Plastid biogenesis and differentiation

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Abstract

Plastids are crucial to plant functionality and develop from proplastids in meristem cells to generate different plastid forms in different types of plant cells. In addition to the photosynthesis of leaf mesophyll cell chloroplasts, plastids contribute to storage and pigmentation capacities in many different specialised cells as well as contributing essential metabolic pathways within the cell in general. Plastids also have the capacity to interconvert between types according to environmental and molecular signals. Progress in understanding the cell biology and morphological control of different plastid types is considered in the light of modern imaging techniques, which have revealed new aspects of plastid morphology. As well as considering molecular aspects of how plastids control their division, this article discusses also how cell-specific differentiation might be controlled and whether master control genes for plastid biogenesis might be in charge.

1 Introduction

Plastids form a distinct group of organelles in higher and lower plants and are one of the defining characteristics by which plants are different to animals. For many years, most plastid based research focused on the chloroplast and trying to understand the mechanism of photosynthesis and the biochemical interactions of the chloroplast with the cell. With the advent of molecular biology and more recently, a variety of novel imaging techniques, a better understanding of how the chloroplast and other plastid types function within the cell in a truly biological manner is starting to emerge. Even so, the chloroplast remains dominant in providing the bulk of our knowledge about plastid biology. In this article, I consider the structure and morphology of the chloroplast and a range of other plastid types as well as how plastids differentiate and undergo interconversions. Finally, I discuss two fields in plastid biology, which have progressed significantly in recent years, namely plastid division and the biology of stromules.

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2 Proplastids

All plastids within a plant are ultimately derived from those progenitor plastids, which are found in meristem cells called proplastids. These in turn have been derived from the few proplastids, which were present in the zygote and derived potentially from both the maternal egg cell and the paternal pollen grain. However, most Angiosperms have mechanisms to exclude or degrade proplastids in the pollen line and hence the plastids present in the majority of plants are inherited maternally (Mogensen 1996; Corriveau and Coleman 1998; Zhang et al. 2003). In those species in which biparental inheritance occurs, plastids within the zygote constitute a mixed population derived from both parent egg and pollen. However, many factors appear to bias the relative proportion of maternally and paternally-derived plastids and plastid populations in resulting plants can be highly variable with respect to the origins of plastids within them (Mogensen 1996).

Considering the fundamental importance of proplastids to plastid biology, the knowledge of proplastid cell biology and their fine ultrastructure is limited, mostly because of the difficulties with analysing small organelles with no pigment in small regions of dense tissue. Knowledge of the physical appearance of proplastids has been derived largely from electron micrographs (Chaley and Possingham 1981; Akita and Sagisaka 1995; Robertson et al. 1995; Gunning 2004), which show proplastids as small organelles containing limited internal structure that are dispersed throughout the cytoplasm. Most proplastids contain rudimentary pieces of thylakoid membrane, but are unpigmented although those in shoot apical meristems appear to contain more thylakoid in a more organized state than those in the root apical meristem (Gunning 2004). In addition, ingrowths from the inner plastid envelope membrane into the proplastid stroma can also be seen occasionally, as well as ribosomes. Starch grains may be present, especially in proplastids of seeds where starch was laid down in the proplastid during seed development (Gunning 2004). In wheat plumules and potato stolons, starch content of proplastids is variable with some containing significant starch grains and others with no starch. This difference in starch content appears to result from differences in the capacity for starch synthesis since immunogold labelling of the enzyme starch synthase reveals two types of proplastids: those with and those without the enzyme (Akita and Sagisaka 1995).

Estimating proplastid numbers is difficult and to date no studies have definitively counted proplastid populations in meristem cells. However, various studies of shoot meristem cells estimate that they contain 10-20 proplastids per cell (Cran and Possingham 1972; Lyndon and Robertson 1976; Pyke and Leech 1992). Using modern fluorescent protein technology, imaging of proplastids in meristems and during cytokinesis should be feasible, although proplastid dynamics during meristematic cell divisions have yet to be studied in detail. Proplastids with fluorescent marker proteins on board, such as GFP, can be imaged in root meristems (Kohler and Hanson 2000) and those in shoot apical meristems can be observed also (Trynka and Pyke, unpublished), although experiments to determine population

sizes and segregation patterns in different parts of the meristem could prove technically demanding.

Differences in proplastid number according to cell position within the meristem or in organs derived from it may well exist (Lyndon and Robertson 1976), but whether such differences are significant to cellular function are unclear and they may simply reflect differences in proplastid division rate compared to local rates of cell division. Differences in proplastid DNA content and morphology have been shown to exist between cell layers within a meristem, suggesting that tissue-specific characteristics of proplastids within a meristem may be important (Fujie et al. 1994). During the cell divisions of embryogenesis and the cell divisions within meristems, proplastids must divide to ensure continuity within cell lines and to ensure that all cells within the plant contain plastids. Little is known of a distinct mechanism by which a correct proplastid segregation is achieved at cytokinesis (Sheahan et al. 2004) and it would appear that aplastidic daughter cells are prevented simply because proplastids are generally distributed in the cytoplasm, thus ensuring segregation into both daughter cells, but also because they locate more particularly in positions close to the nucleus prior to the onset of mitosis. Positioning in the peri-nuclear cytoplasm during protoplast division is driven by the actin cytoskeleton leading to entrapment of plastids close to the nucleus (Sheahan et al. 2004). Whether a similar process happens during cytokinesis in meristems is unknown. Nuclear mutations, which affect proplastid division and give rise to populations of few, enlarged proplastids in meristematic cells (Robertson et al. 1995) do not result in the appearance of aplastidic cells in meristems, which implies that giant proplastids can still maintain a mechanism by which they segregate correctly. Giant plastids in tomato fruit cells appear able to replicate by a budding/fragmentation mechanism (Forth and Pyke 2006) and therefore it is feasible that the generation of small budded proplastids could ensure correct segregation in meristematic cells containing giant proplastids.

Efforts to study the extent of proplastid metabolism and DNA transcription and translation have been limited but those which have examined proplastid transcription at the tissue level have shown such activity to be low and that the initiation of a differentiation pathway, such as chloroplast differentiation, is necessary to upregulate transcriptional activity (Harak et al. 1995; Mache et al. 1997; Sakai et al. 1998; Baumgartner et al. 1989). Indeed, expression of nuclear genes for proplastid ribosomes is required prior to the expression of those genes, which are plastid encoded. Overall proplastids remain an exasperating organelle, occupying a pivotal place in plastid cell biology but yet about which there is so much still to learn.

3 The morphology and structure of different plastid types

As cells within developing seedlings and developing plant organs differentiate, plastids embark on different patterns of differentiation according to the differentiation pathway that the cell itself takes. Proplastids have the ability to give rise to a

variety of different types of plastid, which form in different types of tissue. Plastids can also interconvert between their different forms in many situations. Thus, for most plastid types, there are two different pathways by which they can arise: directly or by re-differentiation of an existing plastid type. Traditionally, characterisation and naming of different types of mature plastids has largely been based on the types of molecules they store or the types of pigments they accumulate, although this may not necessarily be the best system for plastid taxonomy since often plastids show a mixture of features from different types making precise naming difficult. Although distinct types of plastid differentiation do exist, a better system for their classification could be based on the biochemical and physiological properties or maybe the extent of their proteome or metabolome. Such a system could ease the difficulties by which plastids displaying intermediate phenotypes have to be named. In this chapter, the basic structure and morphology of the major types of differentiated plastids found in higher plants will be consider and subsequently, what is known of the differentiation pathways which give rise to each of the types will be discussed.

3.1 Chloroplast structure and morphology

Chloroplasts are the most prominent form of plastid occurring in all green plant tissues and enable photosynthetic carbon fixation to occur in addition to a variety of other biochemical processes central to cellular metabolism. Like all plastids, they are bounded by a double plastid envelope membrane, which acts as a major control point for chloroplast import and export as well as being a major site for biochemical synthesis (Joyard et al. 1998). Chloroplasts in leaf mesophyll cells are typically ellipsoidal in shape but with defined poles, a feature that is crucial to their division. However, chloroplasts can also be highly pleiomorphic and can take up irregular morphologies in different cell types. Indeed, the potential plasticity in plastid shape has become clear in recent years with the analysis of giant plastids, which occur when plastid division is perturbed. In these giant plastids, which are up to 50-fold larger than normal chloroplasts, the morphology is highly irregular (Pyke et al. 1994) yet apparently stable when osmotically challenged (Pyke 2006) suggesting that a mechanism exists which controls and exerts stability on plastid morphology. A suggestion that an FtsZ-based internal plastoskeleton might function in controlling plastid morphology (Reski 2002) needs further experimentation since most of the FtsZ molecules within the plastid appear to be involved in division rather than morphological control. The recent discovery of mechanosensory proteins within the plastid envelope (Haswell and Meyerowitz 2006) showed that perturbation of such proteins by mutation affects plastid morphology, implying that tension monitoring in the plastid envelope somehow plays a role in morphological control.

A major structural component, which typifies the chloroplast, is the extensive thylakoid membrane system, which extends throughout the body of the chloroplast and dominates its internal architecture. Thylakoid membranes are the site of photosynthetic electron transport and ATP synthesis and delimit a distinct compart-

ment within the chloroplasts: the thylakoid lumen. Thylakoids are composed of lamellae, which are arranged into a highly complex system of stacked lamellae called grana interconnected by single lamellae called stromal lamellae.

Models for thylakoid membrane structure have been developed largely from analysis of electron micrographs of sectioned chloroplasts, a system that is fraught with difficulty in interpretation in generating three-dimensional models from two-dimensional images. Three different models have been proposed (Arvidsson and Sundby 1999; Mustardy and Garab 2003; Shimoni et al. 2005) but differ in their conclusions, although all show the highly complex nature of thylakoid membrane arrangement within the grana. The model of Mustardy and Garab (2003) shows the grana as fused stacks of membrane which look like fan blades, with stromal lamellae joining stacks together at alternating levels within the stack, and the whole structure forming a right handed helix. The reason for this complex thylakoid membrane morphology is to provide a large surface within the plastid on which light capture by chlorophyll and electron transport can occur. Consequently, the area of thylakoid membrane within a mature plastid is large and much greater than simple invaginations from the plastid envelope membrane.

Surprisingly, the mechanisms by which the construction of the thylakoid membrane system is initiated, synthesised in large amounts and then built into a complex three-dimensional architecture is poorly understood. Electron micrographs showing invaginations of the inner plastid envelope into the stroma gave credence to the hypothesis that thylakoid membrane is derived, at least initially, from such invaginations as proplastids differentiate into chloroplasts. Proplastids usually contain small amounts of thylakoid membrane and the extensive biogenesis of more thylakoid membrane may simply involve building off of extant membrane. However, recent studies have clearly shown that both chloroplasts and proplastids contain vesicles within the stroma (Westphal et al. 2003; Gunning 2004) and that a vesicle trafficking system occurs in plastids primarily between the plastid envelope and the stroma (Westphal et al. 2003). Vesicles are budded from the inner plastid envelope and accumulate close to the inner membrane, particularly when fusion processing at the thylakoid membrane is curtailed by low temperature (Morre et al. 1991). The main purpose of plastid vesicle transport is probably that of providing galactolipids, which are synthesised in the plastid envelope membranes (Joyard et al. 1998), for continued synthesis of thylakoid membrane, although they could also deliver hydrophobic proteins, which reside in the thylakoid membrane. Plastid vesicle trafficking appears to utilize several homologous components of the cytosolic ER Golgi trafficking system, encoded by nuclear genes, in that the chloroplast contains both ARF1 and Sar1 GTPases (Andersson and Sandelius 2004), which are involved in vesicle assembly. In addition, the chloroplast also contains dynamin (Park et al. 1998) and proteins required for vesicle fusion (Hugeney et al. 1995). Two other nuclear-encoded proteins involved in the vesicle directed thylakoid biogenesis are VIPP1 (Kroll et al. 2001) and Thf1 (Wang et al. 2004). Mutations in either gene result in abolition of vesicles and perturbed synthesis of the thylakoid membrane. VIPP1 forms a high molecular weight complex on the inner envelope membrane, which could conceivably be involved in vesicle production (Aseeva et al. 2004). An intriguing problem for the future will be to

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