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Nucellar and integumentary embryony in angiosperms

T. N. NAUMOVA

Komarov Botanical Institute, Academy of Sciences, Leningrad, USSR

Abstract

The form of adventive embryony is determined by the type of ovule. Nucellar embryony is possible in crassinnucellate ovules, and integumentary embryony in tenuinucellate ovules.

Adventive embryony may be considered as one of the most common type of apomixis among angiosperms. More than 130 species from 34 families of angiosperm embryos are formed in the nucellus or the integument. An attempt was made to summarize the available data, but they are incomplete and do not cover this form of apomixis on the whole (Naumova, Yakovlev, 1972). We studied microgametogenesis, megasporo- and megagametogenesis, double fertilization, differentiation of initial cells of adventive embryos, embryo- and endospermogenesis in: *Euonymus* (*Celastraceae*) (Naumova, 1970a, b, 1978b), *Opuntia* (*Cactaceae*) (Naumova, 1977, 1978a; Naumova, Yakovlev, 1978), *Sarcococca* (*Buxaceae*) (Naumova, 1979, 1980), *Citrus*, *Poncirus*, *Fortunella* (*Rutaceae*).

Investigation of microgametogenesis showed the percentage of the fertile pollen grains to be varying. *Euonymus* and *Opuntia* have a high percentage of fertile pollen grains; *Citrus* and *Fortunella* have a certain amount of sterile pollen grains. Species of *Sarcococca* have sterile pollen grains.

The process of megagametogenesis is also unstable in these species. Embryo sac formation in *Euonymus* follows to the *Polygonum*-type, *Opuntia*, *Citrus* and *Poncirus* show some deviations in this process; asynchronous nuclear division and abnormality of nuclear distribution are usual at nuclear embryo sac stages. Many embryo sacs degenerate at various stages of their development, but fertile embryo sacs are also formed. In *Sarcococca* the deviations in the embryo sac formation are quite usual, and mature embryo sacs are rare. The egg cells of these embryo sacs from the very beginning have an abnormal structure and later degenerate. The antipodal cells are not always formed and chala-

zal nuclei remain together with the polar nuclei in the central cell which is alone viable.

Double feritilization in these species occurs quite seldom. In *Euonymus* which has normal micro- and megagametogenesis, this process is prevented by unfavourable environmental conditions alone. In this case, the growth of pollen tubes may be inhibited by low temperature. In *Opuntia, Citrus* and *Poncirus* double fertilization is also prevented by abnormal micro- and megagametogenesis. Thus, the possibility of double fertilization in these cases is low. In *Sarcococca* which has sterile pollen grains and abnormal megagametogenesis double fertilization is not observed.

Thus, embryological development in species with adventive embryony before anthesis is not similar: some of them show only partial changes (*Euonymus*) while other exhibit considerable changes (*Poncirus, Citrus, Sarcococca, Opuntia*) in these processes.

In spite of irregularieties in the embryonal development of these species, a sufficient amount of mature and viable seeds is formed, largely owing to adventive embryony.

It was found that the type of the ovule determines the form of adventive embryony. Nucellar embryony is possible if the ovule is crassinucellate (*Opuntia, Citrus, Poncirus* etc.); integumentary embryony occurs in the tenuinucellate ovule (*Euonymus*).

The nucellus of the crassinucellate ovule includes: the nucellar cap, parietal tissue, hypostasis and cells neighbouring the embryo sac, generally these tissues only have a vegetative function. But in angiosperms with adventive embryony these tissues as shown in our investigations play a particular part in development of the ovule. Parietal tissue as distinct from the rest of somatic tissues is mitotically active for a long time. This is particularly often observed after flowerings when the number of parietal tissue cells sharply increases. In this period the parietal tissue as a cap surrounding the embryo sac. Each of the cells of the parietal tissue may differentiate into an initial cell of a nucellar embryo. This phenomenon has been observed in *Opuntia elata, Sarcococca humilis, Citrus limon, Poncirus trifoliata,* etc. The other somatic tissues of the nucellus from no embryos. In the case of integumentary embryony the epidermal and subepidermal cells of the inner integument take part in the formation of somatic embryos. Integumantary embryos occur both in the micropylar and chalazal region of the inner integument neighbouring with the embryo sac.

The differentiation of initial cells in the nucellus and integument is evidently the same. Preliminary data show that the differentiation is due to somatic tissue disintegration: some cells degenerate and others become more active. The morphology and intracellular structure of these

active cells change in the process of their differentiation. This phenomenon requires further investigation.

The differentiation of nucellar and integumentary embryos in these species begins 3-10 weeks after flowering. The cell divisions of the proembryos are chaotic. Mature nucellar, integumentary and sexual embroys seem to be quite similar. The possibility of adventive embryos formation is closely connected with endosperm existence.

Endosperm in the species investigated may be either of sexual or of apomictic origin. The sexual endosperm has been observed in *Poncirus trifoliata* and *Citrus limon*. Apomictic endosperm seems to be formed in two ways: by fussion either of polar nuclei alone (*Euonymus macroptera*) or polar and 1-3 chalazal nuclei, the latter being possible when antipodes are not formed (*Sarcococca humilis*).

The embryological development of adventive embryony species is characterized by numerous peculiarities. Which are not described in other angiosperms showing only double fertilization. Plants reproducing both sexually and apomictically grow on extensive areas have a considerable number of species in their genera (*Euonymus*, *Citrus*, etc.), whereas plants reproducing apomictically grow on small areas and have a small number of species in the genus; *Sarcococca* includes 1-5 species. Adventive embryony is of great significance for seed reproduction in plants where double fertilization is limited.

Investigation of the embryology of species with adventive embryony is of great significance for the solution of evolutionary, systematic and embryological problems of angiosperms.

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