Peanut: Origin and Botanical Descriptions

3

Shyam P. Tallury

Abstract

Since the first description of the cultivated peanut, *Arachis hypogaea* L. by Linneaus in 1753, to the recent monograph on the taxonomy of genus *Arachis* (Krapovickas and Gregory in Bonplandia 8(1–4):1–186, 1994; Krapovickas and Gregory in Bonplandia 16(Supl.):1–205, 2007), our knowledge of the genetic structure of the genus including its origin, variability, and geographical distribution of various species has significantly improved. Large germplasm collections have been accumulated in several countries to preserve the genetic diversity and characterize the germplasm resources for efficient utilization in peanut improvement programs. Plant growth and development including the origin and botanical classification of the cultivated species have been revisited here to summarize our current knowledge of the taxon. In spite of these advances, taxonomic and phylogenetic ambiguities still exist. It is likely that the recent advances in peanut genome sequencing and the availability of new and additional molecular markers and other genomic tools might help clarify the genetic structure of genus *Arachis* and of the cultivated species, *A. hypogaea*.

3.1 Introduction

Peanut (*Arachis hypogaea* L.), is an important grain legume crop and is primarily valued as a source of protein as well as fat to human nutrition. The seeds contain about 20–25% protein and 45–55% oil, in addition to useful vitamins and minerals, and offer an easily affordable source of protein for many, particularly in the developing countries. Of the 81 described species, *A. hypogaea*, is the only domesticated species and is cultivated for its seeds for human consumption, although a few other species have been reported to have uses for nutrition, forage and ornamental value (Krapovickas and Gregory 1994, 2007; Gimenes et al. 2000; Simpson et al. 2001; Galgaro et al. 1997; Stalker and Simpson

S.P. Tallury (✉)
Plant Genetic Resources Conservation Unit, USDA-ARS, 1109 Experiment Street, Griffin GA 30223-1797, USA
e-mail: Shyam.Tallury@ars.usda.gov

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1995). *Arachis hypogaea* is a herbaceous annual with plants of about a 45–60 cm tall and 30 cm wide with a deep taproot. The roots typically contain the nitrogen fixing bacterial nodules of *Rhizobium*, which coexist in a symbiotic relationship by providing the necessary nitrogen for plant growth while deriving sustenance from it. The plants are self-fertilizing and have a unique mode of reproduction where flowers are produced on the plant and following fertilization, the gynoecium enters the soil through formation of a peg. Then, pods containing the seeds are produced underground. All species in the genus produce underground pods and in a sense are "pegged" to the ground as mentioned in Krapovickas and Gregory (1994, 2007). Because of this unique reproductive feature, peanut is also known as groundnut in many parts of the world.

3.1.1 Origin and Distribution of Genus *Arachis*

Arachis is a native South American genus with natural populations found growing in Argentina, Bolivia, Brazil, Paraguay, and Uruguay (Valls et al. 1985). The genus likely originated in the highlands of southwestern Mato Grosso do Sul state in Brazil (Hammons 1973; Gregory et al. 1980; Simpson et al. 2001) where the most ancient, trifoliate species, *A. guaranitica* Chodat. and Hassl., and *A. tuberosa* Bong. Ex Benth. were collected. *Arachis guaranitica* is the most genetically isolated species and looks more like a grass plant. These two species are still found growing in this region (Simpson et al. 2001). Subsequently, with water movement, the species spread to drier lowlands in all directions and evolved into various river valleys and drainage systems (Gregory and Gregory 1979; Stalker and Simpson 1995; Simpson et al. 2001) with *Arachis* species growing in sandy to heavy clay/loamy soils and on schist rocks with no soil (Simpson et al. 2001). One of the species, *A. burkartii* Handro was collected in southern Brazil in black gummy clay mixed with small stones with a soil pH of 3.2 (Stalker and Simpson 1995), indicating the wide adaptation of *Arachis* species to extremely diverse geographical environments. The geocarpic reproductive development probably protected the pods/seeds from the predators and helped in sustained survivability and distribution of the genus in South America. However, it is also possible that the geocarpic pod limited the rapid spread of the genus as estimated by Simpson et al. (2001) that the species moved only one meter/year across the continent.

Currently, the genus contains about 81 described species and several new species are likely to be described in the near future (Stalker et al. 2016; Simpson, personal communication). Krapovickas and Gregory (1994, 2007) delineated the species diversity into nine different sections based on geographical distributions, plant, pod and chromosome morphologies and cross-compatibility relationships. The cultivated species, *A. hypogaea*, was assigned to section *Arachis*, which also contains a number of wild species. They concluded that *A. hypogaea* hybridizes readily with the species in section *Arachis* whereas the species in the remaining eight sections are incompatible with it. Although the genus *Arachis* originated in the highlands of Brazil, the 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 parental 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). Additionally, 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 archeological evidence and prevalence of favorable environmental conditions for survival of plants for long periods of time.

Arachis hypogaea is an allotetraploid ($2n = 4x = 40$) with a genomic composition of

AABB. It is considered to have originated from natural hybridization of two closely related diploid wild species followed by either chromosome duplication or fusion of unreduced gametes, thereby, resulting in an allotetraploid with two sets of chromosomes of each of the constituent parental genomes (Seijo et al. 2004, 2007). The general agreement among peanut researchers is that *A. duranensis* Krapov. & W.C. Gregory and *A. ipaënsis* Krapov. & W.C. Gregory are the A and B genome donor species, respectively (Kochert et al. 1991, 1996; Seijo et al. 2004, 2007). Recently, Bertioli et al. (2016) reported the genome sequences of these two species and demonstrated that they are very similar to the A and B subgenomes of *A. hypogaea*.

A list of primitive and advanced traits was compiled by Stalker and Simpson (1995) to demonstrate the evolution of domesticated peanut. Krapovickas (1968) suggested that *A. hypogaea* subsp. *hypogaea* var. *hypogaea* (see Sect. 1.1.2 below for the subspecies descriptions) was the most ancient cultivar type. His observation was based on the available records that it was the most predominant type found in the chaco region between southern Bolivia and northwestern Argentina, the likely area where *A. hypogaea* is believed to have originated. Additionally, the types 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. The above observations led Krapovickas and Gregory (1994, 2007) to conclude that south east Bolivia is the center of origin as well as diversity for subsp. *hypogaea*, whereas subsp. *fastigiata* differentiated in north western Bolivia and possibly in Peru, along with vars. *fastigiata*, *peruviana* and *aequatoriana*. However, genetic diversity analysis among botanical varieties using simple sequence repeat (SSR) markers by Ferguson et al. (2004) revealed 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* were not closely related and suggested 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*. Thus, there still exists, considerable 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 (Hammons 1982; Krapovickas 1968).

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). To characterize and describe the vast amount of morphological variation present in *A. hypogaea*, peanut descriptor lists were compiled (IBPGR and ICRISAT 1992; Pittman 1995). These descriptors included a standardized set of plant, pod, and seed traits to help classify the cultivated germplasm into related groups. The USDA National Plant Germplasm System peanut collection maintained at the Plant Genetic Resources Conservation Unit (PGRCU) in Griffin, GA, USA, routinely uses the U S peanut descriptors developed by Pittman (1995) to characterize the collection. Digital images of the various plant, pod and seed features are also compiled. This information is made available to

researchers around the world on the Germplasm Resources Information Network Global at www.ars-grin.gov site.

It is paradoxical that in spite of the extensive morphological variation among the subspecies and botanical varieties of *A. hypogaea*, little molecular (DNA) polymorphism was observed in the cultivated species (Kochert et al. 1991; Halward et al. 1991, 1992; Moretzsohn et al. 2004, 2013; Pandey et al. 2012). A likely hypothesis for the lack of molecular polymorphisms in the cultivated species was that a single hybridization event accompanied by polyploidization coupled with the autogamous reproduction led to the genetic isolation of the raw tetraploid from the surrounding species diversity with no apparent gene flow between them (Kochert et al. 1996; Seijo et al. 2007). It is likely that following domestication, the early humans selected desirable types from the original population possibly for compact habit, and increased pod and seed sizes producing the different subspecies and varieties of the cultivated taxon, as we have today. Consequently, the vast amount of morphological variability observed in the cultivated taxon is likely to have resulted from natural and/or artificial selection rather than from the introgression of genes from different species (Seijo et al. 2007). However, Varshney et al. (2009) using simple sequence repeat (SSR) markers with a diverse set of 189 *A. hypogaea* accessions observed significant polymorphisms and grouped the accessions into four different clusters. It is also encouraging that the recent advances in peanut genome sequencing and new genomic tools might help clarify the origin, evolution, variability and distribution of the genus and that of the cultivated species, *A. hypogaea*. An initial application of these technologies, particularly, of molecular markers for quantitative trait analysis was demonstrated by Pandey et al. (2012, 2013) for use in marker assisted breeding in cultivated peanut.

Contrarily, the wild species have exhibited extensive molecular variation among and within the different sectional groups (Halward et al. 1991, 1992; Tallury et al. 2005; Upadhyaya et al. 2008a, b; Friend et al. 2010; Moretzsohn et al. 2013). Molecular profiling of a composite collection consisting of 1000 diverse peanut accessions which included both cultivated and wild species demonstrated rich allelic diversity within the wild species with more than 100 unique alleles (Upadhyaya et al. 2008a, b) whereas the number of unique alleles in the two *A. hypogaea* subspecies, *hypogaea* and *fastigiata* were only 11 and 50, respectively. Further, the highest number of unique alleles were found in *A. hypogaea* accessions from the Americas with few unique alleles among the accessions from Asia and Africa. This study also demonstrated that the two subspecies, *hypogaea* and *fastigiata* accessions shared 70 alleles among them. Although the wild species shared only 15 alleles with subspecies *hypogaea* and 32 alleles with subspecies *fastigiata*, the wild species accessions grouped with subspecies *hypogaea* accessions (Upadhyaya et al. 2008a, b).

3.1.1.1 Geographical Spread *of A. hypogaea*

Following the Spanish and Portuguese explorations to South America, the cultivated peanut spread from the centers of origin and diversity in South America to Europe and then to Africa and Asia via trade voyages. There is no substantiated evidence for the occurrence of cultivated peanut in North America during this time. It was suggested that peanut was introduced into U.S. 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. were from Brazil rather than from Africa (Stalker and Simpson 1995).

3.1.1.2 Botanical Classification of *A. hypogaea*

Krapovickas and Gregory (1994, 2007) indicated that genus *Arachis* is defined by its morphological features of the underground structures, including the pods, rhizomatous stems, root systems, and hypocotyls. They showed that these defining characters grouped the *Arachis* collections into different geographic areas and ecological features. This, along with crossabilities of species, allowed them to group the collections

into nine different sections (Gregory and Gregory 1979; Krapovickas and Gregory 1994, 2007). *Arachis hypogaea* belongs to section *Arachis*, which also contains 30 other wild species.

Further, *Arachis hypogaea* was divided into two subspecies, subsp. *hypogaea* and subsp. *fastigiata* by Krapovickas and Rigoni (1960) based on the absence versus presence of flowers on the main stem. They also proposed two botanical varieties of subsp. *fastigiata*, vars. *fastigiata* and *vulgaris* based on the pod traits. Later, Krapovickas (1968) proposed that subsp. *hypogaea* should also be divided into vars. *hypogaea* and *hirsuta*. 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 as described below, which also includes the four major market types grown in the U.S.

A.
***A. hypogaea* subsp. *hypogaea* L.**
No flowers on main stem
Alternating pairs of floral and vegetative axes on branches
Branches short and less hairy
Dark green leaves
Prostrate or spreading growth habit
Late maturing
Seed dormancy present

var. *hypogaea*:

Leaflets with glabrous dorsal surface; with a few hairs on the midrib
Prostrate/spreading (runner) or bunch type growth habit

Market type: Virginia

Less hairy short main stem and leaves
Large pods, two seeded
Slight constriction and reticulation

Market type: Runner

Less hairy main stem and leaves
Small pods, two seeded
Slight constriction and reticulation

var. *hirsuta*:

Leaflets with 1–2 mm long hairs dispersed on entire dorsal surface
Long main stem and very hairy,

Market type: Peruvian runner

More hairy leaves
Late maturing
Long pods, 2-3 seeded
Deep constriction and prominent reticulation

B.
A. hypogaea* subsp. *fastigiata
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

var. *fastigiata*

Leaflets with glabrous dorsal surface or hairs only on the midrib
Few branches, short and slender
Pods with smooth or slight reticulation

Market type: Valencia

Sparsely branched; curved branches
Erect growth habit
Usually 2–4 seeded, long pods
Red seed coat

var. *aequatoriana*

Erect plants with large leaves

Leaflets 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

var. *peruviana*

Thick, large leaves; leaflets glabrous on both sides
Hairy on the margins and dorsal surface on midrib of leaflets
Long, robust reproductive branches
Flowers on both main stem and lateral branches
3–4-seeded pods
Seed coat colors vary from black, violet, cream to variegated
Prominent longitudinal ribs on pods with deep pod reticulation

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

3.2 Description of Seed to Adult Plant

3.2.1 Germination and Plant Morphology

Arachis hypogaea seed is covered by a thin seed coat or testa (commonly called as "skin"). It varies in color from white to tan to black and different shades of red or pink and provides protection to the seed from soil microorganisms. The seeds also vary in size from the large Virginia market types to the small, rounded Spanish types. The seed is composed of two cotyledons, which are the first true leaves. They contain stored food reserves for the young seedling during germination and to establish a plant. The peanut seed contains the dormant shoot (plumule/leaf primordia) and the root initials (radicle). When a seed is planted under optimum soil moisture and temperature conditions, the process of germination is initiated in about three to five days. First, the radicle starts to grow forming the upper hypocotyl and the lower primary root. This is accompanied by the rapid elongation of the hypocotyl which pushes the cotyledons above ground within a week. The cotyledons split open to expose the shoot primordia which extends to form the epicotyl. The epicotyl forms the main stem whereas the lower hypocotyl elongates to form the tap root (Gregory et al. 1973). From the taproot, lateral roots emerge within 3–5 days after germination and are extensively developed by about 7–10 days. Occasionally, on mature plants, adventitious roots are formed where branches are in contact with soil.

Peanut plant is an erect or prostrate type where plants are usually about 30–45 cm tall and the lateral branches spread to about 30 cm wide. However, on many wild species, the lateral branches are a few meters long with a very short main stem. Plants have compound leaves with four leaflets (tetrafoliate) which are located alternately on the main stem and lateral branches. However, three species from the section Triserectoides, namely, *A. guaranitica A. tuberosa* and *A. sesquijuga* have leaves with three leaflets (trifoliate). The leaves are connected to the stems by an adnate stipule and leaflets vary in size and shape, usually oblong and lanceolate in some wild species. The *A. hypogaea* subsp. *hypogaea* has dark green leaves compared to the lighter green leaves in *A. hypogaea* subsp. *fastigiata*. The stems are angular, mostly green with the exception of Valencia and *aequatoriana* types which are reddish purple. As summarized in the

previous section, in some botanical varieties hairy stems are commonly seen. Stem pigmentation, hairiness on stems and leaves has been shown to deter leaf feeding insect pests (Campbell et al. 1976; Stalker and Campbell 1983; Stalker et al. 1984; Sharma et al. 2003).

3.2.2 Flower Morphology, Fertilization and Pod/Seed Development

Generally, peanut plants produce flowers about 30 days after germination. It is an indeterminate plant and as a result, flowers are produced throughout the growing season leading up to harvest. Flowers are usually present in leaf axils on the branches and also on the main stem in subspecies *fastigiata* types. Commonly, three flowers are present in each inflorescence, which is a raceme. At any given time, usually only one flower opens and the interval between the openings of flowers in the same inflorescence vary up to several days. Since the flowers contain fertile, male and female reproductive parts, natural self-fertilization leads to the development of pods.

The flower has five brightly colored petals (corolla) consisting of a large standard (Banner), two wing petals and two fused keel petals. The calyx is green with five lobes of which, one lobe is opposite the keel whereas the other four are fused and cover the back side of the standard. 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 fused for two-thirds of their length and contains eight functional stamens and two, small sterile ones. The stamens produce pollen (male gamets) for fertilization of the egg cell. The flower is attached to the stem (at the leaf axil) by a long tube like structure called a hypanthium or "calyx tube". The flowers are subtended by a bract and are sessile although they appear as pedicillate because of tubular hypanthium. The style is enclosed within the hypanthium and is connected to the ovary (female part) located at the base of the hypanthium in the leaf axil. The tip of the style, called stigma is at the same level or slightly above the anthers so pollen grains can reach it. Differences in stigma morphology were observed 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 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). However, in the wild species, *A. lignosa*, the truncated shape of the stigma and its elevated position relative to the anthers restricts natural self-pollination (Banks 1990). In this case, manual tripping of flowers is needed for pollen to reach stigma for fertilization and later pod development. Outcrossing is possible with bees or other insects, however, it is limited to less than 10% under natural field conditions (Hammons 1973; Knauft et al. 1992).

The process of fertilization begins with anthesis, which occurs within a few hours after sunrise with the opening of the flower. The mature pollen grain is two-celled with two generative nuclei (Xi 1991). The ovary usually has two ovules, and up to three or more in Valencia 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. When pollen germinates on a receptive stigma, the pollen tube containing the mature pollen grain (male gamete) with the two generative nuclei travels through the style and eventually enters the embryo sac through the micropyle. 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. Following syngamy, the starch grains breakdown to provide initial nutrition for the proembryo to grow which eventually develops into a mature seed. The entire process of fertilization usually

takes about 18–24 h from anthesis to syngamy (Pattee et al. 1991). Each ovule develops into a peanut seed and the ovary becomes the pod.

Following syngamy, pod development is initiated as a pointed, stalk like structure which is called the "peg" (Smith 1950). During the early embryo growth (24–72 h after fertilization), an intercalary meristem at the base of the ovary actively divides forming the peg with the fertilized ovules at its tip. Pegs are usually observed between 4 and 7 days after self-pollination and are positively geotropic (Zamiski and Ziv 1976) and require darkness for pod formation (Ziv 1981). As the peg is extending to enter the soil (aerial phase), the embryo remains in a quiescent stage, usually, as an 8-celled proembryo (Pattee and Mohapatra 1987). It is only after soil penetration that the elongation of the peg is arrested, to initiate pod formation. The first sign of pod development involves the swelling of the peg 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). A mature peanut pod is developed in about 60–80 days after pollination. However, due to the indeterminate nature of peanut plants, flowering continues throughout the growing season until harvest. Consequently, pods at different maturities are seen on plants even at harvesting time. Detailed descriptions of peanut embryology including the growth and development of pegs, pods, and seeds are well documented in literature (Smith 1950; Gregory et al. 1973; Periasamy and Smapoornam 1984; Pattee and Mohapatra 1987; Xi 1991; Moss and Rao 1995).

3.3 Conclusion

Plants of genus *Arachis* are characterized by their unique underground structures, including the root systems, rhizomatous stems, pods, and hypocotyls. These features led to the adaptation and grouping of *Arachis* germplasm into different geographical regions and evolution of botanical varieties. *Arachis hypoagea* is a native, new world taxon and exhibits large morphological variation as described above with a wide range of adaptation to many different ecological conditions. An understanding of preservation and characterization of this genetic diversity is crucial to future genetic improvement of *A. hypogaea*.

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