

POLYEMBRYONY IN ANGIOSPERMS

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THE phenomenon, known as polyembryony or the occurrence of more than one embryo in a seed, has attracted considerable attention ever since its initial discovery in orange by Leeuwenhoeck (1719). Ernst (1918) and Schnarf (1929), who have reviewed the older literature, classify it into two types — “true” and “false” — according to whether the embryos arise in the same embryo sac or in different embryo sacs in the same ovule. In true polyembryony, which is the more important, the additional embryos may arise either by a splitting of the zygote or proembryo (cleavage polyembryony), or from cells of the embryo sac other than the egg (apogamy), or from nucellar or integumentary cells outside the embryo sac (adventive embryony).

CLEAVAGE POLYEMBRYONY

Although common in gymnosperms (see SCHNARF, 1933; BUCHHOLZ, 1946) cleavage polyembryony occurs only sporadically in the angiosperms. Jeffrey (1895) described it in *Erythronium americanum*. After fertilization, the synergids degenerate and disappear and the zygote divides to form a small group of cells which do not show any definite order or arrangement. This group continues to increase in volume and outgrowths arise at its lower end which eventually function as independent embryos. The production of two or three embryos from such an “embryogenic mass” was common, but sometimes as many as four were found.

Subsequent to Jeffrey's discovery, which has been confirmed by Guérin (1931) for another species of *Erythronium*, a similar proliferation of embryonic cells was reported in *Tulipa gesneriana* (ERNST, 1901) and *Limnocharis emarginata* (HALL, 1902). In the latter, the first division of the zygote is transverse and results in the formation of a large basal and a small terminal cell. As a rule the former increases in size without undergoing any division but in some cases

it was found to undergo repeated divisions to form a small group of cells from which several small embryos bud forth as in *Erythronium*. No older stages were seen, however, and it could not be ascertained whether these embryos grow to full maturity.

Most other cases of cleavage polyembryony, which have been reported since then, are in the nature of abnormalities. Cook (1902) noted one embryo sac of *Nymphaea advena* showing twin embryos which he interpreted as having originated by the “splitting of a very young embryo”. Later, the same author (1924) noted one instance of two, and a second of four embryos at the micropylar end of the embryo sac of *Crotalaria sagittalis*. Since the synergids are quite ephemeral in this species, these embryos are also believed to have arisen from a splitting of the single zygotic embryo. Samuelsson (1913) reported a similar splitting of the proembryo in *Empetrum nigrum*, Guignard (1922) in *Vincetoxicum nigrum* and Johansen (1931) in *Zauschneria latifolia*. In *Lobelia siphilitica* (Crété, 1938) frequently one and sometimes two embryos develop at the expense of the suspensor. In *Nicotiana rustica*, Cooper (1943) noted an ovule with two embryos of which the smaller had apparently arisen as an outgrowth from the apex of the primary embryo. Kausik and Subramanyam (1946) figure an embryo sac of *Isotoma longiflora*, in which an additional embryo seems to have budded out from a suspensor cell. Frost (in WEBBER & BATCHELOR, 1946) states that out of about 1,200 hybrid seeds of *Citrus*, produced at the California Citrus Experiment Station, 10 gave rise to two hybrid seedlings each. Since these were identical he concludes that the twins were produced by the development of two embryos from the same zygote.

Swamy (1943, 1946b, 1949) believes that cleavage polyembryony is of frequent occurrence in orchids. In *Eulophia epidendracea*, which may be cited as an example, he (1943) records the following variations:

1. The zygote divides irregularly to form a mass of cells of which those lying at the

lower end grow simultaneously and give rise to multiple embryos.

2. The filamentous proembryo becomes branched and each of the branches gives rise to an independent embryo.

3. The embryo gives off buds or outgrowths which may themselves function as embryos.

It is possible, however, that some of the examples of cleavage polyembryony reported above are really cases of an intimate juxtaposition of two separate embryos derived from the same embryo sac or adjacent embryo sacs in the same ovule (see FAGERLIND, 1944). Viewed in this light some of Swamy's (1946b) twin embryos of *Habenaria* (see his FIGS. 31, 32 & 33) may not be products of cleavage but are probably derived from the egg and one synergid. The other orchids in which he has reported cleavage polyembryony also deserve a fresh study.

APOGAMY

Embryos may also be produced sometimes from cells of the embryo sac other than the egg. The most common source is the synergids which frequently become egg-like and may become fertilized¹ or even develop without fertilization (as in diploid embryo sacs). As examples may be cited *Alchemilla sericata* (MURBECK, 1901), *Taraxacum* (MURBECK, 1904), *Burmannia coelestis* (ERNST & BERNARD, 1912), *Alnus rugosa* (WOODWORTH, 1930), *Atraphaxis frutescens* (EDMAN, 1931), *Crepis capillaris* (GERASSIMOVA, 1933), *Sagittaria graminea* (JOHRI, 1936), *Hieracium vulgatum*, *H. ramosum* (GENTCHEFF, 1937), and *Poa alpina* (HÅKANSSON, 1943).

In rare cases haploid and unfertilized synergids may also develop into embryos. In a recent study of *Orchis maculata*, *Platanthera chlorantha* and *Listera ovata*, Hagerup (1944, 1947) noted a number of embryo sacs in which the egg was fertilized and gave rise to a normal embryo but simultaneously with it an unfertilized synergid also began to develop so that two embryos were formed, one diploid and the other haploid. Further, in one ovule of *Orchis*, in which the pollen tube had not yet entered the embryo sac, the egg as well as one of the synergids had commenced to divide, thus indicating a

possibility of the production of twin haploid embryos. In some species of *Lilium* (COOPER, 1943) one of the synergids begins to divide in approximately one per cent of the ovules. However, the haploid synergid embryo usually degenerates at an early stage of development and only the zygotic embryo develops further.

Production of embryos from antipodal cells is much rarer. Derschau (1918) reported the fusion of two sperms with an antipodal cell of *Nigella arvensis*. Shattuck (1905) noted that the antipodal cells of *Ulmus americana* often present an egg-like appearance and in some embryo sacs he actually found embryos in this position. Ekdahl has confirmed this in *U. glabra*, and Modilewski (1931), Mauritzon (1933) and Fagerlind (1944) have figured similar cases in *Allium odorum* (see p. 323), *Sedum fabaria* and *Elatostema eusinuatum*. The further fate of these embryos has not been determined, however, and it is not known whether they are viable.

There are a few reports of embryos arising from the cells or nuclei of the endosperm. Rosenberg (1908), Schnarf (1919), and Gentcheff (1937) reported such an occurrence in some species of *Hieracium*, but later Rosenberg (1930) withdrew this interpretation. He now thinks that in these cases several aposporous embryo sacs develop in an ovule and become irregularly fused with one another so that the boundaries between them get lost and the embryos, although really arising from eggs belonging to different embryo sacs, become included in a common mass of endosperm. Possibly the same explanation applies to the endosperm embryos reported in *Alnus rugosa* (WOODWORTH, 1930). Jeffrey and Haertl (1939) reported endosperm embryos in *Trillium*, but this has been refuted by Swamy (1948). The only remaining case is that of *Isomeris arborea*, in which, according to Billings (1937), the embryo arises as an outgrowth of an endosperm "nodule". As pointed out by Maheshwari (1946a, b) this needs clarification, and we may conclude that to date there is no authentic record of the origin of embryos from endosperm tissue.

ADVENTIVE EMBRYONY

In adventive embryony the embryos originate from the diploid cells of the ovule lying outside the embryo sac and belonging

1. Fertilization of both egg and synergids is possible when more than one pollen tube enters the embryo, or if the same pollen tube contains more than two sperms.

either to the nucellus or the integument. A common feature of this process is that the cells concerned in such development become richly protoplasmic and actively divide to form small cell masses which protrude into the embryo sac and eventually grow further to form true embryos. Frequently the zygotic embryo also develops at the same time and is distinguishable from the adventive embryos only by their somewhat lateral position and lack of a suspensor.

A favourite and oft quoted instance of adventive embryony is that of *Citrus* (STRASBURGER, 1878; OSAWA, 1912; see also WEBBER & BATCHELOR, 1946; & LEROY, 1947) in which four or five embryos are common and sometimes as many as 13 may be seen in the same seed. Among other examples may be cited *Euphorbia dulcis* (CARANO, 1926), *Sarcococca ilicifolia* (WIGER, 1930), *Eugenia jambos* (PIJL, 1934), *Capparis frondosa* (MAURITZON, 1934), *Mangifera indica* (ARNDT, 1935; JULIANO, 1937)² and *Hiptage madablota* (SUBBA RAO, 1940). The chief variation in development concerns the place of origin of the embryos. Whenever the nucellus is intact, the adventive embryos originate from the nucellar cells, but when it becomes disorganized, the cells of the integument may take over this function. Also, sometimes a single cell may become the progenitor of an embryo, while on other occasions it is a small group of cells.

An especially interesting type of adventive embryony occurs in the Scandinavian forms of the orchid, *Nigritella nigra* (AFZELIUS, 1928, 1932).³ As in other members of the family the nucellus is reduced to a single layer of cells surrounding the megaspore mother cell. The latter forms three or four daughter cells, of which the chalazal functions and proceeds to form the embryo sac. Its development stops at the four-nucleate stage, but, meanwhile, one or two cells of the nucellar epidermis show a considerable increase in size and begin dividing to give rise to adventive embryos which lie very close to the apex of the embryo sac and are enclosed by the integuments. *Zeuxine sulcata* (SWAMY, 1946 a), a terrestrial orchid from

India, is very similar except that here, owing to disturbed meiosis, there is no regular megaspore formation and if any embryo sacs are produced, they are incapable of further development. On the other hand, the cells of the nucellar epidermis possess a remarkable capacity for growth and differentiation. One or two of them elongate considerably to give rise to filamentous proembryos (often four-celled and, therefore, looking like megaspore tetrads) which may undergo a secondary increase in number by further proliferation, budding, or cleavage.

As a rule the nucellar embryos originate either from the cells towards the micropylar end of the embryo sac or from those situated on its sides. In *Trillium undulatum* (SWAMY, 1948 b), however, the embryos are said to originate from "the nucellar layer of cells abutting the pouch-like depression at the chalazal end of the embryo sac". This is a somewhat unusual place for the origin of adventive embryos and there is a possibility that the so-called embryos are really antipodal cells which have become active and have undergone a number of cell divisions.⁴ This point, therefore, needs further clarification.

As in *Mangifera indica* and *Nigritella nigra*, the occurrence of adventive embryony may not be a constant feature of all the individuals of a species. Swamy (1948 a) reports that in the U.S.A. there are at least three races of the orchid *Spiranthes australis*. The first shows normal sexual reproduction and a single zygotic embryo is produced in each seed. In the second race, which is apomictic, the male and female gametophytes are both functionless. Fertilization does not occur but the cells of the inner layer of the inner integument give rise to adventive embryos of which two to six may mature in a single seed. In the third race, which is of an intermediate type, some ovules of an ovary follow the course outlined for the first race and others that for the second.

Adventive embryony may be autonomous, i.e. independent of pollination and fertilization, or it may be induced by one or both of these factors. The former condition prevails in *Alchornea ilicifolia* (STRASBURGER, 1878), *Euphorbia dulcis* (CARANO, 1926) and

2. According to Arndt (1935) the multiple shoots arising from seeds of *Mangifera indica* may also be caused by the development of adventitious buds on the seedlings before or during germination.

3. It is interesting to note that those forms of this species, which occur in the Alps, show normal sexual reproduction (see GUSTAFSSON, 1947).

4. Swamy himself says that "the antipodal cells of *Trillium* are very conspicuous and persist even after fertilization", and his Figs. 9, 10, 12, 13 and 14 confirm it.

Sarcococca pruniformis (WIGER, 1930). In *Nigritella nigra* (AFZELIUS, 1928), neither pollination nor fertilization are essential, but the occurrence of pollen tubes in the ovary seems to accelerate the tendency towards formation of adventive embryos. In most other plants, however, either pollination, or pollination followed by fertilization, are important factors in stimulating the development of adventive embryos, although their exact rôle has not been properly elucidated. In the orchid *Zygopetalum mackayi* (SÜSSENGUTH, 1923), unpollinated flowers were found to degenerate and fall off shortly after blooming, but on treating the stigma with pollen from another genus, *Oncidium*, the adventive embryos developed to maturity and viable seeds were formed. Here the foreign pollen, although quite incapable of effecting fertilization, nevertheless exercised some kind of a chemical influence which affected the growth of the embryos in a favourable manner. In *Eugenia jambos* (PIJL, 1934), the adventive embryos may originate quite independently of pollination, but do not attain their full development unless fertilization has taken place. In the "carabas" mango (JULIANO, 1937) and *Citrus* (see WEBBER & BATCHELOR, 1946) fertilization is considered to be essential for the maturation of the adventive embryos.

In all cases of adventive embryony there is a formation of the endosperm whether it originates as the result of triple fusion or without it. The only exception (excluding the Orchidaceae where endosperm formation does not take place) is *Opuntia aurantiaca* (ARCHIBALD, 1939).⁵ Here the egg, synergids, and antipodals are said to degenerate and later also the polar nuclei, so that an endosperm is not formed at all and the whole embryo sac is reduced to a long, irregular, darkly staining cavity. The nucellar tissues become more massive, however, and certain cells lying below the nucellar cap and bordering on the cavity of the embryo sac enlarge and become rounded. Their walls thicken and each cell undergoes two divisions at right angles to each other to form a four-celled "proembryo". With further divisions the proembryo increases in size, ruptures the mother cell wall and

enters into the cavity of the sac. Several embryos are formed in this way but owing to mutual competition only one or two reach maturity.

FALSE POLYEMBRYONY

As mentioned in the introductory paragraph, the polyembryonate condition may also be due to the occurrence of multiple embryo sacs within the ovule. These may arise either (a) from the derivatives of the same megaspore mother cell, or (b) from two or more megaspore mother cells, or (c) from nucellar cells (apospory). To mention a few instances, Bacchi (1943) has found that sometimes more than one embryo sac is present in an ovule of *Citrus* so that two zygotic embryos may arise in a seed. Nielsen (1946) and Swamy (1948 c) have recorded the same in *Poa pratensis*⁶ and *Casuarina equisetifolia* respectively. In *Atraphaxis* and *Trifolium* (FEDORTSCHUK, 1935, 1944) the additional embryo sacs sometimes arise from the cells of the chalaza but the embryos formed in them become arrested at an early stage in their development. In several members of the Loranthaceae there are no clearly demarcated ovules and the endosperms of all the embryo sacs fuse to form a common mass containing several embryos (see SINGH, 1951; MAHESHWARI & JOHRI, 1950).

SOME SPECIAL CASES

In some plants multiple embryos are produced by the simultaneous operation of more than one of the methods named above. The most interesting of these is *Allium odorum*. Long ago, Tretjakow (1895) and Hegelmaier (1897) recorded the occurrence of synergid and antipodal embryos in as many as one-third to one half of the ovules of this species. Later, Haberlandt ((1923, 1925) reported that even in castrated flowers there is an increase in the size of the ovules accompanied by the production of embryos from several sources — egg, synergids, antipodals and the cells of the inner integument. He found the diploid number of chromosomes in all the embryos. Modilewski (1925, 1931), who had obtained somewhat divergent

5. It should be noted, however, that Ganong (1898), who found nucellar embryony in another species, *O. vulgans*, records normal fertilization and the formation of "an abundant endosperm".

6. Species of the genus *Poa* also show other abnormalities in the origin of the embryo, for which a reference may be made to the works of Tinney (1940), Engelbert (1941), Åkerberg (1939, 1943) and Håkansson (1943, 1944).

results, made a further study of the plant and found that it forms two kinds of embryo sacs, some with the haploid number of chromosomes and others with the diploid number. In the diploid embryo sacs there is a fertilization of only the polar nuclei resulting in a pentaploid endosperm; embryos arise from the unfertilized but diploid egg and the antipodal cells. In haploid embryo sacs, on the other hand, viable embryos are found only as a result of fertilization. In conclusion, four possibilities are mentioned:

1. In a haploid and normally fertilized embryo sac, embryos may begin to develop from all cells of the embryo sac and even from the adjacent integumentary cells, but only the zygotic embryo survives so that the mature seed contains a single embryo.

2. Embryos may also begin to form from one or more cells of a haploid and unfertilized embryo sac, but owing to the lack of an endosperm (which can arise only after triple fusion) their growth is soon arrested and they become inviable.

3. In a diploid but unfertilized embryo sac, any of its cells (also the cells of the integument) may begin to form an embryo, but eventually they all degenerate owing to the absence of an endosperm.

4. In diploid embryo sacs, where syngamy fails but triple fusion takes place normally, all the cells of the embryo sac are capable of giving rise to proembryos but only the egg embryo usually attains maturity.

Woodworth (1930) has called attention to the frequent occurrence of polyembryonate seeds in *Alnus rugosa*. Meiosis was disturbed and only 2-3 per cent of the pollen grains were found viable. Pollen tubes were not observed and bagged catkins produced perfectly normal and viable seeds similar to those obtained from unbagged catkins. Embryo sac formation was not preceded by meiosis and more than 50 per cent of the seeds showed diploid egg embryos at the micropylar end of the ovule. A few seeds had an embryo oriented in the opposite direction suggesting its origin from an antipodal cell. One ovule showed three embryos at the micropylar end, two of which are believed to have originated from synergids and the third from the egg. Nucellar budding was frequent. Some embryos were found imbedded in the endosperm without any connection with nucellar cells and

several ovules showed more than one embryo sac, each with one or more embryos. From the occasional occurrence of four to seven cotyledonary buds on certain embryos it further appeared that originally separate embryos could sometimes fuse to form a composite structure.

Woodworth's work, although of much interest, lacks the early stages in embryonal development and, therefore, some of his conclusions about the origin of the polyembryonate condition need confirmation. In particular, his inference that endosperm cells may also give rise to embryos must be regarded as very doubtful, for it is quite likely that such appearances resulted from a fusion of adjacent embryo sacs (see p. 320).

In *Atraphaxis frutescens*, Edman (1931) has described some interesting cases of polyembryony. Haploid embryo sacs are produced only rarely and require fertilization before they can give rise to embryos. More often, meiosis fails and the embryo sacs are diploid. Frequently two or more occur in the same ovule and each of them may produce an embryo. Usually all the sacs lie parallel to each other but sometimes an embryo sac arises from a chalazal cell of the nucellus and is inversely oriented in relation to the normal embryo sac. Further, since embryos of nucellar and apogamous origin may also occur, the resulting picture is quite complicated in some ovules.

Fagerlind's (1944) recent work on some apomictic species of *Elatostema* has also revealed some interesting features of a similar nature. Briefly, the polyembryonate condition here is due to one or more of the following causes: (a) the occurrence of multiple embryo sacs in the same ovule; (b) the formation of embryos from synergids and antipodal cells; and (c) nucellar budding. Sometimes the separating wall between two embryo sacs dissolves so that they form a common cavity and if adjacent embryos come in close contact, they may fuse to form masses of tissue which are difficult to analyse in later stages.

TWINS AND TRIPLETS

When multiple seedlings arise in a species in such a low frequency that it is not practicable to make a developmental study of the embryogeny, there is a good deal of speculation about their origin. Of special interest

are the diploid-diploid, haploid-haploid, diploid-triploid, and haploid-triploid twins.⁷

Considering the diploid-diploid twins first, Randolph (1936) sometimes saw two embryos arranged side by side in kernels of *Zea mays* and the twin plants resulting from such kernels were found to be genetically identical even in heterozygous stocks. He also saw occasional seedlings with two plumules and a single radicle. Skovsted (1939) reported twins in *Trifolium pratense* both of which had an extra chromosome. In all these cases the seedlings are interpreted as having originated by the cleavage of a single embryo. While this may be true, it is necessary to note that cytologically similar diploid seedlings may also be formed in other ways, the most important source being the fertilization of more than one cell of the embryo sac.⁸ Diploid-diploid twins may also arise from embryos produced in two separate embryo sacs in an ovule, or by nucellar budding. It is also conceivable that sometimes a haploid cell of the embryo sac may give rise to a diploid embryo by a process of "endoduplication". A monozygotic origin may, therefore, be assumed only when the seedlings are completely identical in all essential respects.

Haploid-diploid twins were reported by Kappert (1939) in *Linum usitatissimum* and Ramiah *et al.* (1933, 1935) in *Oryza sativa*. Since then, they have been recorded in several other plants, viz. *Triticum durum* (KIHARA, 1936), *Solanum tuberosum*, *Phleum pratense* (MÜNTZING, 1937), *Triticum vulgare* (KASPARAYAN, 1938), *Secale cereale* (KOSTOFF, 1939), *Capsicum annuum* (CHRISTENSEN & BAMFORD, 1943), *Dactylis glomerata* (MÜNTZING, 1943) and *Gossypium barbadense* (HARLAND, 1936; WEBBER, 1938; SKOVSTED, 1939; SILOW & STEPHENS, 1944). Kappert (1933) explained his twins on the basis that the diploid member of the complex was derived from the fertilized egg and the haploid member from an unfertilized cell of the same embryo sac. Ramiah *et al.* (1933) also made the same interpretation but later (1935) considered it probable that

7. See in this connection Webber's (1940) review of "polyembryony"

8. Except in the bi- and tetrasporic embryo sacs all the nuclei of an embryo sac are genotypically alike and identical embryos may also arise as the result of a fertilization of two cells of the embryo sac by the male gametes discharged from a single pollen tube. Possibilities of this nature seem to be indicated in some orchids (HAGERUP, 1947).

the development of more than one embryo sac within an ovule could also account for the origin of the twins. Harland (1936) agreed with this view, adding that the fertilization of the egg in one embryo sac might stimulate a parthenogenetic development of the egg in an adjacent embryo sac. The remaining authors, mentioned above, fall in line with one or the other of these explanations. Briefly, then, in a case of haploid-diploid seedlings, the haploid member is either derived from an unfertilized cell belonging to the same embryo sac or to an adjacent embryo sac.

Diploid-triploid twins have been reported in *Triticum vulgare* (YAMAMOTO, 1936), *Secale cereale* (KOSTOFF, 1939) and a few other plants (see especially SKOVSTED, 1939). According to Kostoff and Yamamoto, the triploid embryos arose from the endosperm. This is, however, merely a supposition without any positive evidence in its favour. Developmental studies in other angiosperms have failed to demonstrate a single authentic instance of embryos arising from endosperm nuclei (see p. 320). It seems more likely that the triploid embryo originated either by the fertilization of an unreduced (aposporic) embryo sac, or by the fusion of a cell of a haploid embryo sac with two male gametes or one unreduced male gamete.

Haploid-triploid seedlings are of comparatively rarer occurrence. Nissen (1937) recorded one such case in *Phleum*. Possibly the haploid embryo arose from an unfertilized cell of the embryo sac and the triploid by one of the methods mentioned in the preceding paragraph.

While these are the possible ways in which twins and triplets arise, it is often almost impossible to be sure of the exact origin of the aberrant member or members of the combination and it is unsafe to make any categorical statements without taking all the possibilities into consideration.

A particularly careful cytogenetic study of the multiple seedlings of *Asparagus officinalis* has recently been made by Randall and Rick (1945). Of 405 multiple seedlings, 97 per cent were twins, 11 were triplets and one was quadruplet. Diploids ($2n = 20$) were the most frequent, but a few showed other chromosome numbers (in order of observed frequency): 30 ($3n$), 21 ($2n + 1$), 10 (n), and 40 ($4n$). Twin seedlings, which were morphologically very similar to each other, usually showed the same chromosome

number. In haploid-diploid pairs, the haploid member was always much smaller than its diploid partner, but aside from this combination the degree of difference in size seldom gave any clue to the chromosome number or the origin of the polyembryonic condition.

The authors critically analyse the possible origins of the multiple seedlings from a study of their chromosome number, stem colour and distribution of sexes, and conclude that about one-fourth of the diploid-diploid twin seedlings must have originated by a process of cleavage polyembryony. The remaining three-fourths are believed to have arisen either from two cells belonging to the same embryo sac or to two embryo sacs in an ovule. In addition, a number of "conjoined" twins were found which were attached to one another in varying degrees but showed themselves to be capable of developing into independent plants. To explain their origin the following alternatives are envisaged: (a) a partial fusion of two adjacent embryos, and (b) an incomplete cleavage of one embryo. From the complete identity in chromosome number and genetic characters between the members of the conjoined type, it is concluded that they originated by an incomplete cleavage of a single initial embryo.

ARTIFICIAL PRODUCTION OF ADVENTIVE EMBRYOS

Since embryos arising asexually from the cells of the nucellus or the integument must give rise to plants which are genetically identical to the maternal parent (except for possible differences due to somatic variation), this phenomenon acquires great importance in the propagation of some of our cultivated plants, especially fruit trees. As mentioned before, some varieties of *Mangifera indica* have adventive embryos; these can be propagated just as safely by seeds as by budding or grafting. In other varieties, with only a zygotic embryo, seed propagation does not give a type true to the mother and one must resort to vegetative propagation. However, as seedlings can be raised much more cheaply, a method of inducing the formation of adventive embryos would obviously be of great economic value. In *Citrus*, nucellar seedlings are in great demand not only on account of their intrinsic worth but also for use as orchard stock upon which grafts from other

types can be made.⁹ Further, clones of *Citrus* tend to deteriorate after repeated vegetative reproduction, but can be fully restored to their original seedling vigour through the use of nucellar embryos.¹⁰

Recognizing the importance of adventive embryony in horticulture, many attempts have been made to induce it artificially. Although the problem has not been solved, the results so far obtained may be reviewed briefly.

About 30 years ago, Haberlandt (1921, 1922) made the observation that in natural adventive embryony the proliferation of the embryo-initiating cells of the nucellus (or integument) is invariably preceded by a degeneration of some of the adjoining cells. This led him to put forward the so-called "necrohormone theory", according to which the stimulus for cell division and proliferation is supplied by certain substances emitted from the adjacent degenerating cells. Proceeding on this basis, he tried to produce adventive embryos in *Oenothera* by pricking the ovules with a fine needle ("Anstichmethode") or by gently squeezing the ovary so as to damage the cells slightly ("Quetschmethode"). In one ovule he obtained two embryos which he considers to be of nucellar origin.

Using the same technique, Hedemann (1931) obtained a two-celled embryo and a free nuclear endosperm in an unpollinated ovary of *Mirabilis uniflora* which had been pricked with a fine insect needle. No chromosome counts could be made, however, to ascertain whether the embryo was haploid or diploid, and the mode of its origin (whether from the egg or the nucellus) does not seem to have been conclusively established.

After Hedemann, no other worker has reported any success in the artificial production of adventive embryos by Haberlandt's methods. Indeed, Beth (1938), who made

9. Nucellar seedlings have a tap root and form better stocks than cuttings which have only a secondary root system and are therefore less suitable (see H. J. WEBBER, 1931, 1932).

10. This vegetative invigoration or "neophysis" is believed to be caused in some way by the powerful morphogenetic influences (perhaps of hormonal nature) exercised by the "magic bath" of the embryo sac (SWINGLE, 1932; COOK, 1938). According to Hodgson (quoted in FROST, 1938), the rejuvenescence may be associated with a high hormone content of young clones and senescence may be an expression of its eventual exhaustion brought about by cell division.

several unsuccessful attempts with *Oenothera* and other plants, denies the nucellar origin of the embryos even in Haberlandt's material. He considers that in Haberlandt's experiments emasculation was either incomplete or it had been performed too late and that the embryos arose from an accidental fertilization of twin embryo sacs.¹¹

Recently, van Overbeek, Conklin and Blakeslee (1941) injected a 0.1 per cent solution or emulsion of the ammonium salt of naphthalene-acetic acid or indolebutyric acid into the ovaries of *Datura stramonium* in the hope of inducing parthenogenetic development of the egg cell. This attempt was unsuccessful but they obtained instead several multi-cellular warty outgrowths which filled the embryo sacs. The shape and contents of the cells closely resembled those of the integumentary tapetum and they also showed the diploid number of chromosomes. It is, therefore, concluded that these structures were derived by a proliferation of the cells of the integumentary tapetum¹² as is the case with many naturally arising adventive embryos. However, in view of their undifferentiated nature and the obscurity regarding their final fate or potentialities the authors wisely refrain from calling them true embryos and designate them instead as "pseudoembryos".

Of interest in this connection are also some recent observations made by Fagerlind (1946) on *Hosta*. Adventive embryony has been known in this genus for a long time, but fertilization is essential for the production of the nucellar embryos. Unpollinated flowers wither and fall away without forming seeds (STRASBURGER, 1878). Fagerlind performed three sets of experiments. In the first experiment he pollinated some of the pistils with a large quantity of pollen and others with a small quantity of it; in the second he used foreign pollen; and in the third he treated the ovaries with growth hormones. Those pistils which had received an adequate quantity of pollen set seeds normally, the embryos being of nucellar origin. In others, where the amount of pollen was insufficient, some of the ovules increased in size but most remained small. On microscopic

examination the former showed the remains of a pollen tube, a more or less well-developed endosperm, and a number of adventive embryos which seemed to be fully capable of further development. On the other hand, those ovules, which had failed to grow showed no pollen tubes, endosperm, or embryos although some of the nucellar cells had acquired a denser cytoplasm than before. In older stages, such "unpollinated ovules" (i.e. ovules not penetrated by a pollen tube) showed a progressive shrinkage and drying up of their tissues accompanied by a degeneration of the embryo sac as well as the possible embryo initials.

In the second experiment in which pistils were treated with pollen from other genera, viz. *Hemerocallis*, *Lilium*, *Galtonia* and *Canna*, all the pistils withered and dropped away just like unpollinated ones.

In the third set of experiments, some of the pistils were treated with one per cent heteroauxin in lanolin and the controls with pure lanolin. The latter dried up within four or five days, but the auxin-treated pistils remained on and three weeks later they showed the presence of young adventive embryos. No endosperm was formed, however, and the embryos seemed to lack the capacity of developing further.

Although of a preliminary nature, Fagerlind's observations seem to indicate that in plants showing adventive embryony it is possible to prepare the ovule for the production of the adventive embryos by the application of suitable growth hormones, but the real difficulty lies in an initiation of endosperm formation. Unfortunately the nature of the stimulus, which may cause divisions of the unfertilized secondary nucleus, remains unknown. Until this is discovered the only way of overcoming the difficulty would probably be to perfect a technique for excising the adventive embryos and growing them in artificial culture.

SUMMARY AND CONCLUSION

Although fairly widespread, polyembryony is much less common in angiosperms than it is in the gymnosperms. The reason for this is that in the latter there are several archeogonia, while in the former there is only one cell in the ovule (the egg) which is normally capable of giving rise to an embryo. Sometimes, however, the proembryo may become separated into two or more portions

11. Twin embryo sacs frequently occur in the family Onagraceae (see MAHESHWARI, 1948, 1950).

12. In the Solanaceae the nucellus comprises only a single layer of cells which soon disorganizes so that the embryo lies in direct contact with the inner layer of the integument.

(cleavage polyembryony); or more than one cell of the embryo sac may develop into an embryo. Less frequently there may be two or more embryo sacs in an ovule, each of which may give rise to embryos. A fourth source of polyembryony is the "budding" or proliferation of the cells of the nucellus or integument (adventive embryony). The adventive embryos are diploid and similar to one another as well as to the plant from which they arise. Embryos produced by the cleavage of a single zygote are also identical in all essential respects. Embryos arising from two or more cells of one or separate embryo sacs may, however, have the same or different chromosome numbers. Even when developmental stages in embryogeny are not available, it is possible in some cases to infer the mode of origin of the polyembryonate condition on genetical evidence.

Intensive studies are needed on the conditions governing the origin of adventive embryos. While a method of inducing

adventive embryony has undoubted economic possibilities, there is also a need sometimes for the elimination of adventive embryos. In *Citrus*, for example, where a number of nucellar embryos may mature simultaneously with the zygotic embryo, it is quite difficult to distinguish the two kinds of seedlings in early stages. Further, the zygotic embryo sometimes becomes suppressed by the nucellar embryos so that all the seedlings are asexual. It would be of distinct advantage to the plant breeder if he could exercise some control over the two processes, eliminating either zygotic or nucellar embryos according to his requirements at the moment.

PS. When this manuscript was in the galley-proof stage, I came across a review of "Polyembryony" by Robyns and Louis (1942) which should be studied by everyone who is interested in the subject. The citation has been included in the list of references.

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