COMMENTS
APOMICTIC FEATURES REVEALED IN A CONIFER

Compared with the elegant apomictic systems that have been evolved in the angiosperms, asexual reproduction in the gymnosperms is poorly developed and rarely extends beyond polyembryony. Apomixis involving diploid parthenogenesis has been regarded as absent from the group (Magie 1992). That the potential to deviate from the normal sexual cycle is nevertheless present in conifers has now been ably demonstrated by Durzan et al. (in this issue) in their experimental work with Norway spruce.

Cleavage polyembryony, by which a single monozygotic embryo subdivides and yields a group of competing embryos, is fairly common in conifers. As seen in sectioned material, this phenomenon appears to lack any resemblance to sexual events. Durzan et al., however, have been able to show that in single cell cultures, obtained from cleaving embryonal suspensor masses, individual cells can behave in a way that shows a remarkable parallel to events in the archegonium. The nucleus of the initially uninucleate cell divides; one nucleus degenerates but the other accumulates an organized cytoplasm ("neocyttoplasm") and develops a thin cell wall. Released into the medium, these "leader cells" display free-nuclear division, so initiating renewed embryo formation. The isolated cell is thus behaving in a manner almost identical with that of the central cell in the archegonium of the female gametophyte, despite its having a diploid nucleus. The divergence from the normal cycle lies in the surviving nucleus, which is analogous to the egg nucleus in normal sexual reproduction of the conifer, developing without fertilization. In cultural conditions, therefore, a gymnosperm has been shown to be capable of behavior that is similar to the formation of an aposporous embryo sac in an angiosperm (e.g., *Ranunculus auricomus*), the diploid pseudoeegg nucleus being capable of parthenogenesis.

One of the many interesting points raised by the results of Durzan et al. is whether the behavior of the embryonic cells was a consequence of the extreme cultural conditions (involving high temperatures, low organic nitrogen, and probably high interstitial levels of CO₂) and were without significance for the normal cycle. These conditions may, however, have reproduced those to which the gymnosperms were subjected in late Mesozoic times, and the reproductive lability revealed may have played a part in their evolution. Although it is unlikely that a question of this kind can ever be answered, the discovery that manipulation of environmental conditions alone can induce a diploid somatic cell to behave as a central cell in an archegonium of the same species is altogether fascinating. This finding is in accord with the concept of the stability of the mode of gene expression, gametophytic or sporophytic, being affected by the state of the internal environment (Bell 1992). A comparable example among the flowering plants is provided by the short-day grass *Dicanthisium* in which both normal and aposporous embryo sacs occur but whose proportions are dependent on the length of the inductive period (Knox and Heslop Harrison 1963), which in turn will affect cell physiology. It is, of course, debatable whether the observation that a cell, the result of experimental treatment, behaves as if it were the precursor of an egg cell is a sure indication of its gametophytic nature. It could be held that, in the system of Durzan et al., the parthenogenetic behavior of the product of the division of the pseudocentral cell disclosed that it was not a true egg cell, but a totipotent cell equivalent to those that initiate embryogenesis in single cell cultures of carrot (Nomura and Komamine 1985).

Semantic discussions of this kind are not, however, likely to be profitable. What is truly striking about the results of Durzan et al. is that the two nuclei resulting from the division within the "central cell" have entirely different fates. In the fern archegonium, the division of the nucleus of the central cell leads to a discrete ventral canal cell above the egg cell. In many conifers no canal cell is formed, and the ventral canal nucleus lies in the egg cytoplasm. In both instances, however, the sister of the egg nucleus becomes pycnotic and is eliminated. Significantly, recent studies of somatic embryogenesis in carrot have shown that the developmental pathway leading to embryogenesis in initially single-cell suspension cultures involves ordered cell death. This appears to be an essential accompaniment to the release of embryonic potential in other cells (Pennell et al. 1992). The nuclei that are destined for elimination typically become pycnotic. Evidence is emerging that the pycnotic condition of nuclei can be taken as an indicator of apoptosis (programmed cell death) (Kerr et al. 1972), a pathway under genetic control (Raff 1992). Will apoptosis prove to be an essential feature of situations in which embryonic activity is regained? It is surely significant that it is encountered in somatic embryogenesis (where a proportion of the cells die), in megasporogenesis in heterosporous ferns and
seed plants (where three of the meiotic products normally die), in archegonia (where usually only the egg cell survives), and in the pseudocentral cells that Durzan et al. have succeeded in inducing in Norway Spruce. The system that Durzan et al. have devised, in which the formation of pseudocentral cells can be induced in defined conditions, gives an opportunity to investigate this intriguing relationship between death and rebirth, present in both normal and abnormal life cycles, in greater depth. This is of greater importance than questions of semantics. Experimental work of the kind that Durzan et al. have been doing makes clear that the standard life cycle is only one way of bringing about the renewal of embryogenic activity, but one feature common to normal cycles and to the experimental treatments that lead to embryogenesis seems to be that controlled death is involved at some stage in one or more of the participating cells. Even in aporous aposporous in angiosperms, the regression of the meiotic sac that accompanies the development of the aposporous may be an apop- 

totic phenomenon. If it could be shown that regression of the meiotic sac was independent of the presence of the aposporous sac, this would be a strong indication that programmed death of the meiotic sac had become encoded in its genome and was not merely the result of competition (Mogie 1992). It is striking that in many instances a conspicuously unequal division precedes cell death, usually of the smaller cell, as in the division of the central cell in archegonia. The reduced cytoplasm of the smaller cell may lead to its genome being exposed to influences that activate the genes controlling self-destruction.

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Peter R. Bell
Department of Botany and Microbiology
Darwin Building
University College
London WC1E 6BT

Literature cited


