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Peanut Growth and Development: From Fertilization to Mature Pod

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ABSTRACT

Due to its importance as a food as well as an oilseed crop around the world, peanut (*Arachis hypogaea* L.) is an economic crop in world agriculture. It is unique among the major food crops with an interesting reproductive biology of above ground flowers and underground pod production. This feature led to a thorough study of the process of fertilization, embryo growth, seed and pod development to understand peanut growth and development. Peanut displays large morphological variation for plant, pod and seed features with a wide range of adaptations to many different ecological conditions. This genetic variation is valuable to researchers for peanut improvement.

INTRODUCTION:

Peanut (*Arachis hypogaea* L.) belongs to the pea family, Fabaceae (formerly Leguminosae), subfamily, Papilionoidae, in the more diverged basal clade, Dalbergioid (Wojciechowski *et al.*, 2004; Weller and Ortega, 2015). The plants are usually compact from 30-45 cm tall and 35-75 cm wide with a deep taproot. The roots harbor a symbiotic relationship with the soil bacterium belonging to genus *Rhizobium* and have the unique ability to convert soil nitrogen into a plant available form. Thus, peanut plants improve soil fertility by reducing their dependence on nitrogen fertilizers, which also results in improved water quality. Peanut is self-fertilizing and exhibits a unique mode of reproduction where flowers are produced on the plant and following fertilization, the pods containing seeds are developed underground. Because of this unique feature, peanut is also known as groundnut in many parts of the world.

Arachis hypogaea is generally recognized as the only domesticated species in the genus and is cultivated for human consumption. The seeds (kernels) contain about 45-55% oil and 20-25% protein (Davis and Dean, 2016; Wang *et al.*, 2022; Dean and Eickholt, 2025). In many parts of the world, they are eaten raw, roasted or salted, or crushed for vegetable oil. However, in the U.S.A., the seeds are mostly crushed for peanut butter or used in the snack industry as roasted/salted nuts and in candies. Although peanut is not a traditional tree nut, compared to all other protein-rich tree nuts, it offers the cheapest and most affordable source of protein, particularly for many in the developing countries who cannot afford animal protein in their daily diets. Additionally, peanuts are a source of several vitamins, minerals and the antioxidant, resveratrol (Dean and Eickholt, 2025). A few other *Arachis* species have also been reported to have uses for nutrition, forage and ornamental value (Krapovickas and Gregory, 1994; Stalker and Simpson, 1995; Galgaro *et al.*, 1997; Gimenes *et al.*, 2000; Simpson *et al.*, 2001; Krapovickas and Gregory, 2007; Stalker *et al.*, 2013; Stalker *et al.*, 2016; Stalker, 2017; Shahid *et al.*, 2023). For example, seeds of *A. villosulicarpa* Hoehne and *A. stenosperma* Krapov. & W. C. Greg., are consumed by the indigenous people in Brazil; the Rhizomatous perennial peanut, *A. glabrata*, provides high protein forage to ruminants and *A. repens* and *A. pintoi* are commonly seen as ornamental ground cover in residential areas and roadsides from S. America to west Africa and China (Mathews *et al.,* 2000; Simpson *et al.*, 2001; Hernandez-Garay *et al.*, 2004; Shahid *et al.*, 2023). *Arachis kempff-mercadoi* grows in the avenue medians in Santa Cruz,

Bolivia and Recife, Brazil as an ornamental (C. Simpson, personal observation). Cultivars derived from *A. glabrata* are also promoted as a groundcover in orchard farms for ease of maintenance, aesthetics, biological nitrogen fixation ability and as an ecosystem for beneficial insect pollinators (Shahid *et al.*, 2023). Thus, peanut is one of the rare crops to be considered a food, oilseed, forage, and an ornamental crop.

HISTORY OF *ARACHIS*:

Genus *Arachis* is native to South America with geographical distribution in Argentina, Bolivia, Brazil, Paraguay and Uruguay (Valls *et al.*, 1985). Currently, 84 species have been named and described (Krapovickas and Gregory, 1994 and 2007; Valls and Simpson, 2005; Valls and Simpson, 2017; Cason *et al.*, 2022; Leal-Bertioli *et al.*, 2024; Seijo *et al.*, 2025) and additional descriptions of new species are being compiled (G. J. Seijo, personal communication). Morphologically, the two most ancient species of the genus, *A. guaranitica* Chodat. and Hassl. and *A. tuberosa* Bong. Ex Benth., are still found growing in the eroded highlands of southwestern Mato Grosso do Sul, Brazil (Gregory *et al.*, 1980; Simpson and Faries, 2001) suggesting that the genus *Arachis* likely originated in this region. Ecologically, many *Arachis* species also grow in deep friable sand to thick, gummy clay and on schist rocks with virtually no soil, to waterlogged conditions, suggesting that they have adapted to highly diverse and harsh environments (Simpson *et al.*, 2001). The genus likely originated in tropical wetland areas, subsequently spread and adapted for survival in dry environments (Gregory and Gregory, 1979; Stalker and Simpson, 1995; Simpson *et al.*, 2001). Consequently, species have evolved to accumulate biotic as well as abiotic stress resistances for survival. These properties make them valuable sources for use in the genetic improvement of *A. hypogaea* (Stalker, 2017).

All peanut species produce underground pods, botanically known as geocarpy. The geocarpic reproduction is likely an adaptive survival mechanism against adverse environmental stresses (Tan *et al.*, 2010) and likely helped in sustained survivability and distribution of the genus in South America. Further, the different root modifications (e.g., rhizomes, stolons, tuberous roots) likely helped the species to adapt and spread to new habitats. Conversely, the geocarpic fruit also impeded rapid spread into new environments as Simpson *et al.* (2001) estimated that the species moved about one meter/year across the continent.

GENETIC RESOURCES:

The world's largest collection of peanut germplasm resources is at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), India with about 15,000 cultivated peanut accessions and also 470 accessions of *Arachis* wild species. In the U.S., the National Plant Germplasm System (NPGS) maintains the peanut germplasm collection at the USDA-ARS Plant Genetic Resources Conservation Unit (PGRCU) in Griffin, GA. It consists of about 9,000 *A. hypogaea* accessions and an additional 600 accessions of *Arachis* wild species. Additionally, Argentina, Bolivia, Brazil, China, and India maintain large peanut germplasm collections at their national germplasm centers with smaller collections maintained in many countries in Africa, and Asia. Further, a core and mini core set of accessions have been assembled for ease of working with a smaller, representative sample of lines from the original collections of ICRISAT and USDA. The ICRISAT collection contains 1704 and 184 lines in the core and mini core, respectively (Upadhyaya *et al.*, 2002 and 2003). Similarly, the USDA collection has 831 lines as part of the core set (Holbrook *et al.*, 1993) and the mini core contains 112 lines (Holbrook and Dong, 2005). The world's largest *Arachis* wild species collection of about 1200 accessions is housed at EMBRAPA in Brazil under the direction of Dr. Jose Valls (Stalker *et al.*, 2016). A large collection of wild *Arachis* is also maintained by Dr. Charles Simpson at the Texas A&M AgriLife Research Station in Stephenville, Texas.

Conservation and characterization of germplasm is the most critical step for proper maintenance and utilization of genetic resources. ICRISAT and USDA have developed different peanut descriptors for characterizing the morphological genetic variability observed within the cultivated peanut (IBPGR-ICRISAT, 1992; Pittman, 1995). They include a standard set of several plant, pod and seed traits and occasional data on resistances or other quality traits to help classify the cultivated germplasm into related groups (Wang *et al.*, 2022). The characterization data provides valuable information to researchers to select suitable germplasm for effective and efficient use in peanut improvement. The U. S. peanut collection characterization data including digital images of the various plant, pod and seed features are publicly available to researchers around the world on the Germplasm Resources Information Network Global at https://npgsweb.ars-grin.gov/gringlobal (GRIN Global).

According to Krapovickas and Gregory (1994; 2007), genus *Arachis* is defined by the morphological features of plants as well as its underground structures of pods, rhizomatous stems, stolons, root systems, and hypocotyls. These defining characters grouped the *Arachis* collections into different geographic areas and ecological features which, along with crossabilities of species, led them to assemble the collections into nine different taxonomic sections (Krapovickas and Gregory, 1994; 2007). Further, evolution of different genomes occurred independently in different sections such as A, B, D, F, G, and K, in section *Arachis*; C, *Caulorhizae*; E, *Erectoides*; EX, *Extranervosae*; H, *Heteranthae*; P, *Procumbentes*; R1 and R2, *Rhizomatosae*; TR *Trierectoides*, and T, *Triseminatae* (Smartt *et al.*, 1978a and Smartt et al., 1978b, Smartt and Stalker, 1982; Seijo *et al.*, 2007; Robledo and Seijo, 2010; Seijo *et al.*, 2014; Stalker, 2017). It is believed that different species originated sympatrically in different sections where isolation barriers developed leading to the geographical separation of the species (Stalker and Simpson, 1995; Seijo *et al.*, 2014). Often two, and as many as five species from four different sections growing sympatrically were observed and collected and in several locations, species of the same section were found growing sympatrically (C. Simpson, personal observations). Section *Arachis* is the largest in the genus and contains about 40% of the species. The cultivated species, *A. hypogaea* is a self-fertilizing allotetraploid ($2n = 4x = 40$; AABB), and belongs to section *Arachis*. In addition to *A. hypogaea*, section *Arachis* also

contains another tetraploid species, *A. monticola* ($2n = 4x = 40$), 28 diploid ($2n = 2x = 20$) and three aneuploid ($2n = 2x = 18$) species (Krapovickas and Gregory, 1994 and 2007; Lavia *et al.,* 2008; Stalker *et al.*, 2013; Stalker *et al.*, 2016; Stalker, 2017). Brazil contains the greatest number of species from all nine sections followed by Bolivia, Paraguay, Argentina and Uruguay.

Although genus *Arachis* originated in the eroded highlands of Brazil, the primary center of origin of the cultivated species, *A. hypogaea*, is believed to be southern Bolivia to northwestern Argentina. This observation was based on the presence of the ancestral diploid wild species of *A. hypogaea* in this region, the wide range of variation observed in pod and seed morphologies and that the germplasm collected in this area exhibited primitive characters associated with wild species, thus supporting the likely origin of *A. hypogaea* in this region (Hammons,1982; Stalker and Simpson, 1995; Ferguson *et al.*, 2004). *Arachis hypogaea* is presumed to have originated as a natural hybrid of two section *Arachis* diploid species, the A genome donor, *A. duranensis* Krapov. & W.C. Greg.and *A. ipaënsis* Krapov. & W.C. Greg. contributing the B genome (Kochert *et al.*, 1996; Seijo *et al.*, 2004 and 2007; Bertioli *et al.*, 2016). Following the hybridization, a single polyploidization event of the sterile diploid hybrid led to the fertile allotetraploid (AABB). Then, the early humans selected desirable types from this and later populations, possibly for compact plant habit, and increased pod and seed sizes leading to the present day cultivated species of *A. hypogaea*. Further domestication in varied geographical environments led to the different subspecies, botanical varieties and market types of the cultivated taxon. Pod size, color, number and size of seeds per pod vary in different market types of *A. hypogaea* (Upadhyaya, 2003; Stalker *et al.*, 2016; Wang *et al.*, 2022). Consequently, the vast amount of morphological variability observed in the cultivated taxon likely resulted from natural and/or artificial selection rather than from the introgression of genes from different species (Seijo *et al.*, 2007). Further, Krapovickas (1968) and Gregory and Gregory (1976) recognized six other regions in South America as the secondary centers of diversity for the cultivated species based on morphological variability of the landraces. Additionally, Africa, China and India are considered as tertiary centers of diversity for *A. hypogaea* because of the large number of landraces and other local germplasm displaying different pod and seed traits (Gibbons *et al.*, 1972). Interestingly, Simpson *et al.* (2001) suggested possible alternate regions for the origin of *A. hypogaea* on the west coast of Peru and/or the eastern slopes of Cordillera in the Andes, based on archaeological evidence and the favorable environmental conditions for survival of plant tissue for long periods.

The Spanish and Portuguese explorations to South America led to the geographical spread of cultivated peanut to Europe, then to Africa and Asia via trade voyages. There was no substantiated evidence for the occurrence of cultivated peanut in North America before the Spanish arrival on the continent. It was suggested that peanut was introduced into the U.S.A. on slave trade ships from Africa via the coast of northeastern Brazil, where peanut was gathered as food source to complete the journey, strongly suggesting that the first peanut introductions into the U.S.A. were from Brazil rather than from Africa (Stalker and Simpson, 1995; Tallury, 2017). Further, Williams (2022) provided a detailed history and dissemination of peanut from its centers of origin and diversity in South America to Europe, Africa and Asia.

BOTANICAL CLASSIFICATION OF *A. HYPOGAEA*:

Krapovickas and Rigoni (1960) classified *A. hypogaea* into two subspecies, subsp. *hypogaea* and subsp. *fastigiata*, mainly, on the presence or absence of flowers on the main stem and the sequence of floral and leaf nodes on the lateral branches (Figure 1). The subsp. *hypogaea* contains no flowers on the main stem with alternate vegetative and floral nodes (two vegetative nodes alternate with two floral nodes) on the lateral branches and a long-life cycle. The subsp. *fastigiata* is characterized by the presence of flowers on main stem with sequential order of vegetative and floral nodes on the lateral branches and shorter life cycle. They also proposed two botanical varieties of subsp. *fastigiata*, var. *fastigiata* and var. *vulgaris* based on pod traits. Later, Krapovickas (1968) proposed that subsp. *hypogaea* should also be divided into var. *hypogaea* and var. *hirsuta* based on pod reticulation. With additional collections of *A. hypogaea*, Krapovickas and Gregory (1994; 2007) not only confirmed the two subspecies of *A. hypogaea* (subsp. *hypogaea* and subsp. *fastigiata*) but also expanded botanical varietal groups to six (vars. *hypogaea, hirsuta, fastigiata, peruviana, aequatoriana* and *vulgaris*) based on plant growth habit, leaf color and branching patterns, which also includes the four major market types grown in the U.S.A. (Table 1; Figure 2).

Krapovickas (1968) suggested that *A. hypogaea* subsp. *hypogaea* var. *hypogaea* was the most ancient type as it was the most predominant type found in the chaco region between southern Bolivia and northwestern Argentina, which is where the ancestral species of *A. duranensis* and *A. ipaënsis* were found and *A. hypogaea* was believed to have originated. Additionally, the plants found in this area exhibited many primitive traits such as the runner growth habit, a branching pattern similar to the wild *Arachis* species, small, two-seeded pods with marked constriction and slight reticulation, and seed dormancy. Further, the above observations led Krapovickas and Gregory (1994; 2007) to conclude that SE Bolivia is the center of origin as well as diversity for subsp. *hypogaea*, whereas subsp. *fastigiata* differentiated in NW Bolivia and possibly in Peru, along with vars. *fastigiata, peruviana* and *aequatoriana*. However, investigation of genetic diversity among botanical varieties using simple sequence repeat (SSR) markers by Ferguson *et al.* (2004) revealed the similarities of three botanical varieties of subsp. *fastigiata*, namely *fastigiata, vulgaris* and *aequatoriana* but did not support the inclusion of var. *peruviana* in subsp *fastigiata.* Further, they also found that the botanical varieties, *hypogaea* and *hirsuta* are not closely related and felt that they should not be grouped under subsp. *hypogaea*. Contrarily, He and Prakash (2001) demonstrated with AFLP markers that vars. *aequatoriana* and *peruviana* were closer to subsp. *hypogaea* than to subspecies *fastigiata*. Interestingly, Grabiele *et al.* (2012) suggested that the six botanical varieties originated from a single genetic origin and that *A. monticola* is the immediate ancestor of *A. hypogaea*. Thus, there still exists, confusion about the

taxonomic classification of the cultivated species. Among the market types, Gregory *et al.* (1980) and Hammons (1982) suggested that the Bolivian and Amazonian geographic regions are the possible sites for the origin of the large-seeded Virginia types. Further, Hammons (1982) indicated that the Guarani area of northeastern Argentina, Paraguay and southern Brazil is the center of variation for the Spanish (var. *vulgaris*) market type whereas, the Valencia type (var. *fastigiata*) probably spread from Paraguay and central Brazil (Krapovickas, 1968; Hammons, 1982).

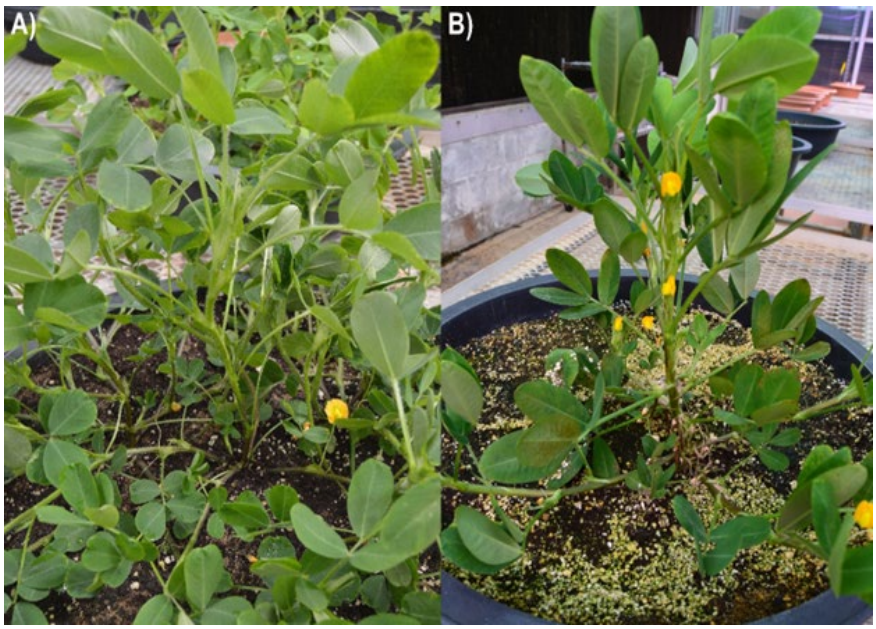

Figure 1. A) *A. hypogaea* subsp. *hypogaea* mainstem flower absent; B) A. hypogaea subsp. fastigiata mainstem flower present.

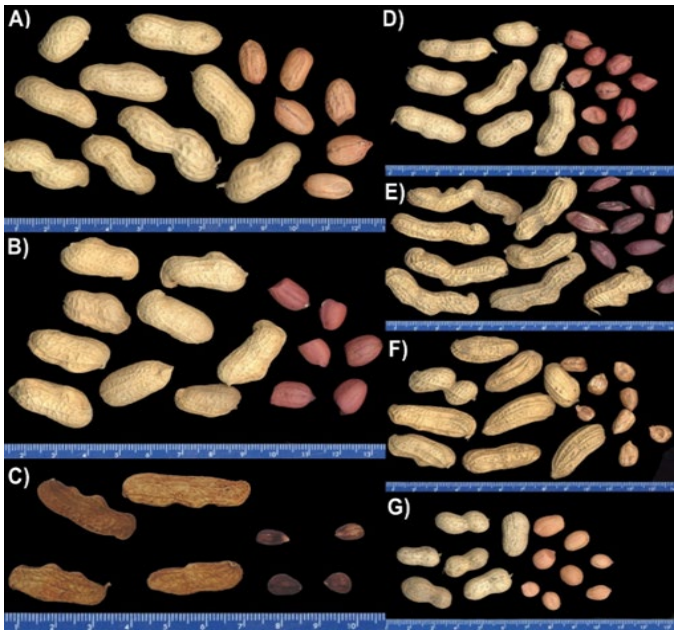

Figure 2. Pod and seed characteristics of *A. hypogaea* botanical varietal groups (cm). Subsp. *hypogaea* var. *hypogaea*: A) Market type: Virginia (PI 536122), B) Market type: Runner (PI 497455); C) var. *hirsuta*, Market type: Peruviana runner (PI 576638). Subsp. *fastigiata* var. *fastigiata*: D) Market type: Valencia (PI 493324); E) var. *aequatoriana* (PI 690056); F) var. *peruviana* (PI 502053); G) var. *vulgaris*, Market type: Spanish (PI 537448).

Table 1: *Arachis hypogaea* taxonomic classification.

A. hypogaea subsp. *hypogaea*	*A. hypogaea* subsp. *fastigiata*
• Main stem with no flowers • Alternating floral and vegetative branches • Branches short and less hairy • Dark green leaves • Prostrate or spreading growth habit • Late maturing • Seed dormancy present • Origin in SE Bolivia	• Flowers on main stem • Sequential floral and vegetative branches • Branches less hairy • Light green leaves • Bunch or erect growth habit • Early maturing • Seed dormancy absent • Origin in NW Bolivia and Peru
var. *hypogaea* • Leaflets with glabrous dorsal surface; with a few hairs on the midrib • Prostrate/spreading growth habit • Pods with moderate reticulation	var. *fastigiata* • Leaflets with glabrous dorsal surface or hairs only on the midrib • Few branches, short and slender • Pods with smooth or slight reticulation • Early maturity • Origin in Bolivia
Market type:Virginia • Less hairy short main stem and leaves • Large, two-seeded pods • Slight constriction and reticulation Market type: Runner • Less hairy main stem and leaves • Small, two-seeded pods • Slight constriction and reticulation	Market type: Valencia • Sparsely branched, curved branches • Erect growth habit • Usually 2-4 seeded, long pods • Red seed coat
var. *hirsuta* • Leaflets with 1-2 mm long hairs dispersed on entire dorsal surface • Long main stem and very hairy • Origin in Peru Market type: Peruvian runner • More hairy leaves • Late maturing • Long pods, 2-3 seeded • Deep constriction and prominent reticulation	var. *aequatoriana* • Erect plants with large leaves • Leaflets with 1-2 mm long hairy dorsal surface, dispersed on entire surface • Main stem with short inflorescences • Long reproductive lateral branches • Prominent longitudinal ribs on pods with deep pod reticulation • Long pods with 3-4 seeded • Seed coat is commonly violet • Origin in Ecuador
	var. *peruviana* • Thick, large leaves; leaflets glabrous on both sides • Hairy on the margins and dorsal surface on midrib • Long, robust reproductive branches • Flowers on both main stem and lateral branches • 3 to 4-seeded pods • Seed coat colors vary from black, violet, cream to variegated • Prominent longitudinal ribs on pods with deep pod reticulation • Origin in Peru
	var. *vulgaris* • Erect growth habit with many upright branches • Medium sized leaves with glabrous surface, long hairs on margins • Mostly 2-seeded, small pods bunched at the base of the plant • Slight pod constriction and reticulation Market type: Spanish • More branched; upright branches • Light green leaves

MORPHOLOGY, GROWTH AND DEVELOPMENT

Seed:

The peanut seeds are contained within a seed pod with a protective outer shell. Peanut seeds vary in color which is a manifestation of the seed coat (testa) or usually referred to as the "skin". The seed coat exhibits different colors ranging from white to tan to black and different shades of red or pink (Wang *et al.*, 2022). In addition, it holds the two cotyledons together to keep them from splitting, thus protecting the seed. The seeds also vary in size from the large-seeded Virginia market type of > 80 g/100 seeds to the small, round seeded Spanish types of < 45 g/100 seeds (Wang et al., 2022; Figure 2). It was reported that the life span of peanut seed is limited when stored under ambient conditions and the seeds generally become inviable within two years (Norden, 1981). However, Rao *et al.* (2002) showed that when seeds were stored in tightly sealed containers at room temperature (23-25 C) with low moisture content (below 4%), they retained viability of over 85% for up to 8 years. Also, Norden (1981) noted that the seed viability of Spanish types decreased faster than Virginia or Valencia types in storage. Seeds of the wild *Arachis* species are more difficult to maintain than the cultivated peanut accessions. Simpson *et al.* (2010) reported *Arachis* seeds, both cultivated and wild species, with germination above 60% after storage for 30+ years in sealed containers stored at -18°C.

The seed is composed of two cotyledons and contains the dormant seedling (Dean and Eickholt, 2025) consisting of the shoot (plumule/leaf primordia) and the root initials (radicle). The cotyledons are stored food reserves and provide the initial nourishment to the young seedling during germination and development. When planted under optimum soil moisture and temperature conditions, the seeds sprout within a week. First, the radicle starts to grow forming the upper hypocotyl and the lower primary root. This is followed by the rapid elongation of the hypocotyl with both cotyledons pushed above ground. As the cotyledons split open to expose the shoot primordia to form the epicotyl which extends into the main stem, the lower hypocotyl elongates to form the tap root (Gregory *et al.*,1973). From the taproot, lateral roots emerge within seven to 10 days. Occasionally, on mature plants, adventitious roots are formed when lateral branches are in contact with soil.

Plant:

The peanut plant is a compact bush with either erect or prostrate growth habit. The main stem is usually about 30-45 cm in height with lateral branches spreading from 35-75 cm wide. Compound leaves with four leaflets (tetrafoliolate) are common and the leaves are located alternately on the main stem and lateral branches. However, wild *Arachis* species in the section *Trierectoides*, namely, *A. guaranitica*, *A. tuberosa*, and *A. sesquijuga* have trifoliate leaves with three leaflets. The leaves are connected to the stems by an adnate stipule and leaflets vary in size, shape and color with dark green leaves in *A. hypogaea* subsp. *hypogaea* to the lighter green leaves in *A. hypogaea* subsp. *fastigiata.* The stems are predominantly green but reddish or purple in Valencia and *aequatoriana* types (see the botanical varieties section for additional information in Table 1). Stem pigmentation, hairiness on stems and leaves have been shown to deter leaf feeding insect pests (Campbell *et al.*,1976; Sharma *et al.*, 2003).

Flower:

The flowers are formed on an inflorescence in leaf axils on the branches and also on the main stem in subspecies *fastigiata* types (Figure 1). The inflorescence is a raceme and usually contains three to five flowers, but as many as 13 have been observed on one inflorescence (C. Simpson, personal observation). Usually, plants start producing flowers about 30 days after seed germination and due to peanut's indeterminate growth habit, flowers are produced throughout the growing season until harvest. Generally, only one flower opens on a given day in each inflorescence and the interval between the openings of flowers within the same inflorescence vary up to several days. However, it is not uncommon to see two flowers at a node. Because the flowers contain both male and female tissues, natural self-fertilization occurs, leading to the development of pods. The flowers are usually orange, reddish orange or yellow in color. Sometimes, white flowers have been seen in at least three *A. hypogaea* accessions and in seven different wild species (C. Simpson, personal observations.) The flower contains five petals (corolla) including a large standard (Banner), two wing petals and two fused keel petals. The calyx is green with five lobes with four fused to cover the back side of the standard and one lobe is opposite the keel (Figure 3). The standard is usually yellow or orange with red veins on the inner face. The wings are usually yellow surrounding the keel. The keel is almost colorless and encloses the stamens and style. The androecium is monadelphous with filaments of stamens fused into a bundle with eight functional stamens and two, small sterile ones. The stamens contain pollen to fertilize the egg cell. Although the flower is sessile, it is attached to the stem (at the leaf axil) by a long tubelike structure called a hypanthium or "calyx tube" and thus appears as pedicillate (Figure 3). The style is enclosed within the hypanthium and is connected to the ovary located at the base of the hypanthium in the leaf axil. The tip of the style, called stigma, is usually at the same height as the anthers so pollen reaches it easily (Figure 3). Differences in stigma morphology were noticed between *A. hypogaea* and the wild species. In *A. hypogaea*, the stigma is of dry papillate type (Lakshmi and Shivanna, 1986) with no surrounding hairs and probably accommodates about 15 pollen grains (Moss and Rao, 1995). On the other hand, the annual *Arachis* species have large, globular stigmatic surface whereas the perennial species have smaller, cuticularized stigmas with unicellular hairs accommodating a maximum of only three pollen grains (Lu *et al.*,1990; Akromah, 2001). In the wild species *A. lignosa*, Banks (1990), observed that natural self-pollination is restricted because of the truncated shape of the stigma and its elevated position relative to the anthers and suggested manual tripping of flowers for pollen to reach the stigma for fertilization and later pod development. Although self-pollination is the predominant mode of reproduction, outcrossing is possible with bees or other pollinators. It was reported that the outcrossing rate is limited to less than 10% under natural field conditions (Hammons,1973; Knauft *et al.*, 1992).

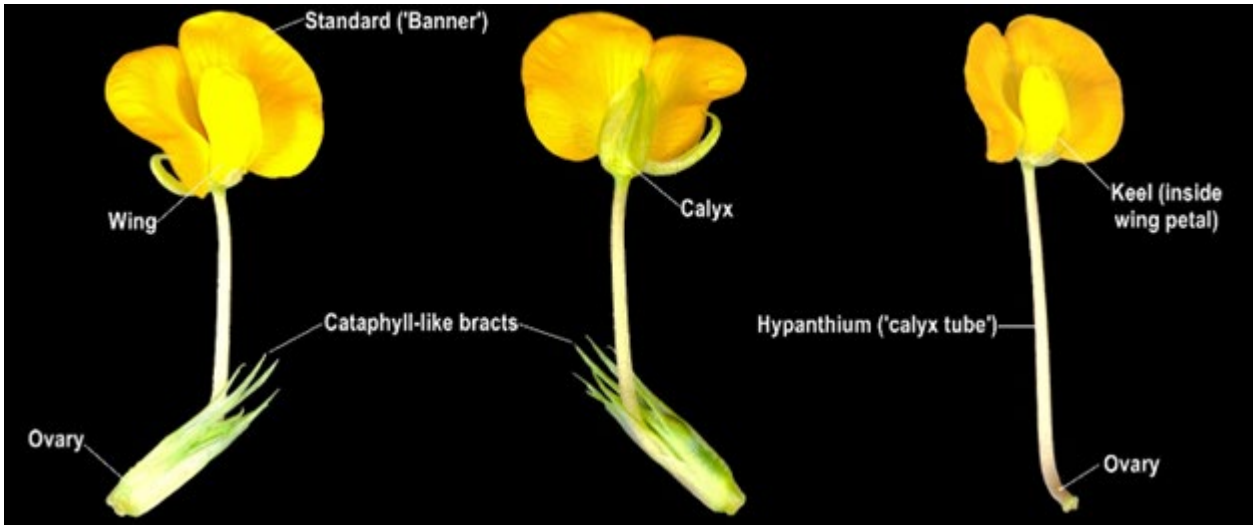

Figure 3. *A. hypogaea* floral and reproductive structures.

Fertilization:

Anthesis (dehiscence of pollen) initiates the process of fertilization, and it occurs within a short time after sunrise with the opening of the flower. Pattee *et al.* (1991) reported that pollen matures approximately 6-8 h before anthesis. The ovary usually has two ovules, and up to three or more in some of the subspecies *fastigiata* types. Each ovule contains a mature embryo sac with a well differentiated egg cell at the micropylar end and a polar nucleus surrounded by starch grains. The mature pollen grain is two-celled with two generative nuclei (Xi, 1991). When a single pollen grain germinates on a receptive stigma, it forms the pollen tube containing the male gamete with the two generative nuclei, travels through the style and eventually enters the embryo sac through the micropyle (Pattee and Mohapatra, 1987). One of the two generative nuclei fuses with the egg cell (syngamy) to form the embryo and the other with the polar nucleus (double fertilization) to form the endosperm. The entire process of fertilization usually takes between 18 and 24 h from anthesis (Pattee *et al.*,1991). Following fertilization, the starch grains breakdown to provide initial nutrition for the proembryo to grow which eventually develops into a mature seed. Each ovule develops into a peanut seed and the ovary becomes the pod.

Pod/Seed Development:

Pod development begins with a pointed structure called the "peg" (Smith 1950), usually observed between 4 and 7 days after self-pollination. Pegs are positively geotropic (Zamski and Ziv, 1976) and require darkness for pod formation (Ziv, 1981). During the early embryo growth period between 24 and 72 h after fertilization, an intercalary meristem at the base of the ovary actively divides leading to peg formation with the fertilized ovules at its tip. In the aerial phase of peg growth before it enters the soil, the embryo remains in a quiescent stage, usually, as an 8-celled proembryo (Pattee and Mohapatra, 1987). Once the peg enters the soil, it stops extending, leading to pod formation with the swelling of the tip along with the horizontal turning of the peg. The peg becomes diageotropic after soil penetration such that the ovules are always located on the upper wall of the pod, with the pod tip pointing away from the plant (Moss and Rao, 1995). Pod enlargement occurs from base towards the tip with simultaneous faster development of the basal ovule (Smith, 1950). The shells of the pods also undergo significant changes during pod development. During the initial development, pods are usually soft, white with approximately 40% moisture content (Dean and Eickholt, 2025). As it starts to develop, pods become drier and the shells firmer with fully developed seeds about 60 days after fertilization. This pod developmental pattern varies slightly among the different botanical varieties with Spanish peanuts maturing earlier than the runner or Virginia-types (Dean and Eckholt, 2025). Also, due to the indeterminate nature of peanut plants, pods at different maturities are seen on plants even at harvest. Detailed descriptions of peanut embryology including the growth and development of pegs, pods and seeds are documented in literature (Smith, 1950; Gregory *et al.*, 1973; Periasamy and Sampoornam, 1984; Pattee and Mohapatra, 1987; Xi, 1991; Moss and Rao, 1995, Tallury *et al.*, 1995).

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