POLLINATION

Pollen grains are formed from microspore mother cells in the anthers. Following a meiotic and a mitotic division a tetrad of cells is formed, which matures as pollen grains (Fig. 12.9). Pollen grains may be either bi- or trinucleate (Brewbaker 1959); that is, they may have one or two generative nuclei in addition to the vegetative nucleus. Members of the Gramineae and Compositae families are characteristically trinucleate as a result of a second mitotic division in the microspore. The binucleate pollen also undergoes a second mitotic division upon germination of the pollen grain and becomes trinucleate in effect.

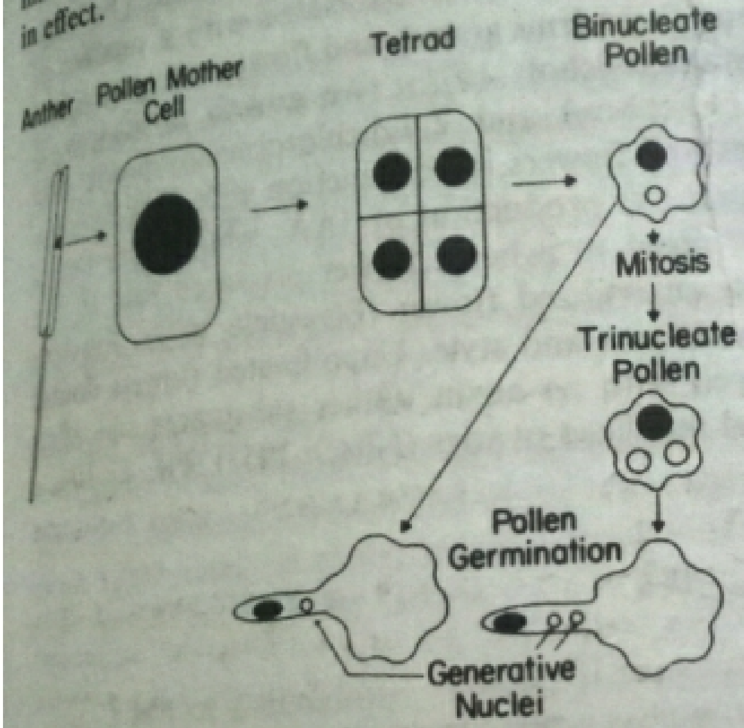
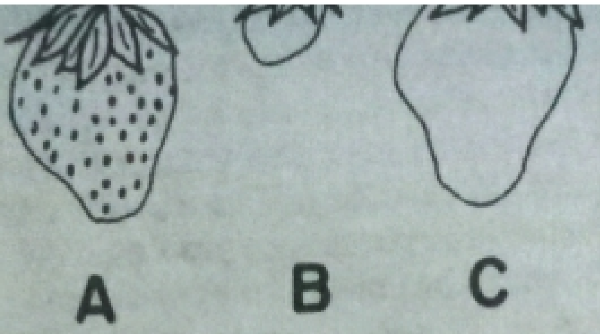


Fig. 12.9. Pollen grain formation in anthesis and germination of di- and trinucleate pollen cells.

Pollen cells germinate almost immediately if brought in contact with a receptive stigma, which provides a suitable substrate stimulation. Germination occurs in vitro using agar or a sugar solution (plus certain minerals, for some species). Germination of pollen is evidenced by a rapid increase in respiration and synthesis of RNA and protein. These processes begin in a span of 2 to 30 min (Leopold and Kriedemann 1975).

A number of factors stimulate pollen germination (Vasil 1960), including favorable concentrations of sucrose, CO_2, boron, and calcium. Boron seems to enhance sucrose utilization. From in vitro studies it appears that growth regulators in the stigma or medium are not requisite to germination, although pollen is rich in auxin and GAs. Increased germination and pollen tube growth from a mass of pollen, compared with that of a single grain, is evidence for growth hormone stimulation. Water extracts of pollen had similar stimulatory effects (Brewbaker and Majumder 1961).



(achenes) on strawberry fruit (receptacle) development. *A*. Fruit with seeds. *B*. Seeds removed at early development stage. *C*. Seeds removed (as in *B*) and replaced with an auxin paste on the young fruit. (From Nitsch 1950)

Numerous GAs have been isolated from seeds (Letham 1963). Seeds produce ethylene as well during germination.

Generally, except for parthenocarpic fruit growth stimulated by pollination alone, seeds are necessary for fruit development. For example, the receptacle of the strawberry does not develop into a fruit without *uchenes* (seeds) (Fig. 12.13). Poor pollination or nutrition resulting in failure of seed set causes dwarfed or deformed strawberry fruits (Nitsch 1950). The role of seed in fruit development of dry fruits is less readily observable. Injury, maturity, and other factors can induce ethylene formation and fruit abortion in most species (Lipe and Morgan 1972), as is common on soybean with stem rot.

MATURATION AND RIPENING

A fruit is mature when full size is reached and the rate of dry weight gain becomes zero. Mature fruits *ripen* by passing through a chain of enzymatic and biochemical events that result in changed chemical composition (Leopold and Kriedemann 1975). In ripening, old enzyme systems senesce and new ones are produced that cause softening and conversion of starches to sugars in fleshy fruits (e.g., apple). The acid level in citrus fruits declines. Chlorophyll is lost, while xanthophyll and carotene increase or are no longer masked out by chlorophyll. Certain of these reactions also occur in grass seeds and legume fruits (pods), although they are less pronounced.

Changes in ripeness are associated with a relatively high respiration rate in *climacteric* (rapid-ripening) fruits. Metabolic activity declines in nonclimacteric fruits, including those of agronomic crops.

Loss of chlorophyll and acceleration of senescence is characteristic of dry, dehiscent fruits (e.g., soybean pods). Carotene increases in yellow maize. Ethylene and abscisic acid play an important role in abscission and dehiscence of pod and capsule dry fruits (e.g., soybean or castor bean).

The number of fruits (e.g., pods of soybean or grains of maize) per plant is established relatively early in the ontogeny of crop plants. In well-watered and well-fertilized plants of adapted cultivars, it is a function of photosynthetic rate or assimilate supply. For a given genotype the number of fruits per plant is a function of spacing and the resulting intercepted light; therefore the number of fruits per unit of land area is related more to intercepted light than to the number of plants. Hence, within limits, light interception and assimilate production per unit of land area determine seed number per unit, regardless of plant number. Once the fruit load is fixed, seed yield becomes a function of seed size. Seed size for a given cultivar is usually relatively constant, but severe stresses during grain filling can cause a reduction in size. This reduction is a consequence of reduced assimilate supply and/or reduced leaf nitrogen. Leaf nitrogen has been considered a principal factor in soybean seed yield (Sinclair 1981). Seed size of peanut has also been shown to be controlled by fruit (pod) size (Nimbkar 1981). Peanut cultivars with small pods produce small seeds because of pod wall constriction, which results in fewer cells and smaller cell size. Peanut cultivars with small pods and seeds usually produce more pods and seeds per plant.

Summary

Flowering, fruiting, and seed set are essential events in crop plant production. These processes are controlled both by environment, particularly photoperiod and temperature, and by genetic or internal factors, particularly growth regulators, photosynthate, and mineral nutrient supply (e.g., nitrogen).

Based on their response to day length (more accurately, length of night), most crop plants can be classified as short-day plants (SDPs), long-day plants (LDPs), or day-neutral plants (DNPs). Soybean, wheat, and tomato, respectively, are examples of these three types. In general late summer to fall flowering indicates SDPs, and spring to early summer flowering LDPs. Tropical plants are usually SDPs but may be photoperiod-insensitive DNPs.

A brief interruption of a long night by red (R) radiation (maximum effectiveness, 660 nm) at low energy levels produces a short-night or long-day effect, preventing flowering in SDPs and promoting flowering in LDPs. An interruption by far-red (FR) radiation (maximum effectiveness, 735 nm) has the opposite effect, promoting flowering in SDPs and preventing it in LDPs. At a warm temperature, FR radiation is equivalent to darkness; the R effect is reversed by the equivalent of darkness. The pigment phytochrome is the photoreceptor of both R and FR radiation. The two forms of phytochrome, P_r and P_{fr}, are photoreversible by R or FR light. The equilibrium concentration of P_r and P_{fr}, and hence the stimulus to flower, is dependent on exposure to length of uninterrupted darkness. P_r is the most biologically active form.

Evidence from grafting experiments shows that the photoperiod stimulus is received by the leaves and translocated to the meristems, causing transformation from a vegetative state to flowering. Evidently the stimulus is not transferred to new or unexposed shoots, or tillers. Grass plants usually have numerous vegetative shoots with flowering shoots on the same plant. Pod initiation of indeterminate varieties of soybean occurs first at the axes of lower nodes and progresses basipetally and acropetally from this point. After the