

in spermidine concentration in the ovariectomized rat uterus 24 hours after intravenous injection. Testosterone has also been noted to effect a gradual increase in ornithine decarboxylase activity in the prostate of orchietomized rats (6).

Certain steroids and polypeptide hormones which induce growth also induce the rapid appearance of ornithine decarboxylase activity in their target organs and an accumulation of amines derived from ornithine. Although an unambiguous biological role for putrescine and the polyamines has yet to be defined, they have been implicated in a large and diverse number of biological processes. For example, polyamines have been reported to stimulate protein synthesis, to stabilize polysomes, to stabilize membranes, to stimulate RNA and DNA synthesis, and to stimulate aminoacyl-transfer RNA formation (7). In many of these reactions the polyamines may replace, at least partially, a  $Mg^{2+}$  requirement, and it has been suggested that polyamines may be more important for protein synthesis *in vivo* than is  $Mg^{2+}$  (8).

The fact that both steroids and polypeptide hormones can act as inducers of ornithine decarboxylase suggests that the induction of the decarboxylase is an early, but not necessarily primary, event in the action of these hormones. It is conceivable that the rapid induction of ornithine decarboxylase and the subsequent accumulation of putrescine or polyamines provide a mechanism by

which the cell may rapidly alter its internal environment to optimize conditions for a variety of biosynthetic reactions.

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## Apospory in *Sorghum bicolor* (L.) Moench

**Abstract.** *A line of Sorghum bicolor* (L.) Moench was discovered to reproduce by apospory, a type of apomixis. The formation of an embryo by a nucellar cell without fertilization was established by cytological observations of ovaries and by progeny tests.

Apomixis, seed production without fertilization, has tremendous potential in the production of cereal grain hybrids. The  $F_1$  hybrids are generally superior and are widely used, but they must be produced by repeated controlled crossing of parental lines. An apomictic hybrid would fix heterosis, since it perpetuates itself through identical offspring for successive generations.

We now report a form of apomixis in a polygynaceous line (I) of *Sorghum bicolor* (L.) Moench in which the embryo is formed by apospory from a somatic cell in the nucellus (2). This

type of embryo development and its significance has been reported in several species (2-4), but we know of no documented report on apospory in a grain crop.

Method of reproduction was determined by cytological study of ovules and was confirmed by evaluation of progeny. Serial sections of ovaries were made at various stages of development and were stained in safranin-fast green in order to observe megasporogenesis and development of the embryo sac. The apomictic line was crossed with a pollen parent that had a dominant genetic marker.

Some ovules of this line had aposporous development, whereas those in other florets had sexual development. In sexually reproduced sorghum the megaspore mother cell differentiates and divides to form a linear tetrad of megaspores (5). The functional chalazal megaspore (Fig. 1A) continues to enlarge, the nucleus divides, and an embryo sac is formed with an egg, two polar nuclei, two synergids, and three antipodals (Fig. 1B).

Megasporogenesis in ovules with aposporous development proceeds identically to that in ovules which develop sexually, up to the time of formation of the functional chalazal megaspore. At this time the nucellar cells become active (Fig. 1C). These nucellar cells enlarge and the nuclei divide to form aposporous embryo sacs, each with two polar nuclei and an egg (Fig. 1, D to F). At this stage the chalazal megaspore apparently degenerates. There are usually two to five well-differentiated aposporous embryo sacs within each ovule.

Rao and Narayana (6) reported "a suspicion of possible apomictic development" in *S. bicolor*. A single fully differentiated eight-nucleate embryo sac arose from a cell at the chalazal end of the tetrad of megaspores. They assumed that the embryo sac originated from a nucellar cell, but the figures they presented may be interpreted as normal development of the functional megaspore. Apparently there was no evidence of additional nucellar activity in the ovule or formation of multiple aposporous embryo sacs as noted in our material, and their studies of progeny were inconclusive.

Apospory in this line of sorghum actually contributes to the formation of seed and progeny. Self-sterile plants which produced no pollen, possessing the polygynaceous character, were crossed with a pollen parent that had a dominant marker gene *Pc*, which causes susceptibility to toxin of the fungus *Periconia circinata* (Mang.) Sacc. The aposporous stock was recessive *pc* and resistant. The seedlings resulting from these crosses were screened for resistance to toxin (7). Up to 25 percent of one progeny of 16 and 20 percent of another progeny of 25 were resistant. We concluded that these resistant progeny arose from aposporic embryo sacs. Pollination was necessary for stimulation, for the development of endosperm, or for both.

To be ideal for plant breeding (8), apomixis should be obligate and trans-

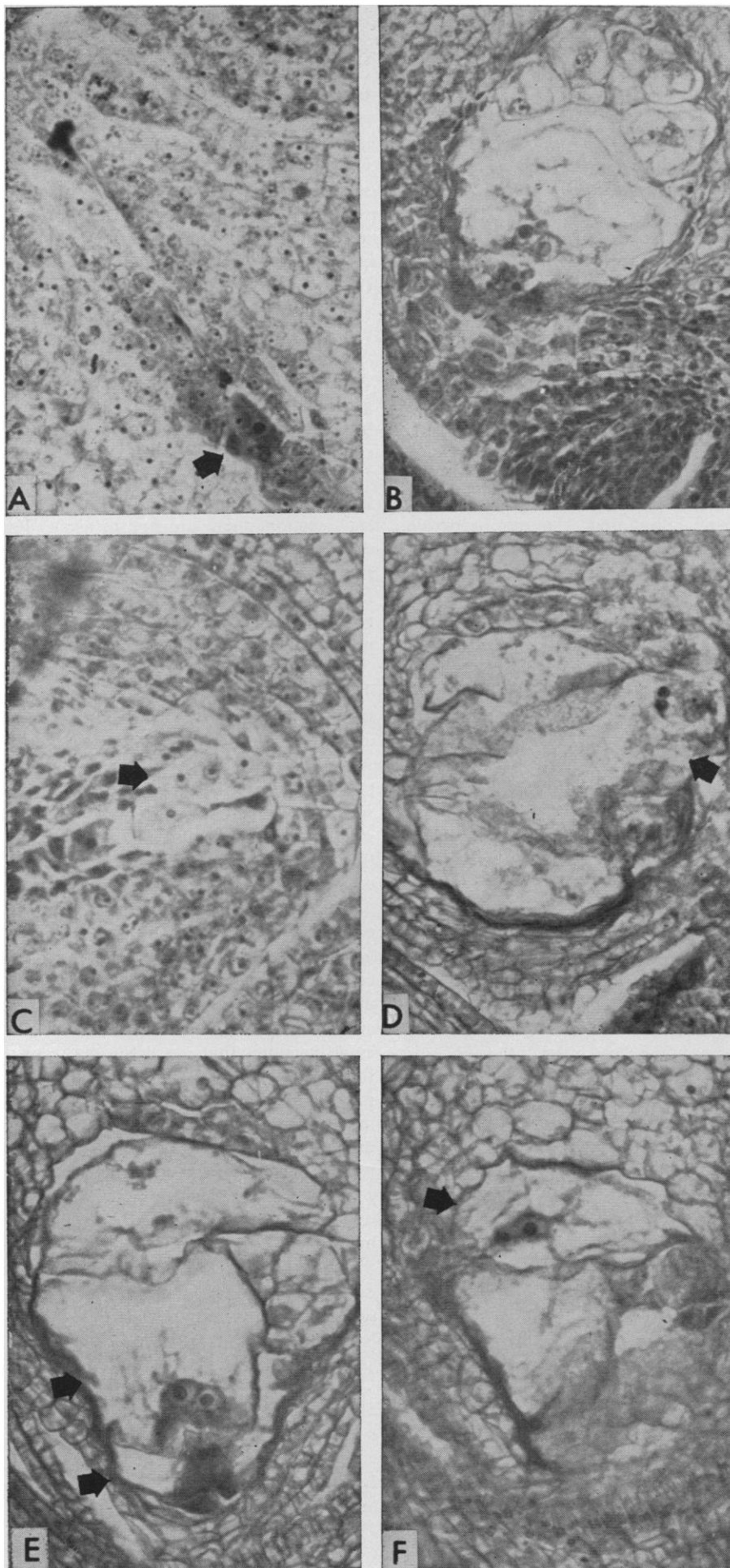


Fig. 1. Sexual and apomictic development in longitudinal sections of sorghum ovaries. Normal sexual development is shown in (A) and (B); aposporous development in (C) through (F). (A) Functional chalazal megaspore (arrow) ( $\times 1800$ ). (B) Mature embryo sac at anthesis ( $\times 900$ ). (C) Nucellar activity near micropylar end (arrow) ( $\times 1800$ ). (D-F) A single ovule with multiple nuclear embryo sacs (arrows) ( $\times 900$ ). (D) Nuclear embryo sac with two polar nuclei (egg was present in adjacent section). (E) Two additional sacs, each with two polar nuclei and an egg. (F) Another sac with a polar nucleus and an egg (other polar nucleus was present in adjacent section). Note prominent antipodal cells in B and their absence in D, E, and F. All magnifications are approximate.

ferable. We recognize the limitations imposed by the facultative form of apomixis in the present *S. bicolor* line. However, purely aposporous offspring may be derived from this material. It has been established in buffelgrass (3) and other species that apomixis is genetically controlled and can be used to develop new useful apomictic varieties. It is probable that an obligate apomict can be found or isolated by proper genetic and breeding manipulations in sorghum.

Apomictic grain sorghum could (i) make available maximum-yielding, true-breeding hybrids of high purity; (ii) simplify hybrid seed production; (iii) lessen the need for highly trained production men; and (iv) increase the opportunity of breeders to use superior gene combinations in hybrids. These advantages have especially important implications for less developed areas.

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