The cultivated peanut (*Arachis hypogaea* L.) is an annual legume that probably originated in Bolivia, South America, along the eastern slopes of the Andes (Krapovickas, 1968). It is now widely grown and well adapted to tropical, subtropical, and warm temperate areas of the world. In the United States, peanuts are utilized primarily as whole seeds and for making peanut butter, while elsewhere in the world they are mainly crushed for oil. Seed of the commonly grown cultivars contain 42 to 52% oil and 25 to 32% protein.

I. PARENTAL MATERIAL

The genus has been classified into seven distinct sections (Gregory et al., 1973). The *Arachis* section includes four annual diploids, (2n = 20), at least five perennial diploid species, and two annual tetraploids (2n = 40), one of which is the cultivated peanut. Gregory and Gregory (1976) postulated, "... the cultivated peanut consists of two genomes, both of which came from species of the section *Arachis*, and ... one of these genomes came from a perennial species and one from an annual."

The cultivated species has been taxonomically classified by Krapovickas (1968) into two subspecies and four interfertile varieties: (i) subspecies *hypogaea*; variety *hypogaea* (includes the U.S. market types Virginia and Runner), and variety *hirsuta*; (ii) subspecies *fastigiata*; variety *fastigiata* (Valencia market type) and variety *vulgaris* (Spanish market type). Although many interspecific crosses in the genus *Arachis* have failed, successful crosses have been reported. The hybrids from the successful crosses are largely sterile, but Smartt (1964) found that some sterility obstacles may be overcome by artificially doubling the chromosome number. Gregory et al. (1973) list several species of *Arachis*, a few of which are freely cross-compatible with the cultivated species. *A. monticola*, a wild annual species, has the same chromosome number, a similar karyotype, and complete interfertility with *A. hypogaea*.
Varnell and McClure (1975) listed a total of 10,790 accessions of the cultivated peanut in nine countries of the world. The Southern Regional Plant Introduction Station at Experiment, Ga. maintains 3,990 accessions and is the most complete and accessible collection in the United States.

II. PLANT CULTURE

A. Field

Like most crop plants, peanuts do best with a balanced supply of available plant nutrients. The soil should be especially well supplied with calcium. Fruits that appear normal may be empty or contain only shriveled seeds due to a lack of readily available calcium in the fruiting zone.

Smith (1954) observed that changes in flower frequency may be influenced by climatic factors which determine relative humidity. In field plantings, flower frequencies reach low values under drought conditions, but high flower frequencies occur within 2 or 3 days after the soil has been saturated by rainfall or irrigation.

Ono et al. (1974) reported optimum soil moisture content in the podding zone to be about 40% of the total soil volume, regardless of the soil moisture content in the rooting zone. Soil moisture content lower than 40% reduced the podding percentage and pod enlargement, but moisture greater than 40% only reduced enlargement.

Gibbons (1977) had very low success rates in India when field hybridizations were performed during the dry season (December to May), presumably due to the low relative humidity.

Optimum plant population depends mainly on the purpose of the planting and secondarily on the subspecies involved. For example, F₁ plants should be spaced from 45 to 90 cm apart in rows 90 to 180 cm apart to produce large quantities of seed. Spacings from 30 to 45 cm apart in rows 91 cm apart are recommended for segregating populations to permit uniform opportunity for the expression of each plant’s potential, and permit visual evaluation and manual separation by the breeder. The closer spacings are satisfactory with erect or semi-erect growing types.

Field nursery plantings of wild peanut species are in isolation type plots, i.e., planted rows have three or four non-planted 90 cm plots between them. Species that will cross are not planted in adjacent plots. If two species will cross, the hybrid should be easily recognized by a genetic marker, such as flower color (Gregory, 1977).

Umen (1933) has reported that Arachis hypogaea is photoperiod-insensitive under constant temperatures, but did show photoperiod sensitivity under variable temperatures. Fortanier (1957) demonstrated that the initiation of flower production was independent of photoperiodism, as well as thermoperiodism. These results were corroborated by Wynne et al. (1973). Peanuts require a high light level of not less than 45% full sunlight (Simpson, 1977). Fortanier (1954) stated that flower bud elongation and opening were light-wave-length-dependent, and that the time of flower expansion was regulated by a light stimulus received by the bud 3 days earlier.
Flower expansion was also shown to be dependent on white and blue wavelength.

Temperatures between 22 and 33 C are most ideal for flowering and fruiting of cultivated peanuts. Ono et al. (1974) noted that the beginning time and rate of pod development were significantly affected by soil temperature in the podding zone. Optimum soil temperature was 31 to 33 C; minimums were 15 to 17 C and maximums 37 to 39 C.

Pollen is sensitive to environmental changes such as light, temperature, and humidity. DeBeer (1963) noted that plants grown at temperatures of 33 C produced pollen of low viability, and that the temperature 36 to 96 hours preceding flower opening also influenced viability.

Hybridization of the cultivated peanut is commonly done in pots or flats in greenhouses so the plants can be moved around. However, in some countries hybridization is done in field nurseries. Many wild species are not successfully hybridized when grown in pots, but must be grown in deep benches or beds. Several wild species do not set fruit inside a greenhouse and hybridization must be done outdoors (Gregory, 1977).

B. Growth Chamber and Greenhouse

The female plants of cultivated species that are to be used in crosses are generally grown in 15-liter, 30-cm diam pots on greenhouse benches. The containers may be rotated to provide convenient access to the flowers during emasculation and pollination. In Florida, hybridization has been more successful from plantings made in the greenhouse in early spring, probably because lower temperatures during the winter season, cloudy days, or both retard floral development and flowering (Norden and Rodriguez, 1971).

Banks and Jordan (1971) experimented with different sources of water (tap, lake, distilled) and different fertilizer treatments for growing peanuts under greenhouse conditions in a high pH soil. They found distilled water was best and acidified tap water second best. They obtained good results using acidifying soluble fertilizers of 21–7–7 and 20–20–20 NPK in combination with distilled water and steam-sterilized sandy loam soil in plastic pots.

New or sterilized soil to be used in hybridization studies should be inoculated with Rhizobium bacteria (Simpson, 1977). He found that 80 to 85% of soil capacity is the best moisture level for greenhouse plantings.

Apparently maintaining a high relative humidity is critical for successful artificial hybridization in greenhouses.

Peanut hybridization usually has been done by emasculating flowers in the evening and pollinating them the following morning. Two modifications that increase crossing efficiency recently have been reported. Profuse flowering can be induced with artificial lighting from 1700 to 0130 hours (Hildebrand, 1974). Following that treatment, buds can be emasculated between 0730 and 1130 hours. Pollen parents can be grown outdoors and will provide ample fresh pollen during this time enabling the breeder to make pollinations immediately after emasculating flowers of the female parent. The average time required for this crossing method is 4 min. Hammons (1973) estimated that the conventional method required 10 min per flower.
A second modification involves the use of a growth chamber to reverse the day-night cycle (Banks, 1976). A 12-hour, 29°C day begins at 1630 and a 12-hour, 21°C night at 0430 hours. Emasculations are made between 0800 and 1000 hours and pollinations are done immediately with fresh pollen coming from plants grown in a greenhouse. He found this crossing method yielded more than 50% viable hybrids per pollination and, because the growth environment was artificially controlled, permitted up to three crossing cycles per year. The crossing methods of Hildebrand (1974) and Banks (1976) share the obvious advantage of allowing hybridization to be done during normal working hours when labor can be more efficiently utilized.

III. FLORAL CHARACTERISTICS

The peanut is normally a self-pollinating species. Anthesis generally occurs prior to flower expansion. In mature flowers, the stigma lies buried among the dehisced anthers in the tightly closed keel petal, thus assuring self-fertilization (Smith, 1950; Capinpin and Guevara, 1951).

The occurrence of natural hybrids in the cultivated peanut was reported as early as 1910 by van der Stok (1910), and plants suspected of having originated by natural hybridization are not infrequent in most breeding nurseries. Hammons (1973) made numerous studies of natural hybridization using a dominant leaf marker called, krinkle. He found rates of outcrossing in breeding nurseries at Tifton, Ga. ranging from 0.25 ± 0.002% to 6.16 ± 0.007%. Culp et al. (1968) obtained much lower rates in Virginia, averaging from 0.09% to 0.27% which is similar to findings in Puerto Rico (Stone et al., 1973). Gibbons and Tattersfield (1969) reported from none to 1.67% outcrossing in Malawi, Rhodesia, and Zambia.

Various wild bee species are the principal vectors of natural cross-pollination in *A. hypogaea*, and the frequency is associated with the production of atypical flowers that vary considerably for different cultivars (Hammons, 1963; Hammons and Leuck, 1966; Leuck and Hammons, 1969).

The inflorescences consisting of three or more flowers are spikelike and always occur in the axils of cataphylls or of foliage leaves. The flowering axis never occur at the same nodes as vegetative branches, although they may appear to do so because of the shortness of the internode below the first cataphyll of a branch. Each flower is subtended by a bract and is borne on a minute branch of the inflorescence which arises in the axil of a second bract. Thus, two bracts are found below each flower, but the lower bract actually occurs on an axis of the inflorescence (Fig. 1a). Mainstem inflorescences occur in the Spanish (*A. hypogaea fastigiata vulgaris*) and Valencia (*A. hypogaea fastigiata fastigiata*) cultivars, while inflorescences occur on the lateral branches of the Virginia (*A. hypogaea hypogaea hypogaea*) cultivars. The calyx and corolla are located at the top of the hypanthium. The staminal column is surrounded by and runs the entire length of the hypanthium (Fig. 1b). The calyx is five-lobed, one lobe being separate and opposite the keel and the other four fused, except for their tips. The keel closely embraces the stamens and style. Flower size varies with environment.
The staminal column is usually composed of 10 filaments, 8 of which normally bear anthers (Fig. 1b). The filaments are fused through one-half to two-thirds of their lengths. At the point of separation, the free ends of the filaments are sharply reflexed toward the standard forming acute angles with their fused bases. The pistil consists of a single ovary 1.5 mm long and 0.5 mm in basal diameter (Smith, 1950). It is surmounted by the long style which extends through the hypanthium, bends sharply through the staminal column, bends sharply again through the filaments, and ends in a club-shaped stigma (Fig. 1b). The style is clothed with upward slanting hairs near its summit on the surface facing the standard (Gregory et al., 1951).

*Arachis hypogaea* is indeterminate in growth, and flowering begins from 25 to 35 days after planting, depending on the cultivar. The most prolific period of flowering occurs between 6 and 11 weeks, depending on the cultivar, with a high proportion of the first flowers producing mature fruits.

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Fig. 1—Peanut inflorescence with flower in leaf axil (a) and longitudinal schematic drawing of the flower (b). (After Smith, 1950.)
Few of the flowers that open late produce mature fruits, unless something in the production environment prevents the early flowers from functioning (Bear and Bailey, 1973). Peanuts produce many more flowers than the plants can support in fruit and seed production. Approximately two-fifths of the flowers fail to begin fruit development and an additional two-fifths produce immature pegs which abort before pod enlargement occurs (Smith, 1954). Removing all flowers every day can cause *A. hypogaea*, normally an annual, to live as long as 240 days or more and insures that flowers are available over a long period (Bear and Bailey, 1973).

Usually only one flower of an inflorescence reaches anthesis on a given day, occasionally two or more in Spanish types. Intervals between successive flowers on an inflorescence vary from one to several days. Twenty-four hours before anthesis, the flower bud is 6 to 10 mm long. During the day, the hypanthium elongates slowly and the buds attain lengths of 10 to 20 mm. At night, elongation accelerates, so that at anthesis flowers are usually 50 to 70 mm long (Smith, 1950). The bud usually opens at the beginning of the light period; however, this may be delayed by cool or wet weather. Pollen liberation may occur as early as 7 to 8 hours before flower opening, but even upon flower opening the anthers may not have dehisced in some flowers (Bolhuis et al., 1965). The stigma is receptive from 24 hours before to 12 hours after the opening of the flower (Hassan and Strivastava, 1966).

On warm, sunny days the flowers often wither within 5 or 6 hours after expansion. In cooler weather, wilting is delayed. Only the ovary and the base of the style remain in a turgid condition after the day of anthesis.

**IV. ARTIFICIAL HYBRIDIZATION AND SELF-POLLINATION**

**A. Equipment**

The main instruments required for emasculating the flowers are a forceps and a sharp penknife, scalpel, or razer blade. Unless one has exceptional eyesight, a 2× to 3× magnifier attached to a head band is helpful.

**B. Preparation of the Female**

Usually only one flower bud per inflorescence is emasculated on the female parent. The flower bud selected should be as near to the main stem as possible. The percentage of successful hybridizations per emasculations is usually higher when the plants are young and in the early stage of flowering.

Stages in the emasculation of the peanut flower are illustrated in Fig. 2. Flower buds appear above the leaf axils during the afternoons of warm, bright days, and emasculations can be accomplished without difficulty as early as 1700 hour (Fig. 2-2). On cloudy or rainy days, fewer flower buds develop, and their growth is usually retarded to the extent that emasculations are easier to accomplish if delayed until 2100 or 2200 hours, or until the bud has emerged approximately 2 cm from the axil and is large enough to be manipulated.
Emasculation begins by grasping the bud with thumb and index finger of one hand (Fig. 2-3). The sepal in front of the keel is removed, and the sepal on the side of the standard is folded down (Fig. 2-4). The standard is opened with the forceps, and the wing petals pulled out and down (Fig. 2-5). As the standard is held back with thumb and index finger, the point of the forceps is used to break the keel and to move up the keel to pull it free of the stigma and anthers (Fig. 2-6). The keel is pulled down and held out of the way with thumb and index finger while all anthers and as much of the filaments as possible are removed with forceps (Fig. 2-7). Some operators find it difficult to hold the wing and the keel petals out of the way during the process; therefore, they remove them without noticeably reducing the percentage of successful hybridizations (Fig. 2-8). After the anthers are removed, the standard is returned to its original position over the stigma. No attempt usually is made to protect the emasculated flowers.

An alternative method was described by Reddy et al. (1970) who used a razor blade to cut around the flower bud two-thirds down from the tip for removal of the standard and a portion of the wing petals. The anthers were then removed and a folded piece of drinking straw inserted over the emasculated flower.

Fig. 2—Stages in the emasculation of a peanut flower. (1) Potted plant, (2) bud at proper stage for emasculation, (3) bud held in position for emasculation, (4) the sepal on the side of the standard is folded down, (5) the standard is opened with the forceps and wing petals pulled out and down, (6) the standard is held back with thumb and index finger and with the forceps the keel is pulled free of the stigma and anthers, (7) anthers and as much of the stamens as possible are removed, (8) and emasculated flower with the wing and keel petals removed, (9) emasculated flower identified with small colored string attached to hypanthium. (Photographs 3 through 7 provided through the courtesy of C. E. Simpson, Stephenville, Texas.)
The emasculated flowers can be identified in a number of ways. A common method is to attach a small thread to the hypanthium of the emasculated flower and drape the other end over the edge of the pot (Fig. 2-9). Different colored strings may be used to identify the flowers emasculated on different days. Mixon (1977) tags an emasculated flower with a strip of heavy duty aluminum foil that is cut 6 to 8 mm wide and 5 to 6 cm long and looped around the hypanthium. Gibbons (1977) marks the emasculated flower with a colored thread and uses a second thread of a different color to show that the flower has been pollinated.

C. Pollination

On the morning of the day following emasculation, the standards are usually expanded and the stigmas exposed, so that application of pollen is possible in many cases without handling the flower. Pollinations are accomplished between 0700 and 1000 hours by removing a healthy flower from the male parent (Fig. 3-1), squeezing its pollen onto a forceps, and transferring the pollen by means of the forceps to the stigma of the emasculated flower (Fig. 3-2). Some operators detach the keel from the male parent flower and squeeze the pollen from it directly onto the stigma; others apply pollen to the stigmas with a small camel hair brush. The plants and flowers must be handled very carefully following pollination because the pollen grains are easily dislodged from the stigma (Fig. 3-3). The operator should dip the forceps and rinse fingers in an alcohol solution before changing from one pollen source to another to reduce the possibility of pollen contamination.

To provide shade and a higher relative humidity for the germination and subsequent growth of pollen, a paper towel, approximately 12 × 12 cm in size, can be dampened with water and placed carefully over the flower without touching the stigma immediately after it is pollinated (Fig. 3-4a). Sharma (1964) found that placing a polyethylene tube cover, punched with a few holes to allow aeration, over the female plants after pollinating resulted in better pollen germination and ultimate fertilization without the necessity of covering the pollinated stigma. He reported little success when he covered the pollinated stigma with the keel, probably because the pollen was dislodged from the stigma in the process.

Peanut pollen is most viable when collected in the early morning (Bolhuis, 1959; DeBeer, 1963). Oakes (1958) found that pollen collected as early as 0300 hours was physiologically immature, but that collected after 0900 hours was overmature. He, as well as Hassan and Srivastava (1966), reported that the period of maximum physiological development of peanut pollen is between 0500 and 0700 hours.

Faucette and Emery (1974) found that pollen desiccated for 6 to 7 days and stored in dry containers for 9 days at 8°C was still viable. Hassan and Srivastava (1966) reported that pollen was viable up to 8 days when stored in a refrigerator at 6°C over calcium chloride in sealed desiccators, but for only 8.5 hours when stored at 28°C and a relative humidity of 56%.

Smith (1956) reported a time lapse of 12 to 16 hours between self-pollination and fertilization, and Oakes (1958) 8 to 9 hours.
After pollinations are completed, all unpollinated flowers on the plant are removed by breaking the hypanthium near the base with forceps by 1000 hours. If fertilization was successful, an aerial peg will usually become visible 7 to 10 days after pollination, rarely as long as 15 days. Smith (1954) and Stokes and Hull (1930) observed that the ovaries of pollinated peanut

Fig. 3—Stages in the artificial pollination and subsequent development of hybrid peanut seed. (1) A flower removed from the male parent plant; (2) pollen that has been squeezed onto forceps and transferred to the stigma of the emasculated flower; (3) cluster of pollen grains on the stigma; (4) a dampened paper towel (a) placed over the pollinated flower to provide a higher relative humidity for germination, and the wilted flower (b) 5 to 6 hours after pollination; (5) a color-coded wire looped around the developing peg (b), which is still attached to the withered flower and its identifying string (a); (6) fruit which is generally harvested 55 to 65 days after the peg is wired. (Photographs by John Swearingen and line drawings by Ashley Wood, Univ. of Florida, Gainesville.)
flowers can remain dormant for several weeks without losing their ability to resume active fruit development.

After fertilization occurs, the ovary elongates because of intercalary meristem growth in its base. This peg grows down into the soil where the peanut develops. Figure 3-5a shows the withered flower attached to the peg and Fig. 3-5b the peg that has been wired for identification. Approximately 2 months later, the mature peanut fruit with the peg still attached can be harvested (Fig. 3-6).

The developing peg, with the withered flower and string still attached, can be identified by means of a color-coded wire which is looped around the peg before it penetrates the soil. The other end of the wire can be attached to the stake that supports the label of the female plant (Fig. 3-4 to 3-6). Discarded sections of telephone cable provide an excellent source of different colored wires for identifying crossed seed. The use of a different wire color each day provides the opportunity for allowing each hybrid seed a prescribed period of time in which to develop and mature. Simpson (1977) identifies the pollinated flowers with nylon string attached to a dated stake. The string is transferred to the peg when it emerges.

Immediately after pollinating a flower, Mixon (1977) records the number of the pollinator plant and the date of pollination on the foil strip that was attached to the hypanthium at the time of emasculation. When the resulting peg reaches 12 to 16 mm, the foil marker is removed from the hypanthium and secured around the elongating peg. This labeling procedure is particularly useful in making random crosses between several plants.

Artificially hybridizing peanuts in the greenhouse has consistently resulted in over 70% success. Gibbons (1977) reported a success rate of 44% in India from field hybridization starting at 0630 hours during the monsoon season (July to August), compared to 27% when pollination was started at 0830 hours.

D. Factors Affecting Efficiency

Flowers and developing pegs without attached strings or wires are removed daily for a period of 10 days after the last cross has been completed. The lateral vegetative growth and fruiting branches that do not contain hybrid pegs are pruned back. When more than 5 to 10 pegs are developing per plant, the efficiency of the operator's time is reduced in terms of the number of crossed seed harvested relative to the number of pollinations made.

To facilitate record keeping, it is recommended that the plant in any container donates or receives pollen from the plant in only one other container. Because plants involved in various crosses do not generally begin to flower at the same time, the flowers are removed daily until the majority of the plants are flowering.

Genetic markers are not commonly used in peanut breeding, but are used in peanut genetic studies and for detecting contamination from natural outcrossing. Hammons (1964) reported a monogenic dominant wrinkled leaf marker that is easily differentiated from normal leaves from seedling leaf expansion through harvest maturity.
V. NATURAL HYBRIDIZATION

Van der Stok (1923) stated that natural hybridization had been used to develop new peanut cultivars in Buitenzorg, Java. Hammons (1973) discussed the utilization of natural crosses as a new genetic technique he termed pedigree natural crossing. This technique permits the production of larger numbers of F1 hybrids than is possible with the same expenditure of time using manual procedures. The chief disadvantage of the technique is that the marker stock must have in its genetic makeup those characteristics desirable for cultivar improvement.

VI. SEED DEVELOPMENT, HARVEST, AND STORAGE

The appearance of the aerial peg with withered hypanthium and string adhering to it is evidence, but no proof that the fertilization was successful (Fig. 4-5). Seed harvest is usually 55 to 65 days after the peg was wired depending on environmental conditions and maturity of the parental lines.

Seed of the cultivated peanut generally becomes non-viable within 2 years when stored at room temperature. Seed storage studies indicate that shelled peanut seeds with not more than 6% moisture can be stored for at least 9 years without appreciable loss in germination when held at −4 to 5°C (Norden, 1975).

VII. TECHNIQUES FOR SPECIAL SITUATIONS

In hybridization programs, the number of F1 seeds sometimes are insufficient to produce the large F1 populations desired, in which case the F1 hybrids may be multiplied by vegetative propagation.

Nuchowicz (1955) cultured excised embryos and sections of embryos of peanuts as a means of increasing the number of descendants, but found that the divided embryos grew poorly. Martin (1970) conducted research on methods of in vitro embryo culture in attempting to overcome some of the barriers to interspecific hybridization. He has been able to produce viable seedlings from ovules measuring 0.3 mm. Banks (1977) has had some success culturing embryos that were differentiated to the extent that cotyledons were visible, but as yet has not been successful with very young embryos.

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