Chapter 1

THE PEANUT—REPRODUCTIVE DEVELOPMENT TO PLANT MATURITY

J. PHILIP MOSS AND V. RAMANATHA RAO

INTRODUCTION

Peanut or groundnut is a member of the genus *Arachis* in subtribe Stylosanthinae of tribe Aeschynomeneae of family Leguminosae. The only species in the genus of significant economic importance is *A. hypogaea* L., of which the seed is the most important plant part. A large percentage of peanut seed is utilized for the production of edible oil, whereas in the U.S. about 60% of production is processed in a variety of ways and eaten as food. The haulms (stems and leaves) also are used as fodder for hogs and cattle in some areas, being economically more significant than the seeds at times of shortage of fodder for cattle in Asia and Africa. *Arachis hypogaea* is an annual herb and is one of the few plant species that form underground fruits (Fig. 1). There are two subspecies of *A. hypogaea*, distinguished primarily on branching pattern and distribution of vegetative and reproductive axes. Subspecies *hypogaea* has two varieties (*hypogaea* and *hirsuta*), whereas subsp. *fastigiata*

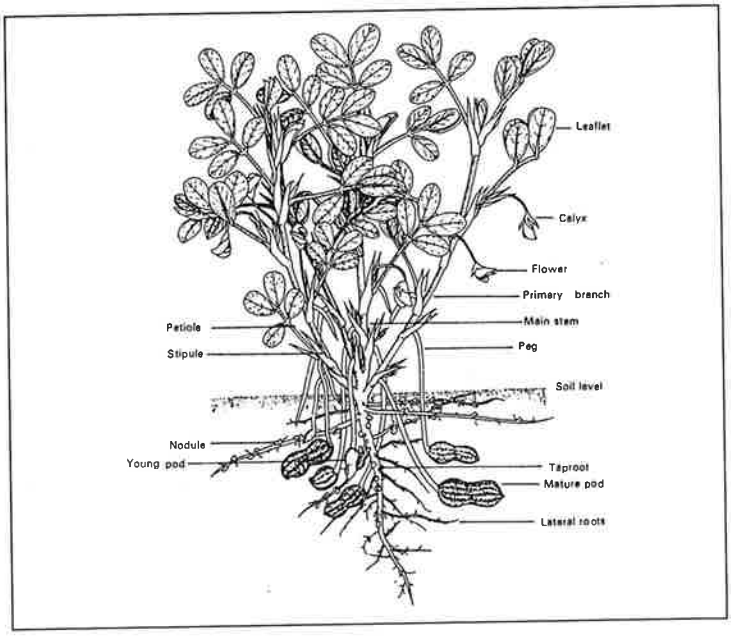

Fig. 1. Stylized plant of *Arachis hypogaea* (reproduced from Rao, 1988).

has four (*fastigiata*, *vulgaris*, *peruviana* and *aequatoriana*) (Krapovickas and Gregory, 1994; see Chapter 2).

Other species in the genus are used for grazing, notably the rhizomatous perennials (Prine *et al.* 1986, 1990; Kretschmer and Wilson, 1987) and *A. pintoi* Krapov. and W.C. Gregory (Kerridge and Hardy, 1994). The major interest in the wild relatives has been as sources of resistance to insect pests and diseases, and a number of programs have concentrated on interspecific hybridization to transfer desirable genes (Stalker and Moss, 1987).

The anatomy, morphology, and botany of the cultivated peanut have been described in a number of books, the most comprehensive being in the chapter by Gregory *et al.* in "Peanuts—Culture and Uses" (Gregory *et al.*, 1973) and the chapter by V. Ramanatha Rao in "Groundnut" (Rao, 1988). This chapter summarizes the developmental morphology and anatomy of the cultivated peanut, with emphasis on agrunomic importance.

Peanut originated in South America and was taken westward by the Spaniards who introduced it into the Malayan Archipelago, China, and Indonesia and eventually to Madagascar (Krapovickas, 1968). Peanut also was carried east to Africa from South America. The first introduction into North America has been speculated to be from Africa, with later introductions from Spain—hence the origin of the term "valencia" to describe var. *fastigiata*. A possible alternative was introduction from South America by way of resupplying slave traders in route from Africa to the U.S. (see Stalker and Simpson, Chapter 2). Regardless of the route for the early introductions, there has been much exchange of seeds in recent years, and breeders have had access to a wide range of *A. hypogaea* germplasm. Accessions of peruvian runner (var. *hirsuta* types), however, have not been freely available, as few living collections are known.

Arachis hypogaea is variable for many morphological and reproductive traits. The range of this variation is described in "Descriptors for Groundnut" (IBPGR/ICRISAT, 1992). As an example, 19 primary seed colors ranging from white to very dark purple are listed, each with reference to the relevant color codes of the standard color chart of the U.K. Royal Horticultural Society.

REPRODUCTIVE DEVELOPMENT

Peanut inflorescences are borne in the axils of leaves on primary or secondary branches, are spike-like, simple or compound monopodia, and each has up to five flowers. However, three flowers per inflorescence are the most common. Only one flower per inflorescence usually is open at any given time. They are modified sessile papillionaceous flowers (although pedicels can elongate) that appear to be stalked due to the presence of an elongated tubular hypanthium or "calyx tube" (Fig. 2). The flower is subtended by a bract, with a second bract on the inflorescence branch (Norden, 1980). The style is contained within the calyx tube, and both structures elongate rapidly with a rate up to 5 cm in the 24 hours prior to anthesis. The ovary is superior,

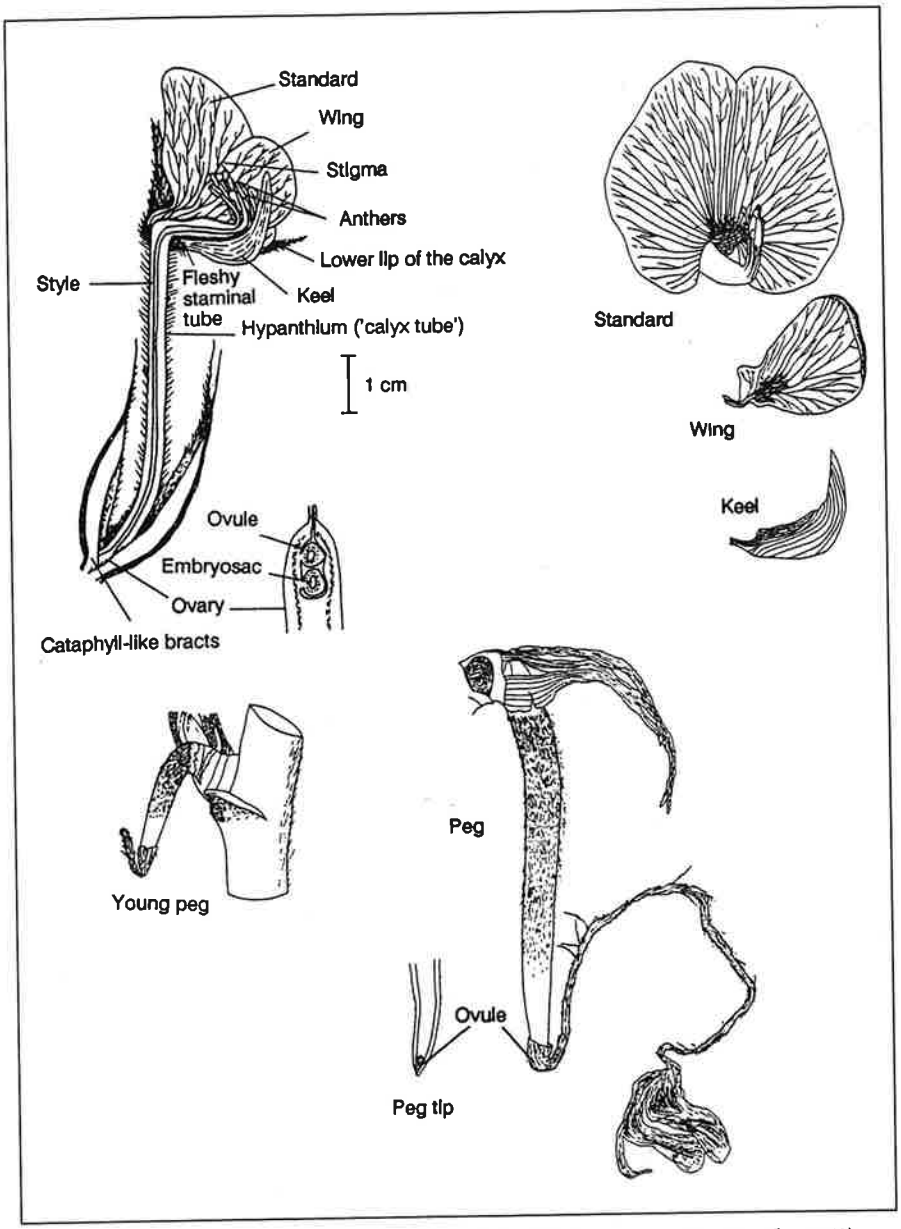

Fig. 2. Floral and reproductive structures of *Arachis hypogaea* (after Smith, 1950).

with the "calyx tube" (hypanthium) attached to the base of the ovary. The corolla (consisting of standard, wing and keel petals), and the calyx (of five sepals) are borne at the distal end of the elongated hypanthium. The standard ranges in color from light yellow to deep orange, or is very rarely white. A central crescent area exists on the face of the standard which can be

deeper in color, or even express a different color, than the rest of the standard (Hayes, 1933; John *et al.*, 1954; Varisai Muhammad *et al.*, 1973). The wing is usually the same color as the standard, but the two flower parts have different mixtures of yellow and orange in several species.

The androecium is a basic monadelphous structure, with a staminal tube notionally bearing five globular and five oblong anthers (Fig. 2), although this number is rarely observed because one or two anthers are usually sterile. Maeda (1972) reported that sterile anthers were more common in the erect spanish and valencia types than in the virginia runner types. The filaments are fused for two-thirds of their length. Microsporogenesis leading to the production of pollen grains has been described in detail by Xi (1991), and pollen matures approximately 6 to 8 hours before anthesis (Gregory *et al.*, 1973; Pattee *et al.*, 1991). At the time of anthesis, the mature pollen grain is two-celled with two generative nuclei.

The stigma is at the same level as, or protrudes beyond the anthers. Self-pollination usually occurs because the stigma and anthers are enclosed by the keel. Cross-pollination occurs when bees visit flowers, and outcrossing has been reported at frequencies ranging from 0 to 6.16% (Hammons and Leuck, 1966; Culp *et al.*, 1968; Hammons, 1973; Norden, 1973). The stigma is of the dry pappillate type (Lakshmi and Shivanna, 1986) and is elongated, strongly curved, and composed of many papillae without surrounding hairs. Pollination takes place at or near the time of anthesis (flower opening) which occurs within a few hours after sunrise (Pattee *et al.*, 1991). The stigmatic surface can accommodate and permit hydration of up to 15 pollen grains. Enzymes associated with pollen germination are produced on the stigmatic surface from 48 hours before to 8 hours after anthesis (Lu *et al.*, 1990). This correlates with observations that success in crossing peanut genotypes declines a few hours after the flower is fully open, although Hassan and Srivastava (1966) reported that the stigma is receptive for up to 12 hours.

Lu *et al.* (1990) observed marked differences between stigma morphology of the annual and perennial species of *Arachis* (Fig. 3). In contrast to the large stigmatic surface of the annuals, the perennial species have very small stigmas surrounded by cuticularized unicellular hairs. The number of pollen grains which can be supported on these stigmas is limited to a maximum of three. The stigma morphology of perennials could be one factor contributing to low seed set and to their poor crossability as female parents in interspecific hybridization attempts. However, Pattee and Stalker (1992a,b) observed that, even though fertilization usually occurs after hand-pollination (if at a low frequencies), the high frequency of embryo abortion in crosses involving both perennial and annual species restricts the number of interspecific hybrids which can be obtained.

The style is enclosed in the staminal tube and extends through the calyx tube to the ovary. The style is hollow, the central canal being continuous with the ovarian cavity (Periasamy and Sampoornam, 1984).

The ovary in peanut is unilocular and commonly has one to three ovules. The development of the ovule has been described as anatropous and bitegmic (Periasamy and Sampoornam, 1984; Xi, 1991). The ovule is green, with

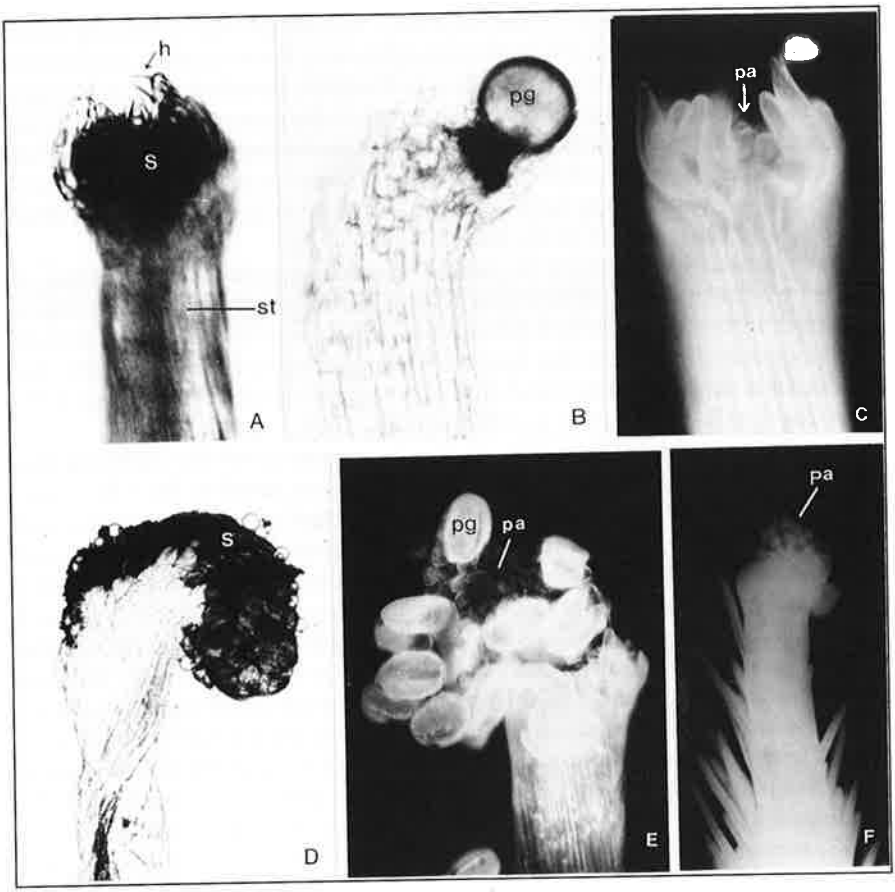

Fig. 3. Whole mounts of stigmas of *Arachis* species (h = hairs, pa = stigmatic papillae, pg = pollen grain, s = stigma, and st = style) (reproduced from Lu *et al.*, 1990). (A) *A. cardenasii* stigma surface densely stained by Coomasie blue, stigma hairs unstained, ×576. (B) *A. cardenasii* stigma with one pollen grain showing size of stigma surface compared to pollen grain, ×576. (C) *A. correntina* stigma stained with Auramine O showing lightly cutinized stigmatic papillae surrounded by heavily cutinized hairs, ×640. (D) *A. hypogaea* stigmatic papillae stained with Coomasie blue, ×256. (E) *A. hypogaea* stigma with at least 10 pollen grains; stained with Auramine O showing limited flourescence of stigmatic papillae compared to stylar cells, ×256. (F) *A. glandulifera*, intermediate type of stigma stained with Auramine O, ×256.

chlorophyll pigments in the inner integument and the hypodermal layer of the chalaza.

The mature embryo sac is composed of a prominent egg with the endosperm nucleus surrounded by starch grains. With the onset of fertilization, starch grains disappear and a multicellular proembryo is formed upon syngamy (Pattee and Stalker, 1991).

The embryology of cultivated peanut has been amply described by Periasamy and Sampoornam (1984), Pattee and Mohapatra (1987), Wu and

Xi (1988), Pattee *et al.* (1991), and Xi (1991). In wild species belonging to the section *Rhizomatosae*, where seed set is either very low or absent, anatomical observations of the pistil 1 day after pollination revealed that the major reason for no seed setting is the breakdown of ovular tissue. Fertilization also triggers the degeneration of the ovular tissues, including the tapetal layer. In section *Arachis* there are differences in embryo sac morphology and in peg, ovary, and ovule ontogeny between the cultivated and wild species (Pattee and Stalker, 1991; Pattee *et al.*, 1991).

Post-fertilization changes in peanut are accompanied by withering of petals by 24 hours after pollination. Normally, the petals open on the day of anthesis and remain fresh for 4-6 hours under field conditions. If fertilization does not occur, then withering may be delayed for up to 24 hours. Following fertilization, the hypanthium and style may remain attached to the base of the ovary for 4 to 5 days (Pattee and Mohapatra, 1986).

Fertilization ultimately results in the development of the underground fruit. The fertilized egg, or proembryo, undergoes three to four divisions, after which time it becomes quiescent until after soil penetration (Pattee and Mohapatra, 1987). An intercalary meristem located adjacent to the basal ovule becomes active within a short time after fertilization, and a structure commonly termed a peg (botanically a carpophore or a gynophore) is formed (Fig. 2). Elongating pegs, which are usually green with a purple tip, exhibit positive geotropism (Zamski and Ziv, 1976) and grow into the soil. The peg becomes diageotropic after penetrating the soil, ceases to elongate, and then fruit development commences. The diageotropism is such that the ovules are always located on the upper wall of the pod, with the pod tip pointing away from the plant (Fig. 1). Although darkness is usually necessary for pod development (Ziv, 1981), aerial pods have been observed. Seshadri *et al.* (1955) reported differences between cultivars in the depth at which pods form. Ono (1979) also reported differences in peg length between cultivars which have different branching patterns. Comparisons between wild and cultivated peanuts indicated that, in *A. hypogaea*, peg expansion occurs, on average, for 16 to 17 days after pollination, and the pegs are about 7 cm long by this time. In contrast, *A. batizocoi* produces pegs 25 cm long by 23-25 days after pollination (Halward and Stalker, 1987). The pegs of *A. hypogaea* are strong and will not break upon maturity. In contrast, the long pegs of wild *Arachis* species are fragile and break, thus serving as a mechanism for seed dispersal. Although comparable measurements are not available for all species, pegs more than 1 meter long have been observed on some wild species, for example *A. pusilla* Benth. (Fig. 4).

In crosses between species, the size and stage of development of the embryo do not correlate with the stage of development of the pod. In attempts to obtain hybrid plants from wide crosses in peanut, the culture of ovules is an advantage because embryos continue to grow *in vitro*. Embryos then can be dissected from ovules and subcultured when they are large enough to survive without associated maternal tissues (Sastri *et al.*, 1980; Stalker and Eweda, 1988; Feng *et al*, 1994).

The immature pod contains a thick layer of parenchymatous tissue between

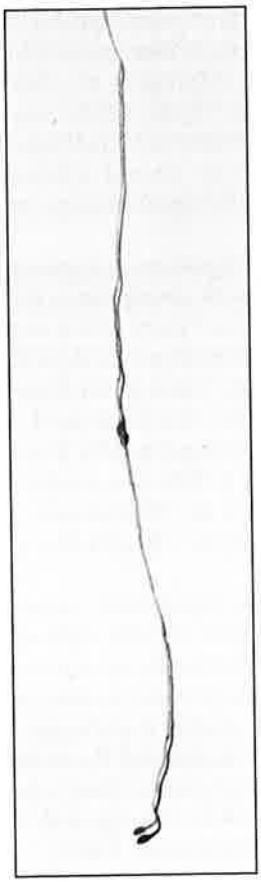

Fig. 4. A 75-cm catenate peg of *A. triseminata*.

the ovules and the shell (Schenk, 1961). This tissue recedes as the ovules grow and, at maturity, the pod wall consists only of an outer spongy layer, a fibrous middle layer, and a papery internal layer. Pod shape depends on the number of seeds per pod and the amount of constriction between seeds (IBPGR/ICRISAT, 1992). Pods with marked reticulation and deep constrictions between seeds retain larger quantities of soil at harvest than smooth pods with shallow constrictions. Differences also exist between genotypes in the amount of surface reticulation and the size of the beak (a protrusion which may be insignificant to large and curved at the tip of the pod).

The seed is enclosed in a thin, papery testa (Zambettakis and Bochellee-Morvan, 1976; Glueck *et al.*, 1979). The testa is maternal tissue derived from the integuments and has a wide range of colors from white to dark purple. Variegated testas are commonly observed in many genotypes. Genetics of testa color is complex (Hammons, 1973), and the testa color usually darkens during storage. Testa color is important for varietal recognition

in markets, and there are strong local preferences by people for particular colors. Integrity of the testa has been associated with resistance to invasion by *Aspergillus flavus* Link (Mehan *et al.*, 1987). Resistance to *Sclerotinia minor* Jagger in germplasm from China has been associated with seed characteristics such as tan testa and small seed size. These are undesirable attributes in the virginia-type peanut market which makes selection for resistance to this disease difficult when large, pink seeds are the desired type (Porter *et al.*, 1992).

The seed consist of two cotyledons, a hypocotyl, epicotyl, and radicle. The epicotyl is well developed, with young leaves formed within the mature seed. All of the leaves and aerial plant parts which the seedling will develop during the first 2-3 weeks after germination are already present in the dormant seed (DeBeer, 1963). There has been controversy, however, whether flower primordia are present in the dormant seed. Staritsky (1973) could not confirm presence of the flower primordia in peanut seeds, but Tahahashi *et al.* (1978) [cited by Ono (1979)] reported that "in ssp. *fastigiata* or intersubspecific hybrid such as Tachimosari, the flower bud had already been formed in seed embryos." It remains an area of debate as to how common this is in *Arachis*.

The cotyledon comprises epidermis, vascular tissue, and parenchyma. The epidermis is a single layer of cells, with stomata only occurring on the inner adaxial surface. The parenchyma consists mostly of large isodiametric cells containing lipid bodies, protein bodies, and starch grains (Young and Schadel, 1984). They also reported that the groove which is normally present in the center of the adaxial surface of the cotyledon is not present in seed from environmentally stressed plants. De-embryonated cotyledons have the ability to regenerate shoots even when growth-regulating substances are not added to culture media (Bhatia *et al.*, 1985).

The two cotyledons comprise about 96% of the seed by weight, are the major storage tissue for the developing seedling, and contribute most to the economic importance of the plant. The peanut seed contains about 20% carbohydrates and 50% oil, thus providing a high energy source (Ahmed and Young, 1982). Pattee *et al.* (1974) found starch to increase until mid-maturity of seed and then sugar, predominantly in the form of sucrose, to reach a maximum at full maturity.

VEGETATIVE GROWTH

Germination is epigeal, the cotyledons becoming green soon after emergence. The seedling consists of cotyledons, vegetative axes, and the main axis. Leaves are spirally arranged on the axes. Detailed descriptions have been published by Richter (1899), Badami (1933, 1935), Bouffil (1947), Yarbrough (1949, 1957a,b), and Prevot (1950).

Hypocotyl length depends on depth of planting. It is initially white and fleshy and can be up to 1 cm in diameter. The hypocotyl is easily distinguished during the early stages of plant growth, but later becomes

indistinguishable from the root. Epicuticular waxes of peanut hypocotyls have been shown to inhibit *in vitro* growth of *Rhizoctonia solani* Kuhn (Reddy *et al.*, 1988). Hadwan and Bhowmik (1991) compared hypocotyl characteristics of one genotype resistant to *Aspergillus niger* van Tieghem with a susceptible cultivar and suggested that hardening of hypocotyl tissues is a factor conditioning resistance.

The root system consists of a rapidly growing tap root and numerous lateral roots (Fig. 1) (Yarbrough, 1949; Gregory *et al.*, 1973). Lateral roots generally first appear on the third day after seed germination, and numerous laterals are formed within 3-5 days (Yarbrough, 1949). Roots are mostly in the 5- to 35-cm zone below the soil surface, but they have been reported to a depth of 135 cm (Narasinga Rao, 1936; Intorzato and Tella, 1960). Peanut roots do not have typical root hairs, but tufts of hairs in the root axils. These hairs have been associated with nodulation resulting from *Bradyrhizobium* infection and subsequent symbiosis (Nambiar *et al.*, 1983). Nodules are formed on roots, but at different frequencies among genotypes (Nambiar and Dart, 1980). Non-nodulating genotypes also have been reported (Nambiar *et al.*, 1983). Nodulation and associated nitrogen fixation in peanut is reviewed in Chapter 8 of this volume.

Stems are angular, green or pigmented with colors ranging from light pink to dark purple. They are usually pubescent, but can be glabrous. Plants can grow to 65 cm high and spread to a width of over 1 m in runner types of *A. hypogaea*. Stems can grow several meters long in several other species of *Arachis*. Adventitious roots also can form where stems come in contact with soil.

The growth habit and branching pattern differ between *A. hypogaea* subspecies and botanical varieties. These characteristics are of botanical and agronomic importance, as they define the overall size and fruiting pattern of the plant as well as affecting plant spacing and other agronomic factors.

Arachis hypogaea subsp. *hypogaea* var. *hypogaea* (virginia type) and *A. hypogaea* subsp. *hypogaea* var. *hirsuta* (peruvian runner type) have no floral axes on the main stem, but have alternating pairs of floral and vegetative axes on lateral branches (Fig. 5). Virginia peanuts have shorter, less hairy branches than the peruvian runner types.

Plants of *A. hypogaea* subsp. *fastigiata* have floral axes on the main stem and sequential floral axes on branches. Valencia types (var. *fastigiata*) have relatively few and curved upright branches. Plants are similar to var. *peruviana* except that plants of this variety have fewer hairs and pods are deeply reticulated. Varieties *vulgaris* and *aequatoriana* are more branched and have erect or very upright stems. The *aequatoriana* types, however, are very hairy, have purple stems and deep pod reticulation (Krapovickas and Gregory, 1994).

Leaves of cultivated peanut and most species in the genus are tetrafoliolate, with the exception of two species in section *Trierectoides* which have trifoliolate leaves. The paripinnate leaves are borne spirally in 2/5 phyllotaxy and their arrangement on the main stem, and higher order branches is distichous. Leaves are subtended by a partially adnate stipule. Leaflets are

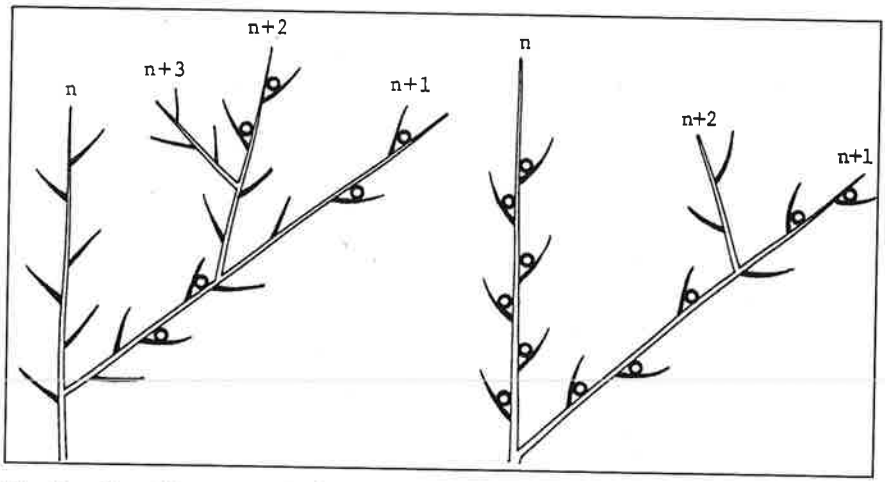

Fig. 5. Branching patterns of *A. hypogaea*. Left: Alternate branching of *A. hypogaea* subsp. *hypogaea*. No floral axes on the main stem (n) but alternating pairs of floral and vegetative axes on branches (n+1, n+2, n+3). Right: Sequential branching of *A. hypogaea* subsp. *fastigiata*. Floral axes on the main stem and sequential floral axes on branches (reproduced from Rao, 1988).

oblong to lanceolate, with stomata on both surfaces. Mutants with different leaf shapes and textures have been identified—krinkle (Hammons, 1964), mottle (Srivastava, 1970), corduroy (Gregory, 1968), and various small or narrow leaved mutants (Ashri, 1970; Bhide and Desale, 1970; Matlock *et al.*, 1970). Differences in leaf color exist between *A. hypogaea* subsp. *hypogaea* (darker green leaves) and subsp. *fastigiata* (lighter green leaves). Hairiness of leaflets differs between genotypes but has not been associated with subspecific status. However, hairiness has been correlated with insect resistance (Campbell *et al.*, 1976). Resistance to peanut leafhopper, *Empoasca ricei* Dworakowska & Power is correlated with trichome density, although the resistant genotypes studied also had harder leaf petioles, as measured by a piercing test, and higher tannin content than the susceptible genotypes (Sison, 1991). Differences in leaf surface texture account for differences in leaf wettability and moisture retention on the leaf surface, although no water is retained after wetting on the adaxial surface (Cook, 1981). A direct relationship between water repellency and susceptibility to rust infection was shown by Cook (1980). Leaf anatomy has been associated with severity of disease symptoms by Kaur *et al.* (1988), who reported significant negative correlations between severity of infection by late leaf spot caused by *Cercosporidium personatum* (Berk. et Curt.) Deighton and number of palisade cells per unit area. Pixley *et al.* (1989) compared stomatal size and frequency in genotypes resistant, moderately susceptible, and susceptible to *C. personatum*. The resistant genotypes had the lowest average stomatal frequency and size, and a positive and significant correlation between stomatal frequency and disease reaction indicated the importance of this trait for determining plant reaction to this disease.

CONCLUSIONS

A great range of morphological and reproductive diversity exists in the genus *Arachis*. The brief descriptions given above, mainly on the cultivated peanut, are intended to be an insight into the basic structures and the range of this variation. The limits of variation are best described in "Descriptors for Groundnut" (IBPGR/ICRISAT, 1992) but, for more detail, the reader is referred to the literature cited. A number of the morphological features of peanut also are agronomically and economically important, and a few that are associated with pest resistance, disease resistance, or other characters have been mentioned.

LITERATURE CITED

Ahmed, E.M., and C.T. Young. 1982. Composition, quality and flavor of peanuts, pp. 655-688. *In* H.E. Pattee and C.T. Young (eds.) Peanut Science and Technology. Amer. Peanut Res. Educ. Soc., Yoakum, TX.

Ashri, A. 1970. Inheritance of small leaflets in a wide cross in peanuts, *Arachis hypogaea*. Oléagineux 25:153-154.

Badami, V.K. 1933. Botany of groundnut-Part I. J. Mysore Agric. Exp. Union 14:188-194.

Badami, V.K. 1935. Botany of groundnut-Part II. J. Mysore Agric. Exp. Union 15:59-70.

Bhatia, C.R., G.S.S. Murty, and V.H.Mathews. 1985. Regeneration of plants from "de-embryonated" peanut cotyledons cultured without nutrients and agar. Z. Pflanzensucht 94:149-155.

Bhide, M.V., and S.C. Desale. 1970. A small leaf mutant in groundnut. Poona Agric. Coll. Mag. 59:113-114.

Bouffil, F. 1947. Biologie, ecologie et selection de l'arachide au Senegal, Direction de l'agriculture de l'elevage et des forets. Bull. Scien. 1:1-112.

Campbell, W.V., D.A. Emery, and J.C. Wynne 1976. Resistance of peanuts to the potato leafhopper. Peanut Sci. 3:40-43.

Cook, M. 1980. Peanut leaf wettability and susceptibility to infection by *Puccinia arachidis*. Phytopathology 70:826-830.

Cook, M. 1981. Susceptibility of peanut leaves to *Cercosporidium personatum*. Phytopathology 71:787-791.

Culp, T.W., W.K. Bailey, and R.O. Hammons 1968. Natural hybridization of peanuts, *Arachis hypogaea* L., in Virginia. Crop Sci. 8:109-111.

DeBeer, J.F. 1963. Influences of temperature on *Arachis hypogaea* L. with special reference to its pollen viability. Verslagen van Landbouwkundige Onderzoekinsen 69:1-81.

Feng, Q.L., H.E. Pattee, and H.T. Stalker. 1994. *In vitro* reproductive development of a diploid wild species *Arachis duranensis*. Peanut Sci. 21:139-143.

Glueck, J.A., L.E.Clark, and O.D. Smith. 1979. Testa comparisons of four peanut cultivars. Crop Sci. 17:777-782.

Gregory, W.C. 1968. A radiation breeding experiment with peanuts. Radiat. Bot. 8:81-147.

Gregory, W.C., M.P. Gregory, A. Krapovickas, B.W. Smith, and J.A. Yarbrough. 1973. Structures and genetic resources of peanuts, pp. 47-133. *In* Peanuts—Culture and Uses. Amer. Peanut Res. Educ. Assoc., Inc., Stillwater, OK.

Hadwan, H.A., and T.P. Bhowmik. 1991. Hypocotyl anatomy of groundnut cultivars, resistant and susceptible to collar-rot caused by *Aspergillus niger* Van Teigh. Beitrage zur Tropischen Landwirtschaft und Veterinarmedizin 29:337-339.

Halward T.M., and H.T. Stalker. 1987. Comparison of embryo development in wild and cultivated *Arachis* species. Ann. Bot. 59:9-14.

Hammons, R.O. 1964. Krinkle, a dominant leaf marker in the peanut, *Arachis hypogaea* L. Science 4:22-24.

Hammons, R.O. 1973. Genetics of *Arachis hypogaea*, pp. 135-173. *In* Peanuts—Culture and Uses. Amer. Peanut Res. Educ. Assoc., Inc., Stillwater, OK.

Hammons, R.O., and D.B. Leuck, D.B. 1966. Natural cross pollination of the peanut *Arachis hypogaea* L. Agron. J. 58:396.

Hassan, M.A., and D.P. Srivastava 1966. Floral biology and pod development of peanut studied in India. J. Indian Bot. Sci. 45:92-102.

Hayes, R.T. 1933. The classification of groundnut varieties with preliminary note on the inheritance of some characters. Trop. Agric., Trinidad 10:318-327.

IBPGR/ICRISAT. 1992. Descriptors for Groundnut. IBPGR, Rome; ICRISAT, Patancheru, India.

Intorzato, R., and R. Tella. 1960. Sistema radicular do amendoim. Bragantia 19:119-123.

John, C.M., G. Venkatanarayana, and C.R. Seshadri. 1954. Varieties and forms of groundnut (*Arachis hypogaea* Linn.). Their classification and economic characters. Ind. J. Agric. Sci. 24:159-193.

Kaur, J., M. Dhillon, S. Kaur, and M. Bala. 1988. Palisade index of groundnut (*Arachis hypogaea* L.) in relation to resistance/susceptibility to *Cercosporidium personatum* (Berk. & Curt.) Deighton. Proc. Ind. Nat. Sci. Acad., B (Biol. Sci.) 54:191-193.

Kerridge, P.C., and B. Hardy (eds.). 1994. Biology and Agronomy of Forage *Arachis*. Cen. Int. de Agric. Trop. (CIAT) Publ. No. 20., Cali, Colombia.

Krapovickas, A. 1968. Origen, variabilidad y diffusion del mani (*Arachis hypogaea*), pp. 427-441. *In* P.J. Ucko and G. Dimbleby (eds.) The Domestication and Exploitation of Plants and Animals. Duckworth, London (Engl. transl.).

Krapovickas, A., and W.C. Gregory. 1994. Taxonomía del género *Arachis* (Leguminosae). Bonplandia 8:1-186.

Kretschmer, A.E., and T.C. Wilson. 1987. A new seed-producing *Arachis* species with potential as forage in Florida. Proc. Soils Crop Sci. Soc. Fla. 47:229-223.

Lakshmi, K.V., and K.R. Shivanna. 1986. Structure and cytochemistry of the pistil in *Arachis hypogaea*. Proc. Ind. Acad. Sci. (Plant Sci.) 95:357-363.

Lu, J., A. Mayer, and B. Pickersgill. 1990. Stigma morphology and pollination in *Arachis* L. (Leguminosae). Ann Bot 66:73-82.

Maeda, K. 1972. Growth analysis on the plant type in peanut varieties, *Arachis hypogaea* L. IV. Relationship between the varietal difference of the progress of leaf emergence on the mainstem during preflowering period and the degree of morphological differentiation of leaf primordia in the embryo. Proc. Crop Sci. Soc. Japan 41:179-186.

Matlock, R.S., D.J. Banks, Y.-P. Tai, and J.S. Kirby 1970. Inheritance of a narrow leaflet character in peanut, *Arachis hypogaea* L. Agron. Abstr. 1970:15 (Abstr.).

Mehan, V.K., D. McDonald, and K. Rajagopalan. 1987. Resistance of peanut genotypes to seed infection by *Aspergillus flavus* in field trials in India. Peanut Sci. 14:17-21.

Nambiar, P.T.C., and P.J. Dart. 1980. Studies on nitrogen fixation by groundnut at ICRISAT, pp. 110-24. *In* Proc. Int.Workshop on Groundnuts. ICRISAT, Patancheru, India.

Nambiar, P.T.C., S.N. Nigam, P.J. Dart, and R.W. Gibbons. 1983. Absence of root hairs in non-nodulating groundnut, *Arachis hypogaea* L. J. Exp. Bot. 34:484-488.

Narasinga Rao, V. 1936. A note on preliminary physiological observations on the groundnut, pp. 1-6. *In* Proc. Assoc. Econ. Biol., Coimbatore, Tamil Nadu, India.

Norden, A.J. 1973. Breeding of the cultivated peanut (*Arachis hypogaea* L.), pp. 175-208. *In* Peanuts—Culture and Uses. Amer. Peanut Res. Educ. Assoc., Stillwater, OK.

Norden, A.J. 1980. Peanut, pp. 443-456. *In* W. R. Fehr and H. H. Hadley (eds.) Hybridization of Crop Plants. Amer. Soc. Agron., Madison, WI.

Ono, Y. 1979. Flowering and fruiting of peanut plants. JARQ 13:226-229.

Pattee, H.E., E.B. Johns, J.A. Singleton, and T.H. Sanders. 1974. Composition of peanut fruit parts during maturation. Peanut Sci. 1:57-62.

Pattee, H.E., and S.C. Mohapatra. 1986. Hypanthium and style senescence in relation to ovary development in *Arachis hypogaea* L. Bot. Gaz. 147:302-311.

Pattee, H.E., and S.C. Mohapatra. 1987. Anatomical changes during ontogeny of the peanut (*Arachis hypogaea* L.) fruit: Mature megagametophyte through heart shaped embryo. Bot. Gaz. 148:156-164.

Pattee, H.E., and H.T. Stalker. 1991. Comparative embryo sac morphology of cultivated and wild species of *Arachis*. Ann. Bot. 68:511-517.

Pattee, H.E., and H.T. Stalker. 1992a. Embryogenesis in reciprocal crosses of *Arachis hypogaea* cv NC 6 with *A. duranensis* and *A. stenosperma*. Int. J. Plant Sci. 153:341-347.

Pattee, H.E., and H.T. Stalker. 1992b. Reproductive efficiency in reciprocal crosses of *Arachis duranensis* and *A. stenosperma* with *A. hypogaea* cv. NC 6. Peanut Sci. 19:46-51.

Pattee, H.E., H.T. Stalker, and F.G. Giesbrecht. 1991. Comparative peg, ovary, and ovule ontogeny of selected cultivated and wild-type *Arachis* species. Bot. Gaz. 152:64-71.

Periasamy, K., and C. Sampoornam. 1984. The morphology and anatomy of ovule and fruit development in *Arachis hypogaea* L. Ann. Bot. 53:399-411.

Pixley, K.V., K.J. Boote, F.M. Shokes, and D.W. Gorbet. 1990. Disease progression and leaf area dynamics of four peanut genotypes differing in resistance to late leafspot. Crop Sci. 30:789-796.

Porter, D.M., T.A. Coffelt, F.S. Wright, and R.W. Mozingo. 1992. Resistance to Sclerotinia blight and early leafspot in Chinese peanut germplasm. Peanut Sci. 19:41-43.

Prevot, P. 1950. Croissance, et development et nutrition minerale de l'arachide. I.R.H.O. Ser. Scien. 4:1-108.

Prine, G.M., L.S. Dunavin, R.J. Glennon, and R.D. Roush. 1990. Registration of 'Arbrook' rhizoma peanut. Crop Sci. 30:743-744.

Prine, G.M., L.S. Dunavin, J.E. Moore, and R.D. Roush. 1986. Registration of 'Florigraze' rhizoma peanut. Crop Sci. 26:1084-1085.

Rao, V. R. 1988. Botany, pp 24-64. *In* P.S. Reddy (ed.) Groundnut. Indian Council of Agric. Res., New Delhi, India.

Reddy, M.N., G.G. Rao, and P. Sujathamma. 1988. Epicuticular waxes of groundnut hypocotyls becoming resistant to attack by *Rhizoctonia solani* (Kuhn). Acta Physiol. Plant. 10:287-292.

Richter, C.G. 1899. Beitrage Zur Biologie von *Arachis hypogaea*, p. 39. *In* A. Schrieber (ed.) Inaug. Diss. Kgl. Bot. Gart. Breslau.

Sastri, D.C., M.S. Nalini, and J.P. Moss. 1980. *In vitro* culture of *Arachis* ovaries and ovules, pp. 366-373. *In* P.S. Rao *et al.* (ed.) Proc. Symp. Plant Tissue Culture, Genetic Manipulation and Somatic Hybridization. Bhabba Atomic Res. Cen., Trombay, India.

Schenk, R.V. 1961. Development of the peanut fruit. Georgia Agric. Exp. Stn. Tech. Bull. N.S. 22:5-53.

Seshadri, C.R., M. Bhavanisankara Rao, and N. Srinivasalu. 1955. Studies on the gynophore in the groundnut. Proc. 6th Scien. Workers Conf., Dept. of Agric., Tamil Nadu, India.

Sison, M.L. 1991. Mechanism of resistance of peanut, *Arachis hypogaea* L. against the peanut leafhopper, *Empoasca ricei* Dworakowska and Pawar (En). MS Thesis. Philippines Univ., College, Laguna, Philippines.

Smith, B.W. 1950. *Arachis hypogaea*. Aerial flower and subterranean fruit. Amer. J. Bot. 37:802-815.

Srivastava, A.N. 1970. Mottled leaf—A mutant in *Arachis hypogaea* L. Madras Agric. J. 57:35.

Stalker, H.T., and M.A. Eweda. 1988. Ovule and embryo culture of *Arachis hypogaea* and interspecific hybrids. Peanut Sci. 15:98-104.

Stalker, H.T., and J.P. Moss. 1987. Speciation, cytogenetics, and utilization of *Arachis* species. Adv. Agron. 41:1-40.

Staritsky, G. 1973. Seed morphology and early development of the groundnut (*Arachis hypogaea* L.). Acta Bot. Neerl. 22:373-89.

Varisai Muhammad, S., T. Ramanathan, and M. Ramachandran. 1973. Variation in morphological characters of *Arachis hypogaea* L. Madras Agric. J. 60:1373-1379.

Wu, M.Z., and X.-Y. Xi. 1988. Embryo and endosperm development in *Arachis hypogaea* L. J. Shandong Agric Univ. 19:11-17.

Xi, X-y. 1991. Development and structure of pollen and embryo sac in peanut (*Arachis hypogaea* L.). Bot. Gaz. 152:164-172.

Yarbrough, J.A. 1949. *Arachis hypogaea*. The seedling, its cotyledons, hypocotyl and roots. Amer. J. Bot. 36:758-772.

Yarbrough, J.A. 1957a. *Arachis hypogaea*, the seedling, its epicotyl and foliar organs. Amer. J. Bot. 44:19-30.

Yarbrough, J.A. 1957b. *Arachis hypogaea*. The form and structure of the stem. Amer. J. Bot. 44:31-36.

Young, C.T., and W.E. Schadel 1984. Effect of environment on the physical structure of the peanut (*Arachis hypogaea* L.). Food Microstruc. 3:185-190.

Zambettakis, C., and A. Bockellee-Morvan. 1976. Research on structure of the groundnut seed coat and its influence on the penetration of *Aspergillus flavus*. Oléagineux 31:219-228.

Zamski, E., and M. Ziv 1976. Pod formation and its geotropic orientation in the peanut, *Arachis hypogaea* L., in relation to light and mechanical stimulus. Ann. Bot. 40:631-636.

Ziv, M. 1981. Photomorphogenesis of the gynophore, pod and embryo in peanut, *Arachis hypogaea* L. Ann. Bot. 48:353-359.