

The cytological basis of the plastid inheritance in angiosperms

Review Article

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Contents

| | |
|---|----|
| Uniparental or biparental plastid inheritance | 57 |
| Four types of distribution and transmission of paternal plastids | 58 |
| <i>Lycopersicon</i> type | 58 |
| <i>Solanum</i> type | 58 |
| <i>Triticum</i> type | 58 |
| <i>Pelargonium</i> type | 58 |
| <i>Pelargonium</i> or <i>Triticum</i> type | 58 |
| Cytological mechanisms underlying plastid distribution and transmission | 58 |
| Plastid degeneration | 58 |
| Plastid exclusion during the first haploid mitosis | 60 |
| Plastid exclusion during sperm cell formation or development | 61 |
| Plastid exclusion during fertilization | 61 |
| Concluding remarks | 62 |

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Uniparental or biparental plastid inheritance

In recent years the study of plastid inheritance in higher plants has given a new impetus to studies on gametogenesis and embryogenesis from a cytogenetic point of view. The starting points for these considerations are as follows:

(a) In the majority of angiosperms there is a uniparental, purely maternal inheritance of plastic characters, for example in *Antirrhinum*, *Beta*, *Hordeum*, *Mirabilis*,

Nicotiana, *Zea*, and many others (Hagemann 1964, Kirk and Tilney-Bassett 1978). In reciprocal crosses between green and white plants (or branches) of these species the plastidal constitution of the mother plant determines the type of progeny. The cross green (female) × white (male) gives only green F₁-seedlings; the cross white (female) × green (male) gives only white F₁-seedlings. A variegated mother plant (crossed with a green or white male) can produce green, variegated and white seedlings; the reciprocal cross with a green female only yields green seedlings.

(b) In contrast, in a minority of species a clear biparental plastid inheritance is found. The best studied genera of this type are *Pelargonium*, *Oenothera*, and *Hypericum*. In these species crosses between green and white plants (or branches) give variegated seedlings—in addition to green and white ones—in the F₁-progenies.

The difference between these two types of plastid inheritance is obviously due to differences in the mode of distribution and transmission of plastids during gamete formation or fertilization (Hagemann 1979, 1981, 1983).

Electron microscopic investigations in several laboratories allowed the characterization of four groups of angiosperm species, in which different cytological and physiological mechanisms, which cause either uniparental or biparental plastid inheritance, are acting. It is possible to define four plant types: *Lycopersicon* type, *Solanum* type, *Triticum* type, and *Pelargonium* type. In the *Pelargonium* type there is biparental plastid in-

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heritance. The other three types show uniparental plastid transmission although the underlying mechanisms are rather different.

On the female side no striking differences in the plastid content of the egg cell or the central cell of angiosperms (in contrast to gymnosperms) have so far been reported. In all angiosperm species so far studied, the egg cell contains many plastids, in addition to the haploid nucleus and mitochondria. The transmission of maternal plastids (and mitochondria) into the zygote and the developing embryo is an established fact.

In contrast, on the male side interesting differences have been found between different taxa. It has been found that, during the development of the male gametophyte and the fertilization process, there are several stages at which plastids can be excluded from the male germ line.

The development of the male gametophyte is initiated by the first haploid mitosis. After the completion of this mitosis, the male gametophyte consists of two cells: the wall-attached generative cell and the larger vegetative cell. Later on the generative cell is detached from the pollen wall; it becomes spindle-shaped and moves into the vegetative cell. The second haploid mitosis divides the generative cell into two sperm cells, the male gametes of angiosperms. This mitosis occurs either within the pollen grain before anthesis (ripe trinucleate pollen grains) or within the growing pollen tube after anthesis and pollination (ripe binucleate pollen grains). The development of the male gametophyte is concluded by the process of fertilization: the fusion of one sperm cell with the egg cell and the fusion of the other sperm cell with the central cell.

Four types of distribution and transmission of paternal plastids

The four plant types mentioned above differ in their plastid content in the following way:

Lycopersicon type

During the first pollen mitosis the generative cell does not receive any plastids: there is an extremely unequal distribution of the plastids into the vegetative cell only. The generative cell does not contain plastids ab initio (cf. Table 1).

Solanum type

The generative cell contains a few plastids immediately after the first haploid mitosis. However, these plastids

disappear during the maturation of the generative cell (or the sperm cells) before fertilization (cf. Table 1).

Triticum type

Both the generative cell and the sperm cells contain plastids. However, during the process of fertilization the plastids are not transmitted into the egg cell. During fertilization the plastids are stripped of the sperm nucleus. The same seems to be true for the mitochondria of these species. Consequently in species of this type—e.g., wheat and *Triticale*—there is uniparental, maternal plastid inheritance.

Pelargonium type

In the genera and species of this type the generative and sperm cells (or the sperm cell fertilizing the egg cell; cf. Russell and Cass 1983, Russell 1984, 1985) contain plastids, which are regularly transmitted into the zygote and thus into the next generation. This results in biparental inheritance of plastids.

Pelargonium or *Triticum* type

In 18 species presented in Table 1 plastids could be detected within generative and/or sperm cells by cytological investigation. For these species, however, no genetical analyses on the mode of plastid inheritance are available at present. Therefore, which species belong to the *Pelargonium* type and which to the *Triticum* type remains unresolved.

The transmission of male plastids into the zygote (in the case of the *Pelargonium* type) does not seem to require any special cytological mechanisms, because equal plastid distribution between the daughter cells is a normal event in somatic plant tissue mitoses. In contrast, the prevention of transmission of male plastids into the zygote via the sperm cell requires special cytological and physiological mechanisms which act during pollen development and fertilization.

Cytological mechanisms underlying plastid distribution and transmission

Until now two different ways which prevent paternal plastids from being transmitted into the progeny have been detected; plastid degeneration and plastid exclusion at different stages of development of the male gametes.

Plastid degeneration

In species of the *Solanum* type the microspore plastids are transmitted into both the vegetative cell and the

Table 1. Plastid content of generative and/or sperm cells in angiosperms and the mode of plastid inheritance

| Species | gc | sc | mi | Authors |
|-----------------------------------|-----|-----|----|---|
| <i>Lycopersicon</i> type | | | | |
| <i>Aloe jucunda</i> | — | | | Schröder and Hagemann 1986 |
| <i>Aloe secundiflora</i> | — | | | Schröder and Hagemann 1986 |
| <i>Ambrosia psilostachya</i> | — | | | Larson 1965 |
| <i>Antirrhinum majus</i> | — | — | um | Hagemann 1976 |
| <i>Agropyron repens</i> | — | | | Lombardo and Gerola 1986 b |
| <i>Bellevalia lipskyi</i> | — | | | Kordyum et al. 1975 |
| <i>Beta vulgaris</i> | — | — | um | Hoefert 1969 a, b |
| <i>Brassica campestris</i> | — | — | | McConchie et al. 1985 |
| <i>Capsella bursa-pastoris</i> | — | | | Schulz and Jensen 1968 |
| <i>Carya pecan</i> | — | | | Larson 1965 |
| <i>Castilleia foliosa</i> | — | | | Jensen et al. 1974 |
| <i>Chlorophytum comosum</i> | — | | um | Schröder 1986 b |
| <i>Epidendrum scutella</i> | — | | | Coccuci and Jensen 1969 |
| <i>Euphorbia dulcis</i> | — | — | | Murgia et al. 1986, Murgia and Wilms 1987 |
| <i>Fritillaria meleagris</i> | — | | | Schröder 1985 a |
| <i>Fritillaria thunbergii</i> | — | | | Chen et al. 1988 |
| <i>Gasteria verrucosa</i> | — | | | Schröder 1985 b |
| <i>Gossypium hirsutum</i> | — | — | um | Jensen 1972 |
| <i>Haemanthus katherinae</i> | — | | | Sanger and Jackson 1971 |
| <i>Heleocharis palustris</i> | — | | | Carniel 1975 |
| <i>Hippeastrum vitatum</i> | — | | | Mogensen 1986 |
| <i>Hyacinthoides non-scriptus</i> | — | | | Angold 1968 |
| <i>Hyoscyamus niger</i> | — | | | Reynolds 1984 |
| <i>Impatiens balsamina</i> | — | | | Dupuis 1974 |
| <i>Impatiens glandulifera</i> | — | | | van Went 1984 |
| <i>Impatiens walleriana</i> | — | | | van Went 1984 |
| <i>Lycopersicon esculentum</i> | — | | um | Krahnert 1980 |
| <i>Lycopersicon peruvianum</i> | — | | | Cresti et al. 1975, 1977; Pacini and Juniper 1984 |
| <i>Mirabilis jalapa</i> | — | | um | Lombardo and Gerola 1968 a |
| <i>Muscari racemosum</i> | — | | | Kordyum et al. 1975 |
| <i>Nicotiana alata</i> | — | | | Cresti et al. 1985 |
| <i>Olea europea</i> | — | | | Pacini (pers. comm.) |
| <i>Parkinsonia aculeata</i> | — | | | Larson 1965 |
| <i>Petunia hybrida</i> | — | | um | Sassen 1964, van Went 1970 |
| <i>Prunus avium</i> | — | | | Pacini et al. 1986 |
| <i>Quercus virginiana</i> | — | | | Larson 1965 |
| <i>Saintpaulia ionantha</i> | — | — | | Ledbetter and Porter 1970 |
| <i>Spinacia oleracea</i> | — | — | | Wilms 1981 |
| <i>Tillandsia caput-medusa</i> | — | | | Brighigna et al. 1981 |
| <i>Tradescantia paludosa</i> | — | | | Maruyama et al. 1965 |
| <i>Tulbaghia violacea</i> | — | | | Schröder and Oldenburg 1989 |
| <i>Tulipa kolpakowskiana</i> | — | | | unpublished data |
| <i>Tulipa turkestanica</i> | — | | | unpublished data |
| <i>Solanum</i> type | | | | |
| <i>Convallaria majalis</i> | (—) | | | Schröder 1986 a |
| <i>Epilobium spec.</i> | (—) | (—) | | Schmitz and Kowallik 1987 |
| <i>Fritillaria imperialis</i> | (—) | | | Schröder 1985 a |
| <i>Hosta ventricosa</i> | (—) | | | Schröder 1984 b |
| <i>Hosta japonica</i> | (—) | | um | Vaughn et al. 1980 |
| <i>Solanum chacoense</i> | (—) | | | Clauhs and Grun 1977 |
| <i>Solanum tuberosum</i> | (—) | | um | Clauhs and Grun 1977 |

Table 1 (continued)

| Species | gc | sc | mi | Authors |
|--|----|----|----|--|
| <i>Triticum</i> type | | | | |
| <i>Hordeum vulgare</i> | + | + | um | Mogensen 1988 |
| <i>Triticum aestivum</i> | + | + | um | Hagemann and Schröder 1985 |
| <i>Pisum sativum</i> | + | | um | Hause 1986 |
| <i>Zea mays</i> | | + | um | Chebotaru 1981 |
| <i>Pelargonium</i> type | | | | |
| <i>Oenothera erythrosepala</i> | + | + | b | Meyer and Stubbe 1974 |
| <i>Oenothera hookeri</i> | + | | b | Diers 1963 |
| <i>Pelargonium zonale</i> | + | + | b | Lombardo and Gerola 1968 a, Khera 1975 |
| <i>Plumbago zeylanica</i> | + | + | | Russell and Cass 1983 |
| <i>Rhododendron spec.</i> | + | | b | Knox et al. 1986 |
| <i>Pelargonium</i> or <i>Triticum</i> type | | | | |
| <i>Castilleja wightii</i> | + | + | | Jensen et al. 1974 |
| <i>Datura metel</i> | + | | | Sangwan and Camefort 1982 |
| <i>Geranium pratense</i> | + | | | unpublished data |
| <i>Haworthia spec.</i> | + | | | unpublished data |
| <i>Hippeastrum belladonna</i> | + | | | Larson 1965 |
| <i>Lilium candidum</i> | + | | | Bopp-Hassenkamp 1960 |
| <i>Lilium martagon</i> | + | | | Schröder 1984 a |
| <i>Lilium regale</i> | + | | | Anderson 1939 |
| <i>Linum usitatissimum</i> | + | + | | Vazart 1970 |
| <i>Lobelia erinus</i> | + | | | Dexheimer 1965 |
| <i>Lupinus luteus</i> | + | | | Ruhland and Wetzel 1924 |
| <i>Lupinus nootkarensis</i> | + | | | Lombardo and Gerola 1968 b |
| <i>Maianthemum bifolium</i> | + | | | unpublished data |
| <i>Ornithogalum nutans</i> | + | | | unpublished data |
| <i>Polygonatum multiflorum</i> | + | | | unpublished data |
| <i>Secale cereale</i> | + | + | | Hagemann and Schröder 1985 |
| <i>Triticale</i> | + | + | | Schröder 1983 |
| <i>Triticum durum</i> | + | + | | unpublished data |

gc Generative cell. sc Sperm cells. mi Mode of plastid inheritance (from Tilney-Bassett 1975)

— Generative and/or sperm cells lack plastids. + Generative and/or sperm cells contain plastids. (—) Plastids degenerate within generative cell and/or sperm cells

um Uniparental maternal plastid inheritance. b Biparental plastid inheritance

generative cell. However, the mature generative cell lacks plastids (cf. Clauhs and Grun 1977). This loss of plastids is a result of their degeneration. Schröder (1986 a) reported the different steps in the degeneration of plastids during maturation of the generative cell in *Convallaria majalis*. The physiological and molecular basis of plastid degeneration is still unknown, but we are sure that plastid degeneration in generative cells of the *Solanum* type must be considered as a specific characteristic of this particular type. This assumption is supported by the fact that exceptionally transferred plastids in species of the *Lycopersicon* type do not show any signs of degeneration in the generative cell until anthesis. Additionally, in *Antirrhinum majus* (*Lycopersicon* type) exceptionally transmitted plastids of the

generative cell could be detected in the progeny by genetical analyses (Diers 1971).

Plastid exclusion during the first haploid mitosis

In species of the *Lycopersicon* type generative cells without plastids are formed. Several species and genera have been studied in ultrastructural investigations, e.g., *Chlorophytum*, *Gasteria*, *Aloe*, *Haemanthus*, *Impatiens*, *Hyoscyamus* (for references see Table 1). In *Chlorophytum comosum*, *Gasteria verrucosa*, and others it was clearly shown that, in young microspores before the onset of the first haploid mitosis, the plastids are randomly distributed in the cytoplasm. But during prophase of this mitosis the plastids become polarized and

clustered in the center or at the proximal pole of the microspore, whereas the dividing nucleus is located at the distal pole. Therefore, all plastids of the microspore are exclusively transmitted into the vegetative cell; the generative cell does not receive any plastids. This plastid polarization is mediated by the cytoskeleton, and probably controlled by biochemical gradients (van Went 1984, Schröder 1985 b). In *Gasteria verrucosa* the microspores and pollen grains contain a three-dimensional network of 7 nm-filaments containing (or consisting of) actin, in which all cytoplasmic organelles, including the plastids, seem to be embedded (Schröder et al. 1988). We presume that this system of microfilaments is responsible for the intracellular movement or positioning of the plastids (and other organelles) during the first haploid mitosis. Microtubules do not seem to be involved in these processes; there is no correlation between the distribution pattern of microtubules (van Lammeren et al. 1985) and the clustering of plastids in microspores (Schröder 1985 b) during the first haploid mitosis in *Gasteria*. The cause of exceptionally transmitted plastids in generative cells of species of the *Lycopersicon* type (e.g., in *Aloe*, *Tulbaghia*, *Prunus*, and in *Euphorbia*; Murgia pers. comm.) seems to be due to a few plastids escaping integration into the cytoskeletal system in the microspores.

On the other hand, there are reports of atypical pollen grains in the mature anthers of species of the *Lycopersicon* type. These pollen grains consist of two cells, of equal size and containing plastids. Obviously, the first haploid mitosis in such pollen grains has been severely disturbed (*Gasteria verrucosa*; Schröder 1985 b). The same could be observed in pollen grains of *Hyoscyamus niger* after microspore culture (Reynolds 1984). The atypical pollen grains could be of a great interest to plant breeders because they might form haploid plants in anther cultures at a higher probability than "normal" pollen grains.

Plastid exclusion during sperm cell formation or development

In *Plumbago zeylanica* (Russell and Cass 1983; Russell 1984, 1985) a very interesting sperm cell heteromorphism has been found. Two dimorphic sperm cells which differ in size, morphology and organelle content are formed by the second haploid mitosis. The larger sperm cell is closely associated with the vegetative nucleus; it contains many mitochondria and no (or hardly any) plastids. The smaller sperm cell is not associated with the vegetative nucleus; it contains numerous (up

to 46) plastids and relatively few mitochondria. In more than 94% of the fertilization events analysed, the smaller sperm cell with many plastids fuses with the egg cell and thus transmits the plastids to the next generation. In contrast, the larger, mitochondria-rich sperm cell (without plastids) fuses with the central cell and so gives rise to the nutritive endosperm. In this case, in terms of plastid distribution, the second haploid mitosis is extremely unequal. The underlying cytological mechanism is polarized plastid distribution during the second haploid mitosis (Russell et al. 1988).

It is easy to imagine the opposite situation: the exclusion of plastids from the sperm cell which fuses with the egg cell. We should keep in mind that such events may regularly occur in other species.

The exclusion of organelles from sperm cells can also be caused by other means. In *Hordeum vulgare* Mørgensen and Rusche (1985) reported a decrease in the numbers of mitochondria within maturing sperm cells. The mitochondria are enclosed in evaginations of the sperm cell plasmalemma and are afterwards transferred into the vegetative cytoplasm. The reduction of the cytoplasm and the cytoplasmic organelles surrounding the sperm nucleus seems to be rather a widespread characteristic of sperm cell maturation. In our research group this was also found for the generative and sperm cells of tomato (Krahnert 1980). In this case mitochondria are the organelles lost. In other species it may apply to plastids.

Plastid exclusion during fertilization

Several cereals, especially wheat and *Triticale*, confront the investigators with a peculiar situation. On the one hand, the generative and sperm cells in pollen grains regularly contain plastids (Schröder 1983, Hagemann and Schröder 1985). On the other hand, there are reports of maternal, uniparental inheritance of plastid differences in wheat (Briggle 1966). Moreover, it is well known, that there is purely maternal inheritance of "cytoplasmic male sterility", which is in all probability connected with the mitochondria. This situation can only be explained by assuming that, during the process of fertilization, during the fusion of a sperm cell with the egg cell, the plastids (and mitochondria) are stripped off the sperm nucleus and therefore not transmitted to the zygote. There are observations and findings to support this idea. In spinach the cytoplasm (including mitochondria) of the sperm cell (fertilizing the egg cell) remains outside the egg cell. Only the sperm nuclei, which are devoid of cytoplasm, merge with the

egg cell and the central cell (Wilms 1981). A similar situation has been described for barley (Mogensen 1982, 1988). However, in barley the plastids seem to be involved in this process. Mogensen (1988) observed the remnants of sperm cell cytoplasm containing three plastids, besides 59 mitochondria, and other cytoplasmic organelles within the degenerated synergid. Unfortunately, even today we do not have sufficient details from several angiosperms about the actual fusion event during the fertilization of the egg cell by the sperm cell. We can therefore only speculate about the mechanisms or the mechanics of separation of the plastids from the sperm nucleus, especially in cereals.

Concluding remarks

The aim of this paper is to provide a general review of the cytological basis of plastid inheritance in angiosperms. We have not given detailed descriptions or figures, because these have been published in many original papers (cf. Table 1), and have been discussed in reviews on several specific topics (see also Knox 1984; Willemse and van Went 1984; van Went and Willemse 1984; Hagemann 1974, 1979, 1983; Sears 1980).

From all the data we can summarize as follows: In angiosperms it has been possible to characterize four different types of plastid distribution during the development of the male gametophyte and fertilization. In only one type—the *Pelargonium* type—is there regular biparental inheritance of plastids, i.e., regular transmission of genetic information of the male plastids into the next generation.

In the other three types different mechanisms prevent the transmission of male plastids into the next generation. We can characterize different cytological mechanisms which are responsible for this uniparental maternal plastid inheritance. These are: plastid degeneration during maturation of the generative cell or the sperm cells, plastid exclusion during the first haploid mitosis, during the maturation of sperm cells or during the fertilization process.

From these observations certain general conclusions can be drawn: Firstly, the processes which prevent male plastids from being transmitted to the next generation are primarily cytological mechanisms. So far there is no convincing evidence that male plastids are transmitted into the angiosperm egg cell and then destroyed by a restriction-like process, differentiating between female and male plastid DNA. Such processes may act in *Chlamydomonas reinhardtii* (Sager 1977, Sager and Grabow 1983), but, to date, there are no hints of such

events in angiosperms. Secondly, in plants of the *Lycopersicon* type we are confronted with the fact that during normal development of the male gametophytes of green plants cells lacking plastids are formed (generative and sperm cells). More generally, in many green angiosperms cells, which play an important role in sexual reproduction, normally lack plastids.

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