

## Embryogenesis of angiosperms: ultrastructural transformations of plastids

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### Abstract

Electron microscopic study of *Alcea rosea* and *Valeriana officinalis* embryogenesis showed the ultrastructural changes in the embryo plastidome. It is assumed that plastids of the mature angiosperms zygote are of one genetic type. Tissue differentiation and changes of plastid functions in the course of embryogenesis and plant development underlie the histological differentiation of plastids and their ontogenic transformations (metamorphosis).

The plastid apparatus of a plant is highly differentiated. It is also obvious that the zygote plastids determine the great diversity of plastidome of a fully developed adult plant. There is little information as to the genetic composition of the zygote plastid set. It still remains obscure whether all zygote plastids are of the same genetic type or if they consist of various genetically different plastids.

Knowledge of the genetic composition of zygote plastids as well as of the patterns of their transformation during embryogenesis is of particular interest primarily in connection with the problem of plastid origin. Moreover, elucidation of the mechanisms underlying plastid behavior in double fertilization as well as in the course of endosperm- and embryogenesis is of great importance for plant breeding, this was clearly demonstrated by genetic studies on hybridization. The data obtained showed that plastids affect such processes as double fertilization and survival of hybrid embryos (Tilney-Bassett, 1970; Ashley, 1972).

However, until now the structure and genesis of embryo plastids are poorly understood. A number of studies have recently been carried out on the ultrastructure of certain angiosperms embryo plastids mainly at individual stages of embryogenesis. Some of them are reviewed with regard to the problem of chlorophyll accumulation in certain angiosperm embryos (Yakovlev, Zhukova, 1973; Zhukova, 1978, 1979).

Electron microscopic study of *Alcea rosea* L. and *Valeriana officinalis* L. embryogenesis showed that embryo plastids underwent complex ultrastructural changes in the course of this process.

The *Alcea rosea* egg cell contains amyloplasts with large starch grains. These are distinctly detectable even by light microscopy. Amyloplasts are also observed in the zygote and in all *Alcea rosea* proembryo cells up to the globular stage. A ameoboid appearance, large starch grains, almost complete lack of peripheral reticulum, occurrence of tubular systems in certain regions of the peristrome and small plastoglobules in clusters are characteristic of these amyloplasts. Single thylakoids occur in these plastids, sometimes rather elongated, arranged parallel to the plastid envelope. Amyloplast stroma is rather electrondense. There are no distinct ultrastructural differences in the amyloplasts of different proembryo cells except some variability in the amounts of plastoglobules in plastids of the suspensor and embryo proper.

It is the heart-shaped phase of *Alcea rosea* embryogenesis that becomes the turning point in plastid ontogenesis. In every embryo cell chloroplasts alone are found. These are small ellipsoidal plastids (Zhukova, 1978), whose internal membrane system consists of grana and intergrana thylakoids, the number of thylakoids in each granum being not more than 10. Occurrence of plastoglobules and neglectable amounts of starch were found in chloroplast stroma. Small starch grains occur only in individual chloroplast sections.

Ultrastructural chloroplast changes occur in the course of further differentiation of the embryo (mesophyll chloroplasts of cotyledons were observed). The chloroplast appearance becomes amoeboid like that of the leucoplasts of the globular proembryo. Along with the development of the inner membrane system gradual accumulation of starch and decrease of plastoglobules in the chloroplasts take place. The cotyledon chloroplasts acquire features described elsewhere (Zhukova, 1975, 1978, 1979). Maturation of *Alcea rosea* seed and its dehydration are accompanied by new transformations of the embryo plastids. The disappearance of chlorophyll and destructive changes in the inner membrane system were found in them. The increase of plastoglobules is characteristic of plastids at this stage of embryogenesis. The chloroplasts of cotyledon mesophyll cells are transformed into amyloplasts.

Similar plastid transformations were observed also in the course of *Valeriana officinalis* embryogenesis. The zygote, two-celled and globular proembryo contain amyloplasts. Their stroma is characterized by high electron density (at fixation with glutaraldehyde followed by  $\text{OsO}_4$ ). Unlike *Alcea rosea* amyloplasts they contain a well developed peripheral reticulum with electron-translucent contents of its tubules. The latter are rather long and twisted. Their fragments are observed throughout

the stroma of each plastid section. The shape of amyloplasts in *Vale-riana officinalis* proembryo has an amoeboid appearance. In the course of proembryo growth up to the globular phase a decrease in stored starch and appearance of plastoglobules are found in plastids.

The mesophyll plastids of developing cotyledons in *V. officinalis* embryos are represented by chloroplasts. Their inner membrane system consists of grana (2-5 thylakoids) and intergrana thylakoids. They practically lack of starch — small starch grains occur only in individual sections. Amoeboid appearance (invaginations of plastid envelope are observed frequently), occurrence of peripheral reticulum and plastoglobules are characteristic of chloroplasts of the *V. officinalis* embryo.

The results obtained as well as the analysis of literature on this subject (Orsenigo, 1964; Bain, Mercer, 1966; Schulz, Jensen, 1968; Marin, Dengler, 1972; Pinfield et al., 1973; Zhukova, 1975, 1978, 1979; Nagl, 1976) allow us to make the following conclusion. Embryogenesis is accompanied by the metamorphosis of plastids; this metamorphosis is not unidirectional. At a certain stage of development leucoplasts are transformed into chloroplasts if the plant is a chloroembryophyte; chloroplasts in their turn undergo a number of ultrastructural transformations, which in certain species are completed by their turning into amyloplasts. Together with ontogenetic transformations of plastids differentiation of the embryo into tissues and organs take place. Examples of plastid differentiation in tissues and organs of certain angiosperm embryos were presented by us previously (Yakovlev, Zhukova, 1973). Sometimes such differentiation at the embryo organ level can be seen even by visual observation. The *Lotus* embryo is an example of such a case. It is characterized by green plumule and achlorophyllous cotyledons.

Of particular interest in this respect is plastid dedifferentiation in certain embryo tissues and organs leading back to the simplest forms. Such plastid transformation is found, for instance, at seed maturation in some angiosperms. Such dedifferentiated plastids are referred to sometimes as proplastids. At seed germination a new step of plastid transformation in the embryo takes place, including redifferentiation.

Differentiation of plastids is characteristic not only of fully developed plants but of differentiating embryos as well. As it was mentioned above, all of the diversity of plastids is a derivative of the plastid set of the zygote. The plastid set of the angiosperm zygote can include plastids of two types — the plastids of the egg and of the sperm. However an alternative assumption can be suggested — the zygote plastids are of one type. They can become uniform as a result of transformation in specific zygote plastids. This can take place in the zygote itself in the course of its preparation for the first division. The elimi-

nation of "male" plastids during zygote maturation as well as fusion of plastids by pairs — derivatives of male and female gametes should be possible. In both cases the zygote plastids become unvariable ones. Further differentiation of plastids and their ontogenic transformations can not be due to genetic heterogeneity of the initial material. Tissue differentiation and changes of plastid functions, in the course of embryogenesis and plant development can underlie these phenomena.

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