, University of California, Davis, CA 95616, USA
[b] Plant Immunity Research Team, RIKEN Plant Science Center, Tsurumi-ku, Yokohama, Kanagawa 230-0045, Japan

ARTICLE INFO

Article history:
Received 24 May 2009
Received in revised form 25 August 2009
Accepted 25 August 2009

Keywords:
Ageing
Algae
Apicoplast
Bleaching
Chloroplast
Coral reef
Death
Degeneration
Endosymbiosis
Giant clam
Kleptoplast
Malaria
Monocarpic
Photosynthesis
Plants
Plasmodium
Plastid
Polycarpic
Sea slug
Survival
Symbiosis
Toxoplasma
Vacuole

ABSTRACT

Chloroplasts (chlorophyll-containing plastids) and other plastids are found in all plants and many animals. They are crucial to the survival of plants and most of the animals that harbour them. An example of a non-photosynthesizing plastid in animals is the apicoplast in the malaria-causing *Plasmodium* species, which is required for survival of the parasite. Many animals (such as sea slugs, sponges, reef corals, and clams) consume prey containing chloroplasts, or feed on algae. Some of these incorporate the chloroplasts from their food, or whole algal cells, into their own cells. Other species from these groups place algal cells between their own cells. Reef-building corals often lose their intracellular algae as a result of environmental changes, resulting in coral bleaching and death. The sensitivity of the chloroplast internal membranes to temperature stress is one of the reasons for coral death. Chloroplasts can also be a causal factor in the processes leading to whole-plant death, as the knockout of a gene encoding a chloroplast protein delayed the yellowing that proceeds death in tobacco plants. It is concluded that chloroplasts and other plastids are essential to individual survival in many species, including animals, and that they also play a role in triggering death in some plant and animal species.

1. Introduction

The history of life knows of many momentous events. One was the invention of photosynthesis, the capacity to use the energy of sunlight and turn this into biochemical bonds. This evolutionary step apparently occurred in a lineage of prokaryotic cells. It resulted in a dramatic change in the earth's atmosphere, as these photosynthetic prokaryotes produced oxygen.

Another enormous evolutionary event was the failed digestion, by a eukaryotic animal cell, of a prokaryotic photosynthetic cell. Most single-celled animals survive by consuming other cells. They capture their prey by engulfing it. Once inside the animal cell, the prey cell becomes degraded by hydrolases. An evolutionary leap took place when the digestion of a photosynthetic cell became somehow impossible. A photosynthetically active prokaryote then remained inside the cytoplasm of the host eukaryote. Further evolutionary adaptations included the ongoing division of the guest prokaryote and the transfer of its offspring during cell divisions of the eukaryotic host (Keeling, 2004; Reyes-Prieto et al., 2007). When all of this was in place the eukaryotic plant cell was born, containing fully active chloroplasts (Greek *khlāros* = green; and *plast* = form, entity; related to *plastēs*, molder). The first true

* Corresponding author at: Mann Laboratory, Department of Plant Sciences, University of California, Davis, CA 95616, USA.
E-mail address: wgvandoorn@ucdavis.edu (W.G. van Doorn).

1568-1637/$ – see front matter
doi:10.1016/j.arr.2009.08.003

plant cell and its multicellular descendants have been able to produce a considerable surplus, enough to sustain a relatively large biomass of non-photosynthetic organisms (animals, including mankind).

Apart from being essential to survival, chloroplasts and other plastids have also been implicated in ageing and death. The term 'ageing' will here be taken to indicate the deteriorative processses that increase the probability of death with increasing chronological age.

Although ageing refers to what happens in individual multicellular organisms, the underlying deteriorative processes are often studied at the levels of tissues, cells, organelles, and molecules. Mitochondria, for example, have been have been implicated in ageing and are therefore studied in detail. Similarly, other organelles can be causal, or at least involved, in deterioration and death. The purpose of this paper is to give an overview of the current insights about the role of chloroplasts (photosynthetically active plastids) and other plastids in the survival and death plants and animals.

Plastid is feminine of the Greek word *plastēs*, molder (from *plastos*, molded). Plastids will here be defined as organelles enveloped by a double membrane, which contain DNA, are capable of reproduction by fission, are the site of manufacture and storage of important chemicals, and do not show the type of respiration found in mitochondria. In this review we will use the term chloroplast if referring to a plastid that carries out photosynthesis. Other plastids generally will be indicated either with their specific names or by the term non-photosynthesizing plastid. The term plastid will be used only when referring to the group of chloroplasts and non-photosynthesising plastids as a whole. Additionally, the term algae will be used for several organisms harbouring chloroplasts, including the blue green algae (phylum Cyanobacteria), green algae (Chlorophyta), diatoms (Heterokontophyta), and dinoflagellates (Dinoflagellata).

Plastids are apparently found in most, if not all, living cells of higher plants. The Chlorophyll-containing, photosynthetically active chloroplasts are found in many plant cells. Non-chlorophyllous plastids are ubiquitous in cells of both photosynthetic and non-photosynthetic plant organs, for example in meristems, roots, the stem interior, leaves, and petals (Pyke, 2009).

Similarly, many animal species harbour chrloroplasts or non-photosynthesizing plastids, and depend on them.

Non-photosynthesizing plastids are found in animals such as the malaria-causing *Plasmodium*. Many other animals contain either chloroplasts or chloroplasts in symbiotic algae. Examples are almost all reef-building polyps, sea anemones, and giant clams. It is thought that all coral reefs have formed because of the symbiosis between the polyps that produce the calcium carbonate skeletons, and photosynthetic algae in the phylum Dinoflagellata. The algae in reef-building polyps provide up to 90% of their energy requirement (Marshall and Schuttenberg, 2006). The relevance of the symbiosis with algae is evident in the massive coral reef bleaching and subsequent death of the reef-building animals, which is due to degeneration and loss of the algae. It is thought that large parts of the coral reefs are currently under threat of disappearing (Lough and van Oppen, 2009; Pratchett et al., 2009).

This paper will discuss, subsequently, endosymbiosis, the types of plastids found in plants and animals, their ultrastructure, their turnover, and their role in programmed cell death (PCD) and in the ageing and death of individuals.

2. Endosymbiosis

The process of acquiring another cell that stays alive inside the cytoplasm is called endosymbiosis (Greek *endo* = inside, *sym* = together, *biosis* = living). The chloroplast endosymbiont in plants apparently descends from cyanobacteria (Keeling, 2004; Reyes-Prieto et al., 2007) while another endosymbiont, the mitochondrion, derives from from α-proteobacteria (Gray et al., 2001).

The prokaryotic nature of these endosymbionts is reflected by their circular DNA, as well as their specific RNA and the full complement of the transcription and translation machinery. This machinery includes ribosomes and a typical set of enzymes involved in proper protein folding (class I chaperonins) which is only found in bacteria, chloroplasts and mitochondria (Fink, 1999). After entering their host cells early on in evolution, the endosymbionts lost most of their own genes. Many endosymbiont genes became translocated to the nucleus of the host cell, in a process called intracellular gene translocation. The activity of both the chloroplast and the mitochondrion thereby became under control of the host cell (Leon et al., 1998).

The chloroplasts of green algae, red algae, blue green algae, and all multicellular plants are considered to be the result of primary endosymbiosis. This is the process whereby a photosynthetic cyanobacterium got enslaved by a eukaryotic animal cell (Cavalier-Smith, 2000). With the mitochondria also in place, this resulted in the first eukaryotic algal cell.

In other groups of organisms secondary endosymbiosis (or even tertiary symbiosis) has occurred. Secondary endosymbiosis is the acquisition of a eukaryotic algal cell, by a eukaryotic protozoan. After the secondary symbiosis, all organelles of the acquired algal cell disappeared, often with the exception of a remnant of the algal nucleus. Secondary endosymbiosis occurred in several taxa including the brown algae, diatoms, dinoflagellates, and apicomplexans (Cavalier-Smith, 1999, 2000, 2002).

Other types of symbiosis will also be described here, including the acquisition of chloroplasts from algae, by animals, and the acquisition of whole algal cells by animals, whereby the algal cells are placed inside the cells or between the cells.

3. Types of plastids in plants and animals

Apart from chloroplasts (Fig. 1), plant cells can contain proplastids, a name often used for plastids that have not yet assumed a definite role. Proplastids are often found in meristematic cells. More differentiated non-chlorophyllous plastids serve a number of functions. The chromoplasts, for instance, contain high levels of carotenoids and other pigments, and provide colour. Storage plastids have been divided into amyloplasts (starch), elaioplasts (lipid) and proteinoplasts. Gerontoplasts (Greek *geront* = old man) are chloroplasts that are undergoing degenerative changes, in senescent tissues (Wise, 2007).

Apicomplexans are unicellular animals, classified to a subgroup in the Protozoa. The apicomplexans include several disease-causing parasites. Their plastid (apicoplast) still has some of its own genome and its own gene expression machinery, but also imports numerous proteins encoded by nuclear genes (Waller and McFadden, 2005; Oborník et al., 2009). For example, *Theileria* parasites cause death in cattle, *Toxoplasma gondii* (Fig. 2) causes fetal death in humans, and the malaria parasites (*Plasmodium*) kills many children and adults. The genus *Plasmodium* has over 200 species, at least 10 of which infect humans. Malaria is mainly caused by four species (*Plasmodium falciparum*, *Plasmodium vivax*, *Plasmodium malariae*, and *Plasmodium ovale*) that all infect human red blood cells, feed on them, and result in their destruction (Fig. 3). The worst type of malaria is caused by *P. falciparum*, which is kills approx. 1–2% of the people that get sick. Other *Plasmodium* species can infect various vertebrate animals.

In contrast to the photosynthetically inactive apicoplast in *Plasmodium* and *Toxoplasma*, a similar, but photosynthetically active, plastid has been described recently in a protozoan. The host