Chapter 2

# GERMPLASM RESOURCES IN *ARACHIS*

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Plants identified under the general term "peanut" or "groundnut" are members of the genus *Arachis* and distinguished from most other genera by having a peg and geocarpic reproductive growth. *Arachis* belongs to the family *Fabaceae*, tribe Aeschynomeneae, subtribe Stylosanthinae. *Arachis hypogaea* L. is the only peanut species to be domesticated and widely used directly for food or for its oil content. However, at least two other species have been cultivated for their seed, including *A. villosulicarpa* Hoehne in the northwestern region of Mato Grosso, Brazil (Gregory *et al.*, 1973) and *A. stenosperma* Krapov. and W.C. Gregory in central and southeastern Brazil (Simpson *et al.*, 1993b). The case of *A. stenosperma* is interesting because seeds of this wild species were apparently transported great distances from the Araguaya River drainage basin in central Brazil to hunting/fishing grounds adjacent to now-abandoned missionary sites along the southeastern Atlantic coast. *Arachis pintoi* Krapov. and W.C. Gregory and *A. glabrata* Benth. also have been cultivated as forage plants in South and North America and Australia, and *A. repens* Handro. has been used as a ground cover in South America. In numerous other locations in South America we have observed village people planting local *Arachis* species as ornamentals in the village square, flower beds, and/or gardens.

The genetic vulnerability of *A. hypogaea* was believed to be high during the mid-1970s because each of the several market types were grown in virtual monoculture (Hammons, 1976). The situation has somewhat improved during the past 15 years (Knauft *et al.*, 1987), but the germplasm base of U.S. cultivars is still narrow. Forty-five cultivars have been released in the U.S. since the early 1900s, of which 32 originated since 1970 (Isleib and Wynne, 1992). Cultivars Dixie Giant and Small White Spanish have contributed nearly one-half of the genes of all U.S. cultivars, and the line GA 207 is found in 28 of the 45 pedigrees (Isleib and Wynne, 1992).

Potential genetic resources for peanut improvement are found in both *A. hypogaea* landraces and in related wild species. Extensive efforts have been made to collect and evaluate *Arachis* germplasm, and programs have evolved during recent years which are attempting to utilize genes from unadapted genotypes. This review addresses questions related to the variation found in the cultivated peanut and related wild species of the genus. To better understand the potential for utilizing *Arachis* species and unadapted *A. hypogaea* genotypes for crop improvement, reviews will be presented of existing diversity within collections; problems and successes with germplasm maintenance and exchange; evolution, biosystematics and gene pools; and, finally, specific traits of genetic and/or agronomic interest.

# PRESENT STATUS OF CLASSIFICATION—DOMESTICATED AND WILD *ARACHIS*

### *Arachis hypogaea*

The domesticated species was described in 1753 by Linneaus as *Arachis* (derived from the Greek "arachos," meaning a weed) *hypogaea* (meaning an underground chamber) or, in botanical terms, a weed with fruits produced below the soil. The center of origin of *A. hypogaea* is believed to be southern Bolivia to northern Argentina because of the primitive characters (pod beak, pod shape, pod reticulation, peg length, plant structure, etc.) associated with germplasm from this region. Subspecies *hypogaea* var. *hypogaea* is the predominant peanut type found in this area, and Krapovickas (1969) hypothesized that var. *hypogaea* may represent the most ancient cultivars because they have a runner habit, branching patterns similar to related *Arachis* species, and no floral compound spikes.

Recent information indicates that there could have been a second event which led to the evolution of *A. hypogaea* in an area north of Lima on the west coast of Peru. Archaeological excavations have recovered single-seeded peanut shells near Casma at Pampa de las Llamas—Moxeke which came from a level dated to approximately 1500 BC (Banks, 1987, 1988; Banks *et al.*, 1993). These samples predate the remains of maize (*Zea mays* L.) found at other Casma Valley sites (Ugent *et al.*, 1984). The single-seeded shells were examined by the junior author and found to be very similar in reticulation, size and shape to wild peanuts collected at Yala, JuJuy, Argentina (*A. monticola* Krapov. and Rig.) (GKPBSSc 30062) and at San Ignacio, Santa Cruz, Bolivia (*Arachis magna* Krapov. and W.C. Gregory, GKSSc 30097) (Banks, 1988). If the pre-Moche peoples of Peru were cultivating crops at 1500 BC, then the logical conclusion is that they were growing wild peanuts; these peanuts then could have given rise to the *A. hypogaea* shells which were found at other nearby archaeological sites (Banks, 1988; Banks *et al.*, 1993). The other alternative is *A. hypogaea*-types were imported from across the mountains; however, the later domesticated types found in archaeological sites in this region are unique and quite similar to the peanuts grown in the Casma region of Peru to this date (Banks *et al.*, 1993). Even the peanuts represented in gold carvings found in ancient tombs just to the north of Pampa de las Llamas—Moxeke (Alva, 1988; Donnan, 1988) closely resemble the reticulation of cultivated types now grown in the Casma area.

Krapovickas (1969, 1973) and Gregory *et al.* (1973) classified *A. hypogaea* into geographical regions which, in general terms, fit the varietal classification of the species. Following subspecific nomenclature and varietal associations proposed by Krapovickas and Gregory (1994), two subspecies and six botanical varieties are recognized (Table 1). Recent collections by Banks and Pietrarelli (Simpson *et al.*, 1992) have shown that a seventh center of diversity may be present in Ecuador. More than half of the collections made in this region have pods similar to those collected in northern Peru (*A. hypogaea* subsp. *fastigiata* var. *peruviana*) (Krapov. and W.C. Gregory, see Table 1). The pods are similar to *fastigiata* var. *fastigiata* types with a deep reticulation and the plants have an upright growth habit which is sparsely branched with purple stems and purple

**Table 1. Subspecies and varieties of *A. hypogaea*.**

| Variety | Market type | S.A. location | Characteristics |
|---|---|---|---|
| | | **Subspecies *hypogaea*** | |
| *hypogaea* | | Bolivia, Amazon | No floral axes on main stem; alternating pairs of floral & reproductive axes on branches; branches short; less hairy |
| | Virginia | | Less hairy; large seeded |
| | Runner | | Less hairy; small seeded |
| *hirsuta* | Peruvian runner | Peru | More hairy |
| | | **Subspecies *fastigiata*** | |
| *fastigiata* | | | Floral axes on main stem; alternating pairs of floral & vegetative axes on branches |
| | Valencia | Brazil— Guaranian Goias Minas Gerais Paraguay Peru Uruguay | Little branched; curved branches |
| *peruviana* | | Peru, N.W. Bolivia | Less hairy; deep pod reticulation |
| *aequatoriana* | | Ecuador | Very hairy; deep pod reticulation; purple stems; more branched, erect |
| *vulgaris* | Spanish | Brazil— Guaranian Goias Minas Gerais Paraguay Uruguay | More branched; upright branches |

seeds. However, the densely pubescent leaflets are relatively small and resemble accessions which have been designated *A. hypogaea* subsp. *fastigiata* var. *aequatoriana* by Krapovickas and Gregory (1994) and called the Zaruma type (A. Krapovickas, pers. comm., 1993). Gibbons *et al.* (1972) also classified the diverse types found in Africa and concluded that this germplasm arose from extensive hybridization and subsequent selection. Africa can be considered a tertiary center of diversity of *A. hypogaea*.

Descriptor lists have been published so germplasm workers and breeders can describe variation found in *A. hypogaea* using a standardized set of characters (IBPGR and ICRISAT, 1992). Simpson *et al.* (1992) applied 53 of these descriptors to 2000 germplasm lines collected from 1977 to 1986 in South America and observed a large amount of variability illustrated by differences in pod and seed characters among different *A. hypogaea* collections (Fig. 1). In addition to "pure" types of subspecies and varieties, many intermediates exist and the taxonomy of the cultivated species is not always clear. Isleib and Wynne (1983) grouped 27 lines using principal component analyses of morphological

traits and associated heterosis with genotypes from different groups; the greatest effects were from members of different subspecies. In the U.S., 70% of the peanuts grown are runners, while 20, 10, and <1% are virginia, spanish, and valencia market types, respectively (Knauft and Gorbet, 1989).

## *Arachis* Species

The center of origin for *Arachis* is believed to be the Mato Grosso region of

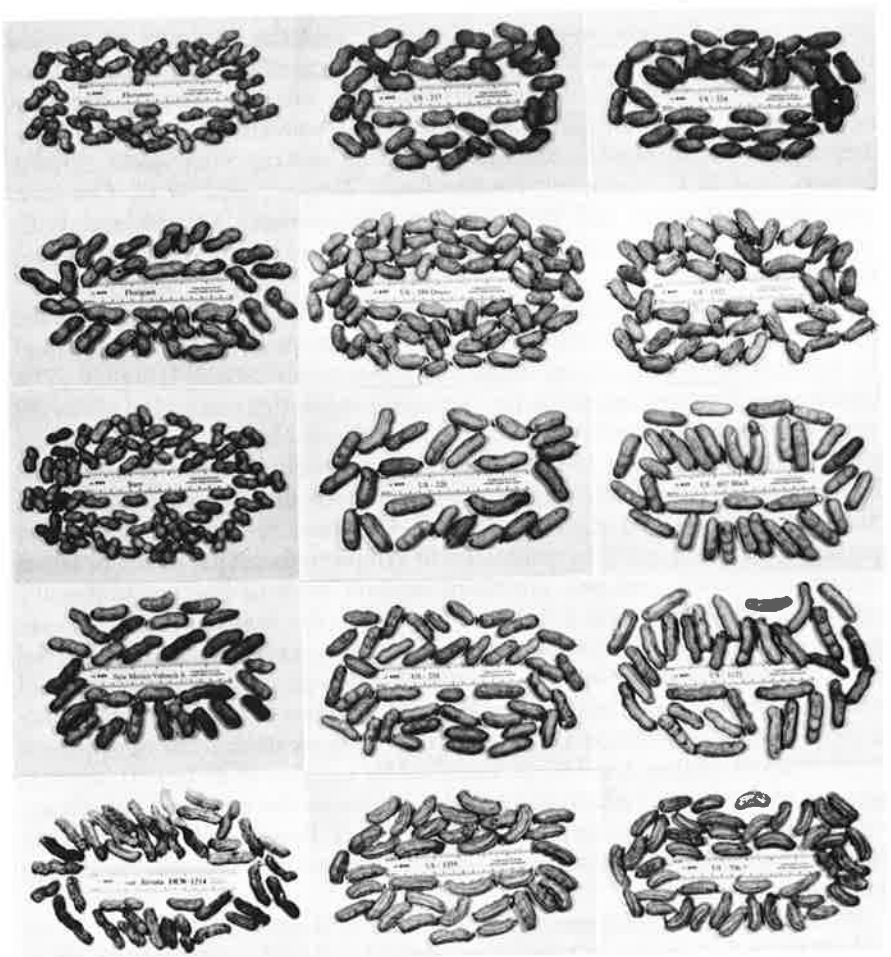

**Fig. 1. Pod variation in *A. hypogaea*. Left to right, top to bottom: Florunner[a], PI 565448 (ssp. *hypogaea* var. *hypogaea*); US-217, PI 475864 (var. *hypogaea*); US-224[a], PI 475871 (var. *hypogaea*); Florigiant[a], PI 565445 (var. *hypogaea*); US-389 (var. *hypogaea*); US-1322, PI 536281 (var. *hypogaea*); US-1322, PI 536281 (var. *hypogaea*); Starr[a], PI 565443 (ssp. *fastigiata* var. *vulgaris*); US-220, PI 475867 (ssp. *fastigiata* var. *fastigata*); US-607 black, PI 497285 (var. *fastigiata*); New Mexico Valencia A[a], PI 565452 (var. *fastigiata*); US-216, PI 475863 (var. *fastigiata*); US-1172, PI 536224 (var. *fastigiata*); DEW-1214, US-1604 (ssp. *hypogaea* var. *hirsuta*); US-1359 (ssp. *fastigiata* var. *peruviana*); US-706-7[a], PI 497631 (ssp. *fastigiata* var. *aequatoriana*).**
**[a]Used as examples in USDA *A. hypogaea* descriptor list.**

Brazil somewhere on the old Brazilian planaltine ellipse (Gregory *et al.*, 1980). The genus evolved before a series of mid-Tertiary uplifts when the slope of the land was generally westward and before the Amazon basin formed. Gregory and Gregory (1979) and Gregory *et al.* (1980) postulated a highland origin for *Arachis* species and subsequent movement via water to the lowlands of South America. As the planalto continued to be uplifted, species of *Arachis* evolved in all directions and became separated into various river valleys and drainage systems. Species in sections *Erectoides* Krapov. and W.C. Gregory, *Extranervosae* Krapov. and W.C. Gregory, and the diploids of section *Rhizomatosae* Krapov. and W.C. Gregory are presumed to be the most ancient because they have highland adaptions including tuberous roots, tuberiform hypocotyls, or rhizomes. Members of sections *Heteranthae* Krapov. and W.C. Gregory (previously cited as *Ambinervosae* Greg. et Krap. *nom. nud.*), *Arachis* Krapov. and W.C. Gregory, *Caulorrhizae* Krapov. and W.C. Gregory, *Procumbentes* Krapov. and W.C. Gregory, *Triseminatae* Krapov. and W.C. Gregory, and the tetraploid *Rhizomatosae* have more recent origins (Gregory *et al.*, 1980).

Wild *Arachis* species are native to a large region of South America from the Atlantic Ocean to the foothills of the Andes Mountains and from the mouth of the Amazon River in northern Brazil to approximately 34°S in Uruguay. The distribution of species appears to be continuous across this vast region wherever suitable habitats are found (Valls *et al.*, 1985). Whereas botanical sections of the genus were once thought to be isolated geographically (Gregory *et al.*, 1973), distributions of subgeneric groups are now known to be greatly overlapped (Simpson, 1984; Valls *et al.*, 1985) (Figs. 2-4). These distributions imply that species in different sections originated in sympatric habitats where isolation barriers developed, and only afterward became more or less geographically separated. Also, the genus is believed to predate the Amazon forest because species belonging in the oldest section (*Extranervosae*) have been collected north of the 10th parallel on both schist rock outcrops and at edges of lowland swamps where the forest has been suppressed. Further distributions of *Arachis* in these areas are restricted by the forest. The westward arc of apparent distribution of section *Arachis*, as described by Gregory *et al.* (1980), appears because of the limited adaptability of the species in the present Gran Chaco region of northwest Paraguay and southeast Bolivia. Recent collections indicate that the progression of section *Arachis* species was continuous during the distant past across the region.

Wild species of *Arachis* were first described by Bentham (1841) during the mid-1800s, and monographs have been written by Chevalier (1933, 1934, 1936) who recognized eight species, Hoehne (1940) who recognized 11, Hermann (1954) who reduced the number to nine, and Krapovickas and Gregory (1994) who listed 69 species (Table 2). Not until the late 1950s were systematic efforts begun to sample the variation in the genus. Most of the collection work during the 1950s to late 1970s was completed by A. Krapovickas and W. C. Gregory, and more recent collections have, in large part, been under the direction of C. E. Simpson and J. F. M. Valls. In total, 1389 accessions of wild *Arachis* have been collected as seeds or plants (Stalker, unpubl. data, 1993).

**Table 2. *Arachis* species identities (type holotype unless otherwise designated) (from Krapovickas and Gregory, 1994).**

| Species and authority | Status | Collector[d] | Coll. no. |
|---|---|---|---|
| **Section *Arachis*** | | | |
| *batizocoi* Krapov. and W.C. Gregory | -- | K | 9505 |
| *benensis* Krapov., W.C. Gregory and C.E. Simpson | *sp. nov.* | KGSPSc | 35005 |
| *cardenasii* Krapov. and W.C. Gregory | *sp. nov.* | KSSc | 36015 |
| *correntina* (Burkart) Krapov. and W.C. Gregory | *com. nov.* | Clos | 5930 |
| *cruziana* Krapov., W.C. Gregory and C.E. Simpson | *sp. nov.* | KSSc | 36024 |
| *decora* Krapov., W.C. Gregory and Valls | *sp. nov.* | VSW | 9955 |
| *diogoi* Hoehne | -- | Diogo | 317 |
| *duranensis* Krapov. and W.C. Gregory | *sp. nov.* | K | 8010 |
| *glandulifera* Stalker | -- | St | 90-40 |
| *helodes* Martius ex Krapov. and Rigoni | -- | Manso | 588 |
| *herzogii* Krapov., W.C. Gregory and C.E. Simpson | *sp. nov.* | KSSc | 36030 |
| *hoehnei* Krapov. and W.C. Gregory | *sp. nov.* | KG | 30006 |
| *hypogae*[ab] L. | -- | Linn. | 9091 |
| *ipaensis* Krapov. and W.C. Gregory | *sp. nov.* | KMrFr | 19455 |
| *kempff-mercadoi* Krapov., W.C. Gregory and C.E. Simpson | *sp. nov.* | KGPBSSc | 30085 |
| *kuhlmannii* Krapov. and W.C. Gregory | *sp. nov.* | KG | 30034 |
| *magna* Krapov., W.C. Gregory and C.E. Simpson | *sp. nov.* | KGSSc | 30097 |
| *microsperma* Krapov., W.C. Gregory and Valls | *sp. nov.* | VKRSv | 7681 |
| *monticola* Krapov. and Rigoni | -- | K | 8012 |
| *palustris* Krapov., W.C. Gregory and Valls | *sp. nov.* | VKRSv | 6536 |
| *praecox* Krapov., W.C. Gregory and Valls | *sp. nov.* | VS | 6416 |
| *simpsonii* Krapov. and W.C. Gregory | *sp. nov.* | KSSc | 36009 |
| *stenosperma* Krapov. and W.C. Gregory | *sp. nov.* | HLK | 410 |
| *trinitensis* Krapov. and W.C. Gregory | *sp. nov.* | Wi | 866 |
| *valida* Krapov. and W.C. Gregory | *sp. nov.* | KG | 30011 |
| *villosa* Benth. | -- | Tweedie | 1837 |
| *williamsii* Krapov. and W.C. Gregory | *sp. nov.* | WiCl | 1118 |
| **Section *Caulorrhizae*** | | | |
| *pintoi* Krapov. and W.C. Gregory | *sp. nov.* | GK | 12787 |
| *repens* Handro | -- | Otero | 2999 |
| **Section *Erectoides*** | | | |
| *archeri* Krapov. and W.C. Gregory | *sp. nov.* | KCr | 34340 |
| *benthamii* Handro | -- | Handro | 682 |
| *brevipetiolata* Krapov. and W.C. Gregory | *sp. nov.* | GKP | 10138 |
| *cryptopotamica* Krapov. and W.C. Gregory | *sp. nov.* | KG | 30026 |
| *douradiana* Krapov. and W.C. Gregory | *sp. nov.* | GK | 10556 |
| *gracilis* Krapov. and W.C. Gregory | *sp. nov.* | GKP | 9788 |
| *hatschbachii* Krapov. and W.C. Gregory | *sp. nov.* | GKP | 9848 |
| *hermannii* Krapov. and W.C. Gregory | *sp. nov.* | GKP | 9841 |
| *major* Krapov. and W.C. Gregory | *sp. nov.* | Otero | 423 |
| *martii* Handro | *sp. nov.* | Otero | 174 |
| *oteroi* Krapov. and W.C. Gregory | *sp. nov.* | Otero | 194 |
| *paraguariensis* | | | |
| ssp. *paraguariensis* Chodat and Hassl. | -- | Hassler | 6358 |
| ssp. *capibarensis* Krapov. and W.C. Gregory | *ssp. nov.* | HLKHe | 565 |
| *stenophylla* Krapov. and W.C. Gregory | *sp. nov.* | KHe | 572 |

**Table 2 (Continued)**

| Species and authority | Status | Collector[d] | Coll. no. |
|---|---|---|---|
| **Section *Extranervosae*** | | | |
| *burchellii* Krapov. and W.C. Gregory | *sp. nov.* | Irwin *et al.* | 21163 |
| *lutescens* Krapov. and Rigoni | -- | Stephens | 255 |
| *macedoi* Krapov. and W.C. Gregory | *sp. nov.* | GKP | 10127 |
| *marginata* Gardner | -- | Gardner | 3103 |
| *pietrarellii* Krapov. and W.C. Gregory | *sp. nov.* | GKP | 9923 |
| *prostrata* Benth. | -- | Pohl | 1836 |
| *retusa* Krapov., W.C. Gregory and Valls | *sp. nov.* | VPtSv | 12883 |
| *setinervosa* Krapov. and W.C. Gregory | *sp. nov.* | Eiten & Eiten | 9904 |
| *villosulicarpa* Hoehne | -- | Gehrt | SP47535 |
| **Section *Heteranthae*** | | | |
| *dardani* Krapov. and W.C. Gregory | *sp. nov.* | GK | 12946 |
| *giacomettii* Krapov., W.C. Gregory, Valls and C.E. Simpson | *sp. nov.* | VPzVlW | 13202 |
| *pusilla* Benth. | -- | Blanchet | 2669 |
| *sylvestris* (A. Chev.) A. Chev. | -- | Chevalier | 486 |
| **Section *Procumbentes*** | | | |
| *appressipila* Krapov. and W.C. Gregory | *sp. nov.* | GKP | 9990 |
| *chiquitana* Krapov., W.C. Gregory and C.E. Simpson | *sp. nov.* | KSSc | 36027 |
| *kretschmeri* Krapov. and W.C. Gregory | *sp. nov.* | KrRa | 2273 |
| *lignosa*[b] (Chodat and Hassl.) Krapov. and W.C. Gregory | *com. nov.* | Hassler | 7476 |
| *matiensis* Krapov., W.C. Gregory and C.E. Simpson | *sp. nov.* | KSSc | 36014 |
| *rigonii* Krapov. and W.C. Gregory | -- | K | 9459 |
| *subcoriacea* Krapov. and W.C. Gregory | *sp. nov.* | KG | 30037 |
| *vallsii* Krapov. and W.C. Gregory | *sp. nov.* | VRGeSv | 7635 |
| **Section *Rhizomatosae*** | | | |
| Ser. *Prorhizomatosae* | | | |
| *burkartii* Handro | -- | Archer | 4439 |
| Ser. *Rhizomatosae* | | | |
| *glabrata* | | | |
| var. *glabrata* Benth. | -- | Riedel | 1837 |
| var. *hagenbeckii*[c] Benth. (Harms ex. Kuntze) F.J. Herm. | -- | Hagenbeck | 2255 |
| *pseudovillosa*[c] (Chodat and Hassl.) Krapov. and W.C. Gregory | *com. nov.* | Hassler | 5069 |
| **Section *Trierectoides*** | | | |
| *guaranitica* Chodat and Hassl. | -- | Hassler | 4975 |
| *tuberosa* Bong. ex Benth. | -- | Riedel | 605 |
| **Section *Triseminatae*** | | | |
| *triseminata* Krapov. and W.C. Gregory | *sp. nov.* | GK | 12881 |

[a]See Table 1.
[b]Type Lectotype.
[c]Type Lecto holotype.
[d]Collectors: B = Banks, Cl = Claure, Cr = Cristobal, Fr = Fernandez, G = Gregory, Ge = Gerin, H = Hammons, He = Hemsy, K = Krapovickas, Kr = Kretchmere, L = Langford, Mr = Mroginski, P = Pietrarelli, Pt = Pittman, R = Rao, Ra = Raymon, S = Simpson, Sc = Schinini, St = Stalker, Sv = Silva, V = Valls, Ve = Veiga, Vl = Valente, W = Werneck, and Wi = Williams. Others = as listed.

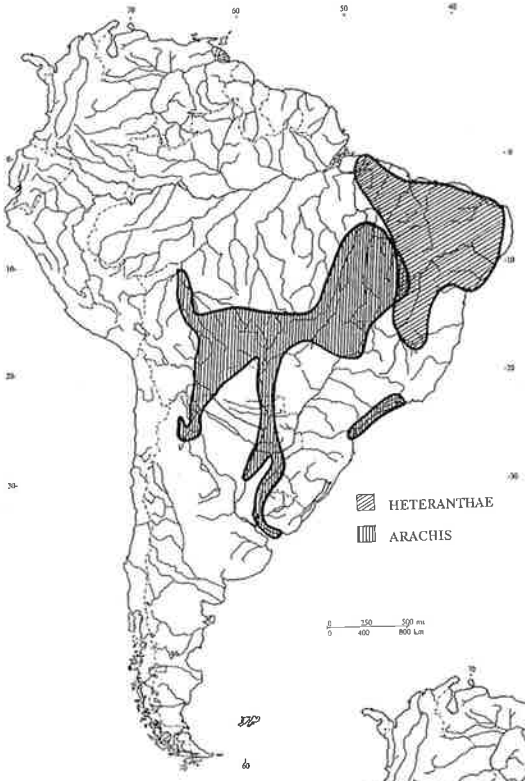


**Fig. 2. Distribution of species in sections *Arachis* and *Heteranthae* in South America. This map was adapted from Simpson (1984), Valls *et al.* (1985), Krapovickas and Gregory (1994), and Simpson (unpubl., 1994).**


**Fig. 3. Distribution of species in sections *Caulorrhizae*, *Procumbentes*, and *Rhizomatosae* in South America. This map was adapted from Simpson (1984), Valls *et al.*(1985), Krapovickas and Gregory (1994), and Simpson(unpubl., 1994).**


**Fig. 4. Distribution of species in sections *Erectoides*, *Extranervosae*, *Trierectoides*, and *Triseminatae* in South America. This map was adapted from Simpson (1984), Valls *et al.* (1985), Krapovickas and Gregory (1994), and Simpson (unpubl., 1994).**

## THE TAXONOMIC SECTIONS OF *ARACHIS*

The genus *Arachis* has been apportioned to nine sections (Krapovickas and Gregory, 1994), and the following is a brief description of their major identifiers.

*1. Arachis:* Leaves tetrafoliolate, plants erect or decumbent, pegs near 45° angle of soil penetration. Plants annual or perennial. $2n=20$, $2n=4x=40$. Type species: *A. hypogaea* L.

2. *Caulorrhizae*: Leaves tetrafoliolate, stems with roots/root primordia at the nodes. Plants perennial. $2n=20$. Type species: *A. repens* Handro.

3. *Erectoides*: Leaves tetrafoliolate, plants erect or decumbent, with flowers and fruits grouped generally at the plant base. Roots with enlarged laterals in most species. Plants perennial. Some pegs up to 1 m or longer. $2n=20$. Type species: *A. benthamii* Handro.

*4. Extranervosae:* Leaves tetrafoliolate, roots with enlargements (tubers?) of various sizes and shapes (but basically cylindrical). Standard petal with red lines on the back side; all flowers "normal" with an expanded corolla. Plants perennial. $2n=20$. Type species: *A. prostrata* Benth.

5. *Heteranthae*: Leaves tetrafoliolate, root system with taproot, but fibrous and without enlargements (tubers?). Standard petals with red lines on front only or on both sides. Flowers dimorphic: normal and open or very small and closed,

small with the corolla not exceeding the calyx. Plants annual or biannual. $2n=20$. Type species: *A. dardani* Krapov. and W.C. Gregory (= *Ambinervosae* Krap. et Greg. *nom. nud.*).

6. *Procumbentes*: Leaves tetrafoliolate, stems with roots occurring in internodes, pegs thickened, horizontal and, in many cases, long. Plants perennial. $2n=20$. Type species: *A. rigonii* Krapov. and W.C. Gregory.

7. *Rhizomatosae*: Leaves tetrafoliolate, plants with rhizomes. Plants perennial. $2n=20$ (Ser. *Prorhizomatosae*), $2n=4x=40$ (Ser. *Rhizomatosae*). Type species: *A. glabrata* Benth.

8. *Trierectoides*: Leaves trifoliolate, hypocotyl tuberiform, plants erect, flowers and fruits primarily at the base of the mainstem. Pegs very long, growing horizontal and superficial. Plants perennial. $2n=20$. Type species: *A. guaranitica* Chodat and Hassl.

9. *Triseminatae*: Leaves tetrafoliolate, fruits with two to four segments, lateral branches decumbent with flowers and fruits along its length. Standard petal with red lines on both sides. Cotyledons with ribs on the upper surface (after plant emergence). Plants perennial. $2n=20$. Type species: *A. triseminata* Krapov. and W.C. Gregory (= GKP 12881, erroneously referred to as *A. pusilla* Benth. in literature).

## COLLECTIONS OF *ARACHIS*

### *A. hypogaea*

Cultivated peanuts were distributed extensively by man over South and Central America during the pre-Columbian period. No evidence exists to indicate that the cultivated peanut reached the continental U.S. during this time, even though peanut culture was thought to be widespread in Mexico in 1492. However, there is some evidence to support the possibility that peanuts journeyed from the western coast of South America to China well before the "rediscovery" of America (Person and Moriarity, 1980). Frost (1982) discounts the evidence for such a theory. During post-Colombian times the cultivated peanut became widely distributed from its primary and secondary centers of diversity in South America to Africa, India, and Asia; and then with the slave trade back to the New World. Because a common practice in the slave trade was to send ships from Africa to the northeast coast of Brazil, at which time new captives were inducted into slavery, it is likely that peanuts from northeast Brazil were used as a food source to complete the voyage to North America. Thus, the first introductions of peanut into North America could easily have been directly from South America rather than from Africa. We believe this to be the more probable scenario versus direct Old World-New World introduction into the present-day U.S.

Cultivated peanuts from the primary and secondary centers in South America have been collected by various methods, but most commonly from markets. Hundreds of collections have been made from one or two vendor markets in small villages; from moderate sized markets in larger population centers (for example, the market at Villa Montes, Bolivia where 12 samples were collected);

and from large markets in centers of trade (for example, the Belem and Mordelo markets in Iquitos, Peru, or the Central Market of La Paz, Bolivia). A large amount of seed diversity exists at these locations because peanuts arrive from many surrounding regions where farmers grow an array of peanut genotypes. Even individual farmers may grow more than one type of peanut; for example, one accession obtained from an Indian farmer in Iquitos, Peru yielded six distinct seed coat colors (SPZ-488, PIs 502091 to 502095). A representative situation for obtaining genetic diversity is the Belem Market of Iquitos. Iquitos is situated on the banks of the Amazon and vendors bring their goods to sell from many small farms along the Napo, Ucayali, Maranon, and Amazon rivers. On one occasion in May 1981, 23 accessions were obtained from Iquitos and, after separation into respective seed testa colors, they yielded a total of 86 distinct lines. Many other markets have yielded 18 to 30 accessions.

The most difficult collections to obtain are directly from the farmers fields because transportation into remote areas is difficult and time-consuming. However, because the crop may be observed and questions about seed history and production practices can be asked, a more complete data base can be obtained. Although farmers are usually willing to share their peanut seeds, often they may have only a very limited seed supply for planting their next crop. Thus, numerous collections from small farms have consisted of very few seeds. Since 1976, a major part of the overall collection effort has been acquiring nodules for isolation of *Bradyrhizobium* spp. An additional benefit to on-farm collections is the opportunity to dig live plants so nodules can be preserved.

Methods for collecting peanuts have been published by several authors, including Hawkes (1976) and Simpson (1984). Efforts to sample representative variation at each location is made but, during some expeditions, carrying many large samples on foot over long distances is not practical. For apparently uniform samples, 1 kg of seed is generally sufficient to assure subdivision between the participants on the collecting trip and the host country. If seeds are obviously variable, then larger samples are desirable. Important information to record at the time of collection includes the location, name of farmer, farmer's name for the variety, planting time, length of growing season, climatic conditions of the area, seeding rate, and pests or diseases associated with the crop.

The major collection expeditions during the past 40 years have included the 1959 and 1960 trips of Gregory/Krapovickas/Pietrarelli funded by the USDA, the 1961 and 1967 trips by Gregory funded by North Carolina State University, and the Hammons/Langford expedition of 1968 funded by the USDA. There were an additional 35 expeditions between 1976 and 1992 that were partially funded by many donors, including the International Board for Plant Genetic Resources (IBPGR); Centro Nacional de Pesquisa de Recursos Geneticos e Biotecnologia/Empresa Brasileira de Pesquisa Agropecuaria (CENARGEN/EMBRAPA), Brazilia, Brazil; Texas A&M University; Instituto Botanico del Nordeste (IBONE), Corrientes, Argentina; Instituto Nacional de Tecnologia Agropecuaria/Estacion Experimental Regional Agropecuaria (INTA/EAA), Manfredi, Argentina; the USDA at Stillwater, OK, Griffin, GA, and Beltsville, MD; North Carolina State University; the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT); and numerous other agencies in South

America. Current funding for U.S. *Arachis* collection expeditions is coming from the USDA Plant Exploration Office at Beltsville, MD; the USDA Plant Introduction Research Unit at Griffin, GA; and Texas A&M University.

The largest single germplasm collection of *A. hypogaea* is maintained at the ICRISAT which has about 13,000 accessions (Singh *et al.*, 1992) (Table 3). The USDA collection in Griffin, GA maintains approximately 6000 accessions (Bettencourt *et al.*, 1989), many of which are duplicated at ICRISAT.

Priorities for future acquisition of *A. hypogaea* germplasm include collecting landraces in regions of Central and South America, Africa, Asia, and China where elite cultivars are replacing more primitive types. Especially important for the immediate future are the var. *hirsuta* accessions because they are poorly represented in both the USDA and ICRISAT collections. Valls *et al.* (1985) outlined three collection priorities in Brazil which include the northwest Mato Grosso State of Brazil (priority 1); all areas in the Brazilian states of Acre, Rondonia, Maranhao, Ceara, Rio Grande do Norte, and Paraiba, plus the northwest region of Goias and northern region of Piaui, Brazil (priority 2); and the southeast Amazon region of Brazil and all of Uruguay (priority 3). (Fig. 5).

***Germplasm Maintenance and Preservation***. Maintenance of *A. hypogaea* accessions is generally straight forward except for handling large numbers of seeds and preventing post-harvest mixtures. The USDA peanut curator increases entries based on seed viability tests, the total number of seeds available in storage, and on the number of requests for individual accessions. To reduce the effects of genetic drift, accessions are stored for the longest possible time (15 or more years in many cases) before they are regrown in seed nurseries. When increases become necessary, reproduction is best done from a large sample of seeds to preserve the original variation and gene frequencies in the population.

Isolation of genotypes to prevent outcrossing or the introduction of diseases and insect pests has been a primary concern to those involved with preservation of *Arachis* germplasm. The first, and often second, seed generation is always grown in the greenhouse under quarantine conditions. Subsequent increases have been in field plots, with 1000 to 6000 seed samples produced for distribution to the USDA peanut curator at Griffin, GA. A portion of this sample is then sent to the National Seed Storage Laboratory at Fort Collins, CO. Small samples also have been distributed to ICRISAT because it has been designated the international germplasm repository for peanut.

Preservation of *A. hypogaea* seed is a relatively easy, albeit an expensive, task. Mature pods are dried so that seed moisture is less than 7%, seeds are shelled and placed in a closed container. Optimal storage conditions were described by Sanders *et al.* (1982) who indicated that the sum of temperature (F) plus relative humidity should be less than 100. Norden (pers. comm., 1990) stored peanut seeds for 20 years with little drop in germination percentage at 10 C and 45% relative humidity. Seeds stored at -17.8 C with no humidity control produce similar results. In areas where optimal seed storage conditions are unavailable, storage in pods is always preferable.

***Germplasm Exchange***. Different countries have varying quarantine policies which have been placed on seed import or exports. These policies generally take into account the region of seed origin and more severe restrictions have been


**Fig. 5. Areas needed for future collection of *Arachis* germplasm (Valls *et al.*, 1985; IBPGR, 1990; Simpson, unpubl., 1994). Dotted lines are areas virtually untouched by *Arachis* exploration teams, solid lines are areas which have been collected but should yield valuable *Arachis* germplasm with additional exploration. 1. Eastern Peru, southern Colombia, and western Brazil for cultivated landraces. 2. Central Amazon basin in north Brazil for cultivated landraces. 3. Eastern Bolivia, west half of Paraguay, and northern Argentina for wild *Arachis* species. 4. Western Ecuador for cultivated landraces. 5. Southeastern Peru and northwest Bolivia for cultivated landraces. 6. Mato Grosso of western Brazil for wild *Arachis* species. 7. Northeastern Brazil for wild *Arachis* species. 8. East-central Brazil for additional accessions of *A. pintoi*. 9. Eastern Argentina, southwest Brazil, and western Uruguay for *A. villosa* and cultivated landraces of *A. hypogaea* var. *vulgaris*.**

imposed on seeds from countries with unique disease, virus or insect problems—for example, rosette virus regions of Africa. However, several countries have highly restrictive quarantines which place all imported seeds into 1- to 2-year observation greenhouses, possibly leading to mixtures and germplasm loss. Peanut seeds imported to the U.S. are visually inspected for insects and disease pathogens, and occasionally plants are grown to detect virus symptoms; but only since the mid-1980s has routine screening for a virus (peanut stripe, PtSV) been employed using bioassays on materials from the Asian countries. The USDA plant introduction station has a policy to observe seed lots from problem areas more closely than from "pathogen-free" regions. U.S. quarantine laws are

**Table 3. Major germplasm collections of *Arachis* (abstracted from Bettencourt *et al.*, 1989; Singh *et al.*, 1992; Stalker, unpubl. data, 1993).**

| Location | Origin of *A. hypogaea*[a] | | | | | | *Arachis* spec. acc. |
|---|---|---|---|---|---|---|---|
| | S.A. | Afr. | Asia | N./Cen.A. | Misc. | Total | |
| | *ca.* no. | | | | | | No. |
| **North America** | | | | | | | |
| INIFAT, Cuba | | | | | | 273 | |
| NSSL, Fort Collins, USA | | | | | | 4229 | |
| USDA, Griffin, USA | 1641 | 2526 | 960 | 238 | 547 | 7432 | 498 |
| Texas A&M, USA | 2750 | 240 | 106 | 130 | 337 | 3563 | 798 |
| NCSU, USA | 1011 | 814 | 98 | 1601 | 5 | 3524 | 275 |
| **South America** | | | | | | | |
| EAA, INTA, Argentina | 1924 | | | | 276 | 2200 | |
| Campinas & CENARGEN, Brazil | 1300 | | | | | 1300 | 450 |
| ICA, Columbia | 68 | | | | 81 | 149 | |
| UNA, Peru | 100 | | | | | 100 | |
| CENIAP, Venezuela | | 35 | 18 | | | 587 | |
| **Africa** | | | | | | | |
| PGRI, Ghana | 25 | | | | | 101 | |
| INAA, Morocco | | | | | | 159 | |
| New Guinea | | | | | | 145 | |
| ISRA, CNRA, Senegal | | | | | | 900 | |
| DRA, Togo | | | | | | 49 | |
| DA, Uganda | | | | | | 900 | |
| **Asia** | | | | | | | |
| BARI, Bangladesh | | | | | | 225 | |
| IGBAC, Israel | | | | | | 200 | |
| ICAR & Nat. Res. Ctr. for Groundnut, India | | | | | | 6299 | 10 |
| ICRISAT, India | 1661 | 3179 | 7076 | 1259 | | 13460 | 195 |
| BORIF, Indonesia | | | | | | 1730 | |
| MARDI, Malaysia | | | 273 | | | 273 | |
| NPGRL, IPB, UPLB, Philippines | | | | | | 753 | |
| **Australia** | | | | | | | |
| Div. Plant Ind., Australia | | | | | | 51 | 11 |
| **Europe** | | | | | | | |
| IPPQ, Hungary | | | | | 260 | | |

[a]Information concerning the origin of accessions of many collections is unavailable, so only total numbers are recorded.

not so restrictive as to hinder movement of germplasm within the U.S. or internationally.

***Property Rights***. As the international community enacts property right laws to protect ownership of elite cultivars or even basic genetic resources, the potential for restricting germplasm movement between countries (or between research locations within the U.S.) is very great. Few lines thus far have been patented, but increasing pressures from administrators to obtain revenues from royalty receipts have occurred during recent years.

## Wild Species of *Arachis*

The native habitats of wild *Arachis* species are highly varied—ranging from semi-arid and almost desert conditions (during the dry season) of the northeast region of Brazil; to the tropical rain forest in the Amazon drainage basin; to humic swamps of the Gran Pantanal of western Mato Grosso, Brazil. *Arachis pintoi* has been collected at several locations in running water, with flowers and fruits developing under the water's surface. *Arachis prostrata* is usually found in schist outcrops with little soil present, and plants have been observed growing in tree-leaf residue between bare rocks and pegging between others. Wild *Arachis* accessions have been collected in course sand with almost no water-holding capacity in western Mato Grosso, Brazil, near Lagunillas, Bolivia, and in other areas. In contrast, the section *Rhizomatosae* species *A. burkartii* Handro has been collected from southern Brazil in black humic clay which is laced with small stones and has a soil pH of 3.2.

More than 35 plant exploration trips have been conducted to obtain *Arachis* species during the past 40 years, and at least 34 individuals have been involved in these germplasm acquisitions. During the mid-1970s, approximately 120 accessions were maintained in germplasm nurseries. Extensive collection efforts since then have been possible through funding from the USDA, IBPGR, ICRISAT, and CENARGEN/EMBRAPA (Fig. 6). The number of accessions


**Fig. 6. Areas of South America for which *Arachis* germplasm collections have been made since 1976 (updated from Simpson, 1984; Simpson, unpubl., 1994).**

maintained in the U.S. and Brazil now number more than 1000 (Stalker unpubl. data, 1993). Of these, 777 *Arachis* species accessions have been introduced into the U.S. and maintained by the USDA at Griffin, GA; Texas A&M University, Stephenville; or North Carolina State University, Raleigh. Many of the other 246 accessions are maintained by CENARGEN in Brazilia, Brazil, which has been designated as a repository for wild *Arachis* species.

To promote continued and systematic field collection efforts, priorities were outlined by Valls *et al.* (1985) and by Simpson (IBPGR, 1990) based on areas where (a) *Arachis* species are believed to exist, but no accessions are available in germplasm nurseries; (b) previously acquired germplasm no longer exists in living collections; and (c) civilization is rapidly spreading into native habitats where *Arachis* grow. The highest priority areas for future collecting include the Mato Grosso and Mato Grosso do Sul states of Brazil plus most of Paraguay (Fig. 5.). Areas of equal priority include Bolivia (especially in the areas where *A. hypogaea* may have originated) and northern Argentina. Simpson (1982) estimated that only 55 to 65% of the potential number of species existing in South America had been collected by the early 1980s, and we now believe the number to have been increased to 75-85%.

***Maintenance of* Arachis *Species***. Preserving wild *Arachis* accessions in germplasm nurseries, either in the greenhouse or field, is difficult even under the best of culturing conditions. Approximately 28% of the 1023 accessions currently maintained in either the U.S. or Brazil are propagated as vegetative plants because of poor or nonexistent seed set. Among this group are all accessions of section *Rhizomatosae*. Additionally, about 23% of the collection has fewer than 50 seeds in storage at the three major *Arachis* germplasm sites in the U.S., and these materials also are being propagated vegetatively. In general, perennial species can be maintained for many years as original plants or cuttings in greenhouse pots. However, greenhouse-grown plants must continuously be observed and separated because most peanut species have long branches with reproductive nodes, and extreme caution must be used to prevent seeding into adjacent containers.

For most annual species and many perennials, sufficiently large numbers of seeds are produced in plant nurseries to maintain accessions through seed propagation. Initial seed increases from South American introductions have all been conducted in the greenhouse, and only limited numbers of seeds have been produced for subsequent distribution. After primary quarantine, and when sufficient numbers of seeds have been obtained for field plantings, space isolation is critical for maintaining genetic purity. Avoiding cross-pollination with accessions in the same or different species is always necessary, but most important when bee populations are present around and in nurseries. Several species of sections *Arachis, Erectoides*, and *Procumbentes* are especially likely to outcross with other taxa within sections. The field nursery system used at NCSU is to transplant seedlings into small blocks consisting of short rows. Because seeds may remain dormant for many years, nurseries are only planted in soils which have not been previously planted with wild peanut species or in fields which have been fumigated with methyl bromide prior to planting. A

minimum distance of 5 m separates adjacent plots in all directions to restrict both outcrossing and pegging into other plots. Further, accessions which will not hybridize (i.e., members of different sections) are planted in adjacent plots in the same and different rows. Plants are grown in sandy soils because the pegs become fragile as seeds mature, and soil must be sifted to recover pods. Much the same system is used in field plots at Texas A&M University, except for the use of methyl bromide which has restricted use in Texas because of soil conditions.

*Arachis* species produce significantly different numbers of seeds per plant at different locations and from year to year. In general, more seeds are produced in field plots than in greenhouses, and for many accessions no pegs have ever been observed while plants were grown under greenhouse conditions. Because seed increases are labor-intensive and require a large amount of field space in sandy soils, few researchers produce seeds for general distribution.

The *Arachis* species occupy an array of different habitats in South America, many of which are highly specialized. Thus, many accessions have been lost during the first few years after they were collected and before adequate propagation conditions could be determined. Species which are most difficult to maintain are those with weak reproductive systems (as opposed to rhizomes or tuberous roots) and do not produce seeds under cultivated conditions. *Arachis marginata* Gard. and most other species of section *Extranervosae* are very difficult to maintain because U.S. plantings grow slowly and are weak. Seed reproduction does not always guarantee species survival, even when standard germplasm procedures are used to maintain an accession. For example, seeds of *A. tuberosa* Benth. and *A. guaranitica* enter a permanent dormancy upon drying, which prevents long-term seed storage (W. C. Gregory, pers. comm., 1978). However, seeds of *A. tuberosa* have been stored for more than 20 months in moist sphagnum moss at room temperature and then germinated (Simpson, unpubl. data, 1983). Environmental influences such as day length and light quality can have significant effects on reproductive development in peanut. Several peanut species are day-neutral and many others produce large numbers of flowers during the summer months under long-day conditions, but very few seeds. Under short-day conditions many species produce very few to no flowers, but most of these flowers self-pollinate and set pegs (Stalker and Wynne, 1983). Thus, compromises must be made to ensure sufficient numbers of flowers to obtain seeds while growing plants at a time of year when reproductive efficiency is relatively high. Flowering peaks have often been observed on several wild species at the 12-hour day lengths at the vernal and autumnal equinox.

Although seed propagation on an annual or semi-annual basis may be necessary to insure adequate seed recovery to conduct replicated experiments, longer term storage is desirable to avoid significant shifts in gene frequencies in the plant population. Large numbers of seeds have been obtained for several species (i.e., *A. duranensis* Krapov. and W.C. Gregory and *A. batizocoi* Krapov. and W.C. Gregory), but for many accessions, the numbers of seeds available remains relatively small.

***Seed Distribution***. Seed distribution and quarantine of *Arachis* species generally follows the same pattern as for the cultivated species. The number of

seeds acquired during collection expeditions to South America has varied greatly with the time of year and plant habit of individual species; obtaining fewer than 25 seeds is common at many collection sites. If collections are made before the annual rains begin, then plants are extremely difficult to find because stems and leaves are dried or decomposed; however, seeds are usually plentiful and easier to harvest when a site can be identified. After the spring rains begin, most of the seeds germinate and plants are easier to find, especially at flowering, but very few viable seeds remain in the soil to be collected. Later in the growing season, nearer the time of seed maturity, would be more optimal for collecting *Arachis*; however, many areas are flooded in regions where wild peanuts grow and transport on poor roads can be extremely difficult or impossible. After collections are made the seed lots are routinely divided between the countries of origin and those countries represented on expeditions. As a result, initial seed increases tend to be from only a few plants and several years may be needed to obtain adequate numbers of seeds for distribution.

Live plants have also been collected during plant explorations when seeds could not be harvested at the original site and then transported to the U.S. Seeds have been harvested from some of these plants, but many have been maintained continuously as vegetative materials. Distribution of vegetative cuttings among research locations has taken significantly longer than for accessions propagated by seeds because of quarantines imposed to assure disease- and insect-free plants. Many of the accessions propagated vegetatively have not been transferred to ICRISAT because they cannot clear their quarantine procedures.

## EVOLUTIONARY TRENDS IN *ARACHIS*

### *Arachis* Species

Peanuts evolved in highland areas of central Brazil (Gregory *et al.*, 1980), and the most ancient species in the genus should have adaptations to relatively harsh, dry environments. Peanut species fitting into this group are those with a perennial growth habit, tuberform hypocotyls, tuberous roots and/or rhizomes. Only two section *Trierectoides* species are known which have trifoliolate leaves (*A. guaranitica* and *A. tuberosa*), and three leaflets on plants could be considered a primitive characteristic for the genus. Traits indicative of more advanced evolution would have adaptations to more lowland areas, such as annual habit, fibrous root systems, and reproductive systems adapted to moister environments (Table 4). Evolutionary trends in the genus were presented by Gregory and Gregory (1979) and Gregory *et al.* (1980) who attempted to synthesize morphological, geographical and crossing data into an evolutionary scheme for the genus. Smartt (1990) also made an extended summary of evolutionary trends in *Arachis*.

***Species Diversity.*** Most species of *Arachis* are diploid ($2n=2x=20$), but tetraploids ($2n=4x=40$) are found in sections *Arachis* and *Rhizomatosae*. Tetraploid species are believed to have evolved independently in the two sections (Smartt and Stalker, 1982). The diploid condition is believed to be the more ancient characteristic and polyploidy more advanced.

**Table 4. Evolution of *Arachis* and domesticated peanuts, *A. hypogaea*.**

| More primitive trait | Group | More advanced trait | Group |
|---|---|---|---|
| **Genus—general** | | | |
| Trifoliate leaves | Sect. *Trierectoides* | Tetrafoliate leaves | |
| Diploid | | Tetraploid | |
| Perennial | | Annual | |
| Tuberiform hypocotyl | Sects. *Erectoides*, *Trierectoides* | Nontuberiform hypocotyl | |
| Tuberous roots | Sect. *Extranervosae* | Fibrous roots | |
| No rhizomes | | Rhizomes | Sect. *Rhizomatosae* |
| Symmetrical karyotype | Most sect. *Arachis* | Asymmetrical karyotype | *A. batizocoi*, *A. glandulifera* |
| **Domestication** | | | |
| Weak peg | Wild species | Stronger peg | *A. hypogaea* |
| Long peg | Wild species | Short peg | *A. hypogaea* |
| Long hypanthium | Wild species | Shorter hypanthium | *A. hypogaea* |
| Prostrate growth | Wild species | Upright growth | *A. hypogaea* |
| Long branches | Wild species | Shorter branches | *A. hypogaea* |
| Long internode between seeds | Wild species | Pod/peg internode suppressed | *A. hypogaea* |
| ***A. hypogaea*** | | | |
| Alternating inflorescences | Subsp. *hypogaea* | Sequential inflorescences | Subsp. *fastigiata* |
| Mainstem w/o flowers | Subsp. *hypogaea* | Mainstem with flowers | Subsp. *fastigiata* |
| Simple (unbranched) | Var. *fastigiata* | Compound inflorescence | Var. *vulgaris* |
| Prostrate habit | Var. *hirsuta* | More upright | Var. *hypogaea* |
| | | Very upright | Subsp. *fastigiata* |
| Late maturing | Subsp. *hypogaea*, esp. var. *hirsuta* | Early maturing | Subsp. *fastigiata* |
| Very hairy | Var. *hirsuta* | Less hairy | Var. *hypogaea* |
| | Var. *aequatoriana* | | Var. *peruviana* |
| 2-seeded pods | Var. *hypogaea* | 2+ seeds/pod | Var. *hirsuta* |
| | Var. *vulgaris* | 4-seeded pods | Var. *fastigiata* |
| Pod beak | | Beak absent | |
| Small seeds | Var. *vulgaris*, some var. *hypogaea* | Large seeds | Some var. *hypogaea* |
| Long lateral branches | Var. *hypogaea* —runners | Shorter branches | Subsp. *fastigiata* |
| Long dormancy | Var. *hypogaea* | Short dormancy | Subsp. *fastigiata* |

The chromosomes of *Arachis* species are small, ranging from 1.4 to 3.9 μm in length. Somatic karyotype studies of *Arachis* species have been limited to fewer than 20 accessions and mostly in section *Arachis* (Stalker and Dalmacio, 1981; Singh and Moss, 1982; Stalker, 1991). Species in this section generally have a symmetrical genome and one distinctively small chromosome pair. The two known exceptions are *A. batizocoi* and *A. glandulifera* Stalker which have asymmetrical and highly asymmetrical genomes, respectively (Stalker, 1991; Stalker *et al.*, 1991a). Principal component analysis of chromosome arm ratios using section *Arachis* species clearly differentiates taxa into three groups: (a) most diploid species, (b) *A. batizocoi*, and (c) *A. glandulifera* (Stalker *et al.*,

1991a). Cytological analyses also have indicated that at least three translocations are present in *A. batizocoi*, with all three present in accession GKBSPSc 30080 (Stalker *et al.*, 1991a). Several translocations have been observed in *A. duranensis* (Stalker, unpubl. data, 1993), and chromosomal rearrangements have occurred in the cultivated species *A. hypogaea* (Stalker and Dalmacio, 1986). Based on Giemsa C-banding *Arachis* chromosomes, Cai *et al.* (1987) also concluded that even chromosomes which are morphologically similar have structural differences.

Studies of pachytene chromosomes (Murty *et al.*, 1982, 1985; Bharathi *et al.*, 1983; Kirti *et al.*, 1983; Jahnavi and Murty, 1985) have indicated that genomes in the genus are comprised of six differentiated chromosomes, one chromosome with a nucleolus organizer region, and three specialized chromosomes (with heterochromatic short arms). Each chromosome has heterochromatic regions on each side of the centromere and are mostly euchromatic distal to the centromere. The collective analyses of the above authors have indicated that species in sections *Erectoides*, *Extranervosae*, and *Triseminatae* are more ancient than species in sections *Arachis* or *Rhizomatosae*. Further, similarities exist in chromosome morphology between species of section *Erectoides* and both sections *Arachis* and *Rhizomatosae*—which also corresponds to chromosome pairing analyses reported by Stalker (1981, 1985).

Molecular studies have indicated that large amounts of genetic variation exist among species of *Arachis*. Kochert *et al.* (1991) and Paik-Ro *et al.* (1992) analyzed accessions in section *Arachis* using DNA restriction fragment length polymorphisms (RFLPs) and then used cluster analyses to group accessions. Tetraploids clearly separated from diploids, and their molecular data generally corresponded with species groups based on cluster analysis using plant morphological traits (Stalker, 1990). Also, the RFLP data closely paired *A. spegazzinii* W.C. Gregory and M.P. Gregory *nom. nud.* (GKP 10038 = *A. duranensis*—see Table 2) with *A. duranensis*, which supports the classification of Krapovickas and Gregory (1994) who grouped the taxa into one species, *A. duranensis*. DNA analyses using randomly amplified DNAs (RAPDs) showed very similar results as RFLPs (Halward *et al.*, 1991, 1992; Lanham *et al.*, 1992). Because a large number of polymorphic molecular markers are present among the *Arachis* species, Halward *et al.* (1993) were able to construct a RFLP map by using progenies of an *A. stenosperma* x *A. cardenasii* Krapov. and W.C. Gregory cross. This map shows 11 linkage groups which will be reduced to 10 after additional markers are analyzed.

Seed storage protein analyses have shown significant variation among species of section *Arachis* (Singh *et al.*, 1991a; Bianchi-Hall *et al.*, 1993), but proteins are not easily used for identifying individual species. On the other hand, isozymes cluster accessions into sectional and species groups very similar to expectations (Lu and Pickersgill, 1993; Stalker *et al.*, 1994). In a study using 113 accessions and 17 isozyme systems, Stalker *et al.* (1994) found variation both between and within species of the genus. Species in different sections generally grouped together, but *Erectoides* species were more variable and taxa appeared to associate with species in several sections. Krapovickas and Gregory (1994) have since divided *Erectoides* into three sections (*Trierectoides*, *Erectoides*, and *Procumbentes*) which may account for much of the sectional variation. When

the analysis was restricted to section *Arachis* species, accessions within a species generally clustered together. Unexpectedly, all *A. batizocoi* accessions grouped apart from other species in the genus and distantly from section *Arachis* (Stalker *et al.*, 1994). In addition to isozyme variation separating species, seed-to-seed variation within accessions has been observed (Stalker *et al.*, 1994). This either indicates that more intra-accession variability exists in natural populations than would be expected in self-pollinating diploid species or that outcrossing has occurred in field nurseries. However, they found no differences in the number of variable accessions when a comparison was made between materials collected during the late 1950s and early 1960s versus more recently acquired accessions during the 1980s. Regardless of the origin of genetic variation within species accessions, several species are now being maintained as highly polymorphic populations in *Arachis* germplasm collections.

The center of genetic diversity in *Arachis* is the Mato Grosso, Brazil into eastern Bolivia (Stalker *et al.*, 1994). However, the greatest probability of finding alleles in *Arachis* species unique from those present in *A. hypogaea* is in the north-central, northeast, south, and southeast regions of Brazil. Species of sections which are distantly removed from both *A. hypogaea* and diploid section *Arachis* species (i.e., they will not hybridize) are found in these regions.

***Evolution of Genomes***. Producing interspecific hybrids among species within a section is not always easily accomplished and is significantly more difficult between taxa of different sections. Gregory and Gregory (1979) presented results from a hybridization program in which 100 *Arachis* accessions were used to evaluate biosystematic relationships in the genus. They found that most hybrids between species in the same section were semifertile, whereas intersectional hybrids were always completely sterile. Amphiploids of species in section *Erectoides* were used to hybridize with diploids of section *Arachis* and chromosome homologies reported between the two groups (Stalker, 1981). Analyses of hybrids between diploids or amphiploids of section *Erectoides* and tetraploid *Rhizomatosae* species also indicated intersectional homologies (Stalker, 1985). Even though intersectional hybridization is possible, plants derived from such crosses are believed to be genetic dead-ends for cultivar improvement because of very high sterility levels and difficulties encountered in restoration of fertility (Stalker, 1981, 1985).

Interspecific hybrids among species within section *Arachis* range from plants which are completely sterile to others which produce many selfed seeds. Fertility levels vary among the species and sometimes among accessions of a single species used in crosses. When *A. batizocoi* or *A. glandulifera* are crossed with other section *Arachis* species, the hybrids are sterile (Stalker and Moss, 1987; Simpson, 1991; Stalker *et al.*, 1991b). However, six to eight chromosomes consistently pair during meiosis in these hybrids, which indicates that a significant amount of chromosome homology exists. Thus, the designations of A, B and D genomes do not represent complete differentiation of chromosome sets.

Hybrids among most A-genome diploids of section *Arachis* have moderate to high male fertility levels, and meiotic chromosomes usually pair as 10 bivalents (Stalker and Moss, 1987; Stalker *et al.*, 1991b). An exception is the cross *A. duranensis* x *A. valida* Krapov. and W.C. Gregory (GK 30011) which

has many univalents and a low chiasmata frequency. More than three genomes (or subgenomes) may thus exist in the section (Stalker *et al.*, 1991b). Intraspecific hybrids are usually fertile, for example, crosses among *A. batizocoi* accessions have greater than 90% pollen stained even though translocations are present in several genotypes (Stalker *et al.*, 1991a). On the other hand, crosses among several *A. duranensis* accessions result in semisterile to sterile progenies (Stalker and Simpson, unpubl. data, 1993).

Stalker (1985) reported that *A. rigonii* Krapov. and W.C. Gregory x A. *paraguariensis* Chod. et. Hassl. hybrids have several nonhomologous chromosomes, but chromosome pairing relationships of few other hybrids among diploids outside section *Arachis* have been reported. Thus, a significant amount of cytological analysis will be needed to resolve species relationships in the genus. The tetraploid species of *Arachis* also create biosystematic problems which must be resolved. For example, based on cross-compatibility data, Smartt and Stalker (1982) proposed that tetraploid *Rhizomatosae* species have one genome in common with the section *Erectoides* and one more closely related to section *Arachis*, but cytological confirmation is still lacking. Additional biosystematic work is needed to sort differences at both the specific and subspecific levels in the genus and to verify the 11 genomic groups proposed by Smartt and Stalker (1982) and Stalker (1991).

***Arachis hypogaea***

Selection within *A. hypogaea* has produced many distinctive morphological types, and patterns of evolution have paralleled most other domesticated species. Evolution of *A. hypogaea* has occurred as a two-step process whereby (a) a new species was formed during domestication at which time "wild" characteristics were selected against and (b) many diverse types were preserved as selection pressures changed.

***Domestication and Evolution of* A. hypogaea**. Morphological alterations to the peanut plant during domestication are analogous to changes found in most other crops which favor mutations to increase seed size, yields and ease of harvesting. Only a few major genetic changes are necessary to transform a wild plant into a domesticated species (which can no longer survive in native habitats without the aid of man) (Table 4). In peanut, these plant alterations included (a) shortening and strengthening of pegs to retain pods during harvest (this also greatly limits seed dispersal and would cause intensive competition among offspring); (b) suppression of meristems between seeds on a single peg or pod, again allowing greater seed recovery and limiting dispersal; (c) selecting a more upright growth habit and shorter branches, which allowed easier harvesting; (d) selecting nondormant types, to induce better plant stands during cultivation; and (e) increasing seed size.

*Arachis hypogaea* is believed to be an allotetraploid species, in large part based on karyotypic data which show only one distinctively small chromosome pair in somatic cells and diploid-like chromosome pairing (most meiotic cells with 20 bivalents) during meiosis. This conclusion has been supported recently by RFLP analyses in which two bands are found in gel lanes when tetraploids are used, but only one band is observed for diploids (Kochert *et al.*, 1991). The

early cytological data also led Smartt and Gregory (1967) to conclude that *A. hypogaea* has both 'A' and 'B' genomes. Accumulated molecular data indicate that either *A. hypogaea* originated from a single cross and was domesticated only once, or the species has encountered a very severe genetic bottleneck during its early evolution (Kochert *et al.*, 1995). Further, introgression from closely related wild species of *Arachis* has been extremely rare or nonexistent during the hundreds of generations since domestication in South America.

The domesticated peanut is in section *Arachis* based on taxonomic rules. Cross-compatibility relationships and morphological similarities have placed numerous other species in this section (Table 2), and the logical conclusion is that two taxa in this group were the ancestral species of *A. hypogaea*. Because most species of section *Arachis* are diploids and the domesticated peanut is a tetraploid, *A. hypogaea* must have either evolved directly from an interspecific cross between two diploids (Husted, 1936) or from a pre-existing wild polyploid (Smartt and Gregory, 1967). The only other tetraploid member of section *Arachis* is *A. monticola*, and the alternatives are that (a) *A. monticola* is the direct progenitor species of *A. hypogaea*, (b) it is a weedy derivative from a cultivated type, or (c) it had independently evolved from the same progenitor species (an unlikely event). In part because *A. monticola* is cytologically most similar to var. *vulgaris* cultivars (Stalker and Dalmacio, 1986), which are more advanced evolutionary than other peanut varieties, the authors believe the most probable evolutionary path is that *A. monticola* is a weedy taxa derived from the domesticated peanut.

At least six A-genome species—including *A. cardenasii*, *A. chacoensis* Krapov., and W.C. Gregory *nom. nud.* (= *A. diogoi* Krapov. and W.C. Gregory), *A. correntina* (Burk.) Krapov. and W.C. Gregory, *A. duranensis*, *A. ipaensis* Krapov. and W.C. Gregory, and *A. villosa* Benth.—and one B-genome species, *A. batizocoi*, have been proposed as progenitors of *A. hypogaea* (for review, see Murty and Jahnavi, 1986; Stalker and Moss, 1987; Kochert *et al.*, 1991). Although *A. batizocoi* is the only known B-genome species, molecular evidence from RFLPs (Kochert *et al.* 1991); DNA polymerase chain reactions (PCRs) (Halward *et al.*, 1991); isozymes (Lu and Pickersgill, 1993; Stalker *et al.*, 1994); and seed storage proteins (Bianchi-Hall *et al.*, 1993) have all indicated that this species is not a progenitor of the domesticated peanut. On the other hand, interspecific hybrids between *A. hypogaea* and amphiploids with an A-B genome are more fertile than ones with A-A genomic groups (Simpson, 1991; Singh *et al.*, 1991b). Chloroplast DNA studies (K. Hilu, pers. comm., 1992) further indicate that *A. batizocoi* is not the female parent of *A. hypogaea*—if it is indeed a parent of the domesticated peanut—and, secondly, that the most likely female genome donor is *A. duranensis*. Although the diploid progenitor species have not been positively identified, the current evidence indicates that *A. hypogaea* originated from two closely related species with similar genomes, thus making it a segmental allopolyploid with $A_1$ and $A_2$ genomes.

Hybrids between *A. hypogaea* and diploid species of section *Arachis* have 4-12 bivalents and 0-4 multivalents (Singh and Moss, 1984; Singh, 1985). The assumption is that bivalents result from chromosome pairing of wild species with *A. hypogaea* chromosome pairing, but preferential pairing among the

domesticated species chromosomes is also possible. After colchicine-treating triploid hybrids to restore fertility at the hexaploid level, the expectation is to observe 30 bivalents (or possibly a few multivalents) in meiotic cells because each chromosome has a homolog. However, in 60-chromosome hybrids of *A. hypogaea* x *A. cardenasii* or *A. hypogaea* x *A. chacoensis* (= *A. diogoi*), up to 32 univalents have been observed (Spielman *et al.*, 1979; Company *et al.*, 1982). Thus, genetic regulators controlling chromosome pairing are believed to be present in *Arachis*. Hexaploids are generally semisterile and many plants do not produce seeds, however, they are usually stable at the 60-chromosome level. If a 60-chromosome hybrid becomes cytologically unstable, then chromosomes are lost and progenies are obtained after one or more (usually more) selfing generations near the tetraploid level. A highly variable population of an *A. hypogaea* x *A. cardenasii* hybrid is believed to have originated by this route (Stalker *et al.*, 1979).

***Variation Within* A. hypogaea**. Many morphological alterations in phenotype were selected after the species was domesticated which transformed *A. hypogaea* into a highly variable array of morphological types. Several of the most obvious mutants are seed size, shape and coloration, plant height, and growth habit. These and other traits probably have been continuously altered since the early days after domestication. The modern plant breeder produces hybrids artificially and then makes selections to produce elite cultivars. The South American farmer, on the other hand, saves both specific characteristics which are pleasing to him and selections better adapted to his individual cultural system and environment. For example, people in eastern Bolivia grow peanuts on river sandbars and have selected types without seed dormancy (so plants quickly become established), a very short time to maturity (to avoid floods), upright habit (to avoid burying plants by blowing sand), and very strong pegs (to keep pods attached to the plant during harvest when they are manually pulled out of the sand) (Williams, 1989).

Cytological differentiation has been reported in meiotic cells of cultivars belonging to different subspecies (seen as univalents in hybrids) (Stalker, 1985) and in somatic cells (seen as different karyotypes of cultivars belonging to three botanical varieties) (Stalker and Dalmacio, 1986). Only 15 of the 20 *A. hypogaea* somatic chromosomes can be differentiated easily. Secondary constrictions have been observed on five different chromosomes in cultivars of varieties *hypogaea*, *fastigiata*, and *vulgaris* (Stalker and Dalmacio, 1986). This indicates that translocations may be relatively common in *A. hypogaea*. Wynne (1974) and Krapovickas (1969) also reported genetic differences between subspecies based on mutant types and lower fertility levels in hybrid progenies.

Molecular evidence indicates that *A. monticola* is nearly indistinguishable genetically from *A. hypogaea*. Analyses of isozymes (Grieshammer and Wynne, 1990; Lacks and Stalker, 1993), RFLPs (Kochert *et al.*, 1991), and RAPDs (Halward *et al.*, 1992) also indicate that little differentiation exists genetically within the cultivated peanut or *A. monticola*. This differentiation is about 5% of the genome based on the work of Kochert and coworkers. Grieshammer and Wynne (1990) and Lacks and Stalker (1993) found only three of 25 isozymes polymorphic among an array of peanut cultivars and plant introductions. Seed

storage proteins appear to be more variable than isozyme or DNA markers (Bianchi-Hall, 1992); however, even though some grouping of cultivars is possible, proteins cannot be used for positive cultivar identification. This problem is complicated by having both subsp. *hypogaea* and *fastigiata* in the pedigrees of most U.S. cultivars. A molecular map derived solely from the cultivated genome will be very difficult to develop using available molecular markers.

## INTERSPECIFIC HYBRIDIZATION BARRIERS IN THE GENUS

Barriers encountered when attempting to produce interspecific peanut hybrids range from complete cross-incompatibility to a low (usually less than 5%) success rate. Factors such as day and/or night temperatures, day length, water stress, humidity, soil fertility levels and other more obscure environmental conditions can alter success rates. Annuals are usually more successful female parents than perennials; and *A. hypogaea*, generally, but not always, is the better female parent. Although producing hybrids in either female-male combination places the genomes from two species within a single cell, if cytoplasmic effects are present, then reciprocal hybrids may also be desirable. In section *Arachis*, attempts to increase frequencies and fertility of hybrids between diploid species and *A. hypogaea* have been attempted with varying success rates by doubling the ploidy level of diploid accessions to produce autoploids or amphiploids (Gardner and Stalker, 1983; Singh, 1986a,b; see Singh *et al.*, 1991b and Stalker, 1992 for reviews). Significant progress has been made to recover many interspecific hybrid combinations during recent years, but major obstacles still prevent crossing most species in different sections of the genus.

Several studies indicate that both pre- and post-fertilization barriers exist which hinder cross-compatibility. Murty *et al.* (1980) and Pattee and Stalker (1992a) reported delayed fertilization of *A. hypogaea* crosses as a major cause of reduced hybridization success. Lu *et al.* (1990) reported that the stigmatic surfaces of annual and perennial species may be different, with annuals having a more filamous stigma and perennials having short, more globular trichomes to which pollen has difficulty adhering. Thus, perennials may be poor pollen receptors. Sastri and Moss (1982) reported that foreign pollen may germinate and then form callus plugs in styler tissues and thus restrict fertilization, but this type of barrier is believed to be incomplete because a few pollen tubes can still reach the egg.

After fertilization, embryo development in peanut is complex and under photo- (Zamski and Ziv, 1976; Thompson *et al.*, 1985), hormonal, and perhaps other control mechanisms (Shushu and Cutter, 1990). Hormone treatments (such as gibberellic acid) may enhance fertilization, but at the same time it inhibits embryo development (Stalker *et al.*, 1987). A combination of auxins and cytokinins applied to the peg a few days after fertilization apparently promotes embryo growth (Sastri and Moss, 1982; Mallikarjuna and Sastri, 1985). In addition to *in vivo* methodology, embryo rescue techniques have been applied

to recover several interspecific peanut hybrids (Sastri and Moss, 1982; Stalker and Eweda, 1988; Mallikarjuna *et al.*, 1992; Ozias-Akins *et al.*, 1992).

In studies of embryo development of interspecific hybrids, Johansen and Smith (1956), Halward and Stalker (1987), Pattee and Stalker (1992a,b), and Tallury (1994) found that abortion may occur before peg elongation, after the peg initiates growth, or during later developmental stages. During normal developmental processes, the peanut proembryo begins to actively divide within a short time after fertilization, but then goes into a quiescent phase as the peg elongates (when the proembryo has eight to 16 cells). After soil penetration, the peg stops elongating and the viable proembryo reinitiates growth and develops into a mature seed. However, most hybrid proembryos observed by the above authors aborted at or before the 16-cell stage. In other aborting hybrids, cell division never starts again and the proembryo eventually dies. A third critical time for onset of abortion is at the time of embryo differentiation from a globular to a heart stage. This stage is critical for embryo recovery because heart-shaped embryos can be rescued *in vitro*, whereas globular embryos are much more difficult, and many times impossible, to rescue in culture (Sastri and Moss, 1982; Stalker and Eweda, 1988; Ozias-Akins *et al.*, 1992). Hybrid embryos which reach the heart or cotyledonary stage will usually develop into a viable seed. Exceptions are known, however, for example, *A. hypogaea* x *A. glandulifera* crosses.

After the embryo reaches physiological maturity several barriers may still restrict hybrid development. Some crosses have a prolonged dormancy period—for example, *A. hypogaea* x *A. monticola*—whereas other hybrid seeds will not break dormancy until several years after harvest regardless of the chemical or physical treatments used to induce germination. One hybrid—*A. batizocoi* x *A. praecox* Krapov., W.C. Gregory, and Valls—was dormant for a period of 32 months even with ethylene treatments at 30-day intervals (Simpson, unpubl. data, 1990). Conversely, pentaploid hybrids derived from backcrossing hexaploids ($2n=6x=60$) onto *A. hypogaea* tetraploids ($2n=4x=40$), all germinate prematurely (1 to 2 weeks prior to the normal harvest time of 55 to 60 days after pollination), and these hybrids must be maintained as plants in the greenhouse rather than seeds in storage. Many other interspecific hybrids at the diploid, triploid, or hexaploid chromosome levels have little seed dormancy and also may germinate prematurely, but hybrid seeds also are usually recovered at harvest time. Some interspecific peanut hybrids are weak and die at the seedling stage, while others develop into vigorous plants which do not produce flowers. When specific *A. hypogaea* genotypes (e.g., cvs. NC 4, Spantex, Tamnut 74, and Florunner) are crossed with *A. diogoi* (acc. GKP 10602, previously *A. chacoensis*), they exhibit virus-like symptoms and the plants are extremely weak. Other hybrids (e.g., cv. Argentine x *A. chacoensis*) are morphologically normal. Because the symptoms have been observed over several years and crossing programs, the cause is believed to be genetic rather than pathological. Smartt (1964) observed similar symptoms in *A. chacoensis* (= *A. diogoi*) crosses. The environment apparently plays some role in gene expression because many of these symptomatic plants will produce normal growth in the early spring for about 30 days after the vernal equinox.

Specialized techniques have been used in *Arachis* to recover interspecific

hybrids. *In vivo* hormone applications (Sastri and Moss, 1982; Mallikarjuna and Sastri, 1985; Stalker *et al.*, 1987) and *in vitro* embryo rescue (Sastri and Moss, 1982; Mallikarjuna and Sastri, 1985; Stalker and Eweda, 1988; Mallikarjuna *et al.*, 1992) have proven useful for rescuing otherwise incompatible interspecific hybrids. Some intersectional hybrids have been obtained between diploid species of several sections even without the aid of hormone applications or embryo rescue techniques (Gregory and Gregory, 1979). However, all hybrids are completely sterile. Directly hybridizing *A. hypogaea* with species outside section *Arachis* has been extremely difficult and only possible with the aid of *in vitro* techniques. Sastri and Moss (1982) reported an *A. monticola* x *A. glabrata* hybrid, and Mallikarjuna *et al.* (1992) reported an *A. hypogaea* x an unnamed section *Erectoides* species hybrid. However, all plants were completely sterile and the domesticated peanut is essentially isolated reproductively from species outside section *Arachis*. Using diploids as bridges between *A. hypogaea* and other *Arachis* species in more distantly related sections is not believed to be a practical plant breeding approach for crop improvement of peanut. Unless new and highly specialized techniques are developed, such as gene transformation, introgression to *A. hypogaea* from *Arachis* species outside of section *Arachis* will not be possible. Thus, the primary gene pool for the domesticated peanut consists of all accessions of *A. hypogaea* and *A. monticola* (lines are cross-compatible and produce fertile progenies). The secondary gene pool consists of diploid species in section *Arachis* (hybrids with *A. hypogaea* are sterile, but fertility can be restored after cytological manipulations). All other species of the genus are completely incompatible with the domesticated peanut and belong to the tertiary gene pool.

## GERMPLASM EVALUATION

Many *Arachis* cultivated and wild species collections have been evaluated for morphological traits, chemical composition, disease resistance and insect pest resistance. However, the effort is still in preliminary stages. Evaluation of the peanut germplasm has lagged behind many other crops because of a perception that peanut is a regional crop, few researchers are working in the area and funds are limited. Characterizing cultivated lines and wild species of *Arachis* for agronomically useful traits is currently a major part of most peanut breeding efforts in the U.S. Large-scale evaluations for resistance to diseases and insects, however, did not occur until the mid- to late 1970s. During this time period ICRISAT was given the mandate for peanut improvement and programs were concurrently initiated at several locations in the U.S. for developing disease- and insect-resistant cultivars. In addition, extensive efforts during recent years have been made to prepare catalogs of passport data as newly collected cultivated and wild species accessions have been introduced from South America (Simpson and Higgins, 1984; Simpson *et al.*, 1992).

### Descriptors and Morphological Traits

The USDA/ARS has developed a Germplasm Resources Information Network

(GRIN) system to compile passport data and lists of agronomically useful traits. Unfortunately, the massive task of collecting and entering data is in the rudimentary stages, and some of the *Arachis* information already in the system is incorrect (R. N. Pittman, pers. comm., 1993). The current status of the GRIN system can be illustrated by reviewing the types of data used by Holbrook *et al.* (1993) to establish a core collection for *A. hypogaea*. For their initial evaluations they used country of origin, plant type, pod type, seed size, testa color, number of seed per pod, and average seed weight for the 7432 accessions in the USDA collection. Only 1776 (23.9%) of the accessions had information for all six morphological traits, whereas no data were available for almost one-fifth of the collection (1597, 21.5%). A major effort will be needed to complete the GRIN data base for even a few traits. Fortunately, problems with the GRIN system have been recognized, and efforts are being made to add information, albeit at a painfully slow pace because of priority and funding constraints.

Because several market types are cultivated, and breeders prefer to use types better adapted to their location, the GRIN system will only become widely used when a large percentage of the *A. hypogaea* collection has been evaluated for important morphological and agronomic characteristics. In contrast, passport data have been entered for 11,400 *A. hypogaea* lines in the ICRISAT germplasm data base, and they represent the most comprehensive listings for the cultivated peanut (Moss *et al.*, 1989). Information exchange between ICRISAT and the USDA germplasm system would facilitate data entry and greatly increase the availability of data to users.

Lists of descriptors have been published for both *A. hypogaea* (IBPGR and ICRISAT, 1992) and wild *Arachis* species (IBPGR, 1990) to standardize the characters used to describe accessions. Although preparing a standard set of measurements is fundamentally a very good idea, funding has not been available to actually measure a large number of traits for a high percentage of the cultivated germplasm and then enter the information into data bases. However, some descriptor work has been accomplished (Veiga *et al.*, 1986; IBPGR and ICRISAT, 1992; Simpson *et al.*, 1992). Describing *A. hypogaea* lines is further complicated because many accessions in the USDA germplasm system were entered originally as seed mixtures, and establishing a single set of descriptors for all entries will be difficult.

**Disease Resistances**

At the forefront of evaluating *Arachis* genetic resources has been identifying sources of disease resistance for developing improved cultivars (Wynne *et al.*, 1991). In large part due to the efforts at ICRISAT, more than 9000 entries have been evaluated for resistance to peanut rust (*Puccinia arachidis*) and late leaf spot (*C. personatum*), two of the most important pathogens worldwide (Moss *et al.*, 1989; Singh *et al.*, 1992). Further, high levels of resistance have been identified in single cultivated lines for both diseases and they are currently being used as parents in breeding programs (Wynne *et al.*, 1991). A significant proportion of the U.S. germplasm collection has also been evaluated for *C. personatum*, and high levels of resistance have been identified (Anderson *et al.*, 1993). In addition to *A. hypogaea*, many of the *Arachis* species are resistant to

both pathogens (Table 5).

Although early leaf spot (*C. arachidicola*) is also a major leaf spot pathogen in many peanut production regions, it has been difficult to evaluate in many areas (Wynne *et al.*, 1991). Researchers at ICRISAT have identified many lines with resistance by conducting field evaluations in Malawi where high levels of natural inoculum are present. However, lines identified as resistant at one location are not always resistant at others (Wynne *et al.*, 1991), and pathotypes (or races) of *C. arachidicola* may be present in different production areas (Waliyar *et al.*, 1993). Foster *et al.* (1981) evaluated 15 "resistant" *A. hypogaea* genotypes to *C. arachidicola* with inoculum originating in North Carolina, and they found that most genotypes were moderately to highly susceptible. Very high levels of resistance have been reported for this pathogen in the *Arachis* species (Table 5), and germplasm releases have resulted from an *A. cardenasii* interspecific hybrid (Stalker and Beute, 1993). Other resistant germplasm has been released from the *A. cardenasii*, *A. diogoi* (GKP 10602, = *A. chacoensis*), *A. batizocoi* source(s) (Simpson *et al.*, 1993a). Evaluation results for resistance also appears to be inconsistent for *Arachis* species among different production regions, especially between Africa and the U.S. (Wynne *et al.*, 1991).

Cylindrocladium black rot has been a major peanut pathogen in the Virginia-North Carolina production area since the early 1970s. More than 1200 accessions have been evaluated, but only a few subsp. *hypogaea* and subsp. *fastigiata* var. *vulgaris* accessions have been identified as resistant (Wynne *et al.*, 1991). Several of these have been used successfully in breeding programs leading to improved cultivars, including NC 8C and NC 10C, which have moderate levels of disease resistance. Unfortunately, the genotypes with the highest levels of resistance have poor seed shape, and highly resistant cultivars are still unavailable. Although few wild peanut species have been evaluated for Cylindrocladium black rot resistance (Table 5), high levels of resistance have been found in section *Arachis*, including the tetraploid species *A. monticola* (Fitzner *et al.*, 1985).

Sclerotinia blight is caused by *Sclerotinia minor*, and is a major peanut pathogen in several production areas. Several plant introductions from China have been reported as resistant, and cv. VA 81B was released with resistance to this pathogen (Coffelt *et al.*, 1984). After evaluating several thousand germplasm lines, Smith *et al.* (1993) identified several highly resistant lines; virtually all of the lines have the resistance source of Tamspan 90, a Spanish cultivar released from Texas (Smith *et al.*, 1991). Several other soil-borne pathogens also attack peanuts, and sources of resistance have been identified for southern stem rot and pythium pod rots (Smith *et al.*, 1991; Wynne *et al.*, 1991).

Aflatoxin has been designated the most important problem in the peanut industry by the National Peanut Council and a large effort has been made to eliminate both the causal fungi (*Aspergillus* spp.) and toxin from the seed chain. Several lines have been reported with resistance, but most of these break down in varying degrees in the field. The largest breeding efforts have been at ICRISAT and at the USDA/ARS station at Tifton, GA. Mehan *et al.* (1991) reported several *A. hypogaea* lines with field resistance to aflatoxin production. The core collection developed by Holbrook *et al.* (1993) has also been screened

**Table 5. Sources of high levels of disease and insect resistance found in *Arachis* species[a] (from Stalker, 1992).**

| | Evaluated | *A. monticola* | *Ara.* | *Cau.* | *Ere.* | *Ext.* | *Het.* | *Rhi.* | *Tri.* | Unknown | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | No. accessions | | | | | | | | | |
| **Diseases** | | | | | | | | | | | |
| *Cercospora arachidicola* | 93 | - | 1 | - | 2 | 3 | - | 24 | - | - | Abdou *et al.*, 1974 |
| *C. arachidicola* | 4 | - | 2 | - | - | - | - | 1 | - | - | Subrahmanyam *et al.*, 1980 |
| *Cercosporidium personatum* | 93 | - | 1 | - | 2 | 3 | - | 14 | - | - | Abdou *et al.*, 1974 |
| *C. personatum* | 95 | - | 15 | 4 | 12 | 2 | - | 50 | 1 | - | Subrahmanyam *et al.*, 1985b |
| Cylindrocladium black rot | 19 | 1 | 12 | - | - | - | - | - | - | - | Fitzner *et al.*, 1985 |
| Cylindrocladium black rot | 6 | 3 | - | - | - | - | - | - | - | - | Stalker, unpubl. data, 1993 |
| *Didymella arachidicola* | 50 | 1 | 23 | 1 | 4 | 1 | 1 | 1 | - | - | Subrahmanyam *et al.*, 1985c |
| *Puccinia arachidis* | 61 | - | 18 | - | 4 | 1 | - | 34 | 1 | - | Subrahmanyam & Moss, 1983 |
| **Nematodes** | | | | | | | | | | | |
| *Meloidogyne arenaria* | 36 | - | 11 | - | 1 | - | - | 14 | - | 9 | Holbrook & Noe, 1990 |
| *M. arenaria* | 116 | - | 23 | - | 1 | - | 4 | 12 | - | 7 | Nelson *et al.*, 1989 |
| *M. hapla* | 33 | - | - | - | - | - | - | 1 | - | - | Banks, 1969 |
| *M. hapla* | ? | - | - | - | - | - | - | - | - | 4 | Castillo *et al.*, 1973 |
| *M. hapla* | 3 | - | 3 | - | - | - | - | - | - | - | Nelson *et al.*, 1989 |
| **Viruses** | | | | | | | | | | | |
| Clump | 38 | - | - | - | - | - | - | - | - | 1 | ICRISAT, 1985 |
| Mottle | 90 | - | 4 | 1 | 4 | - | - | 39 | - | - | Demski & Sowell, 1981 |
| Mottle | ? | - | 3 | - | - | - | - | 3 | - | - | Melouk *et al.*, 1984 |
| Mottle | 50 | - | 1 | - | - | - | 1 | - | - | - | Subrahmanyam *et al.*, 1985a |
| Ringspot | ? | - | 1 | - | - | 1 | - | 1 | - | 5 | Klesser, 1965 |
| Rosette | 11 | - | - | 1 | - | - | - | 1 | - | - | Gibbons, 1969 |
| Rosette | 7 | - | 1 | - | 1 | - | - | - | - | - | Wynne *et al.*, 1991 |
| Stripe | 8 | - | 1 | - | - | - | - | 3 | - | - | Culver & Sherwood, 1987 |
| Stunt | 90 | - | 3 | 1 | 4 | - | - | 39 | - | - | Hebert & Stalker, 1981 |
| Tomato spotted wilt | 42 | | 3 | - | - | - | 1 | - | - | - | Subrahmanyam *et al.*, 1985a |

**Table 5 (Continued)**

| | Evaluated | *A. monticola* | *Ara.* | *Cau.* | *Ere.* | *Ext.* | *Het.* | *Rhi.* | *Tri.* | Unknown | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | ----------No. accessions---------- | | | | | | | | | |
| | | | | | **Insects** | | | | | | |
| *Aphis craccivora* | 7 | - | 4 | - | 1 | - | - | - | - | 3 | Amin, 1985; ICRISAT, 1990 |
| *Elasmopalpus lignosellus* | 27 | - | - | - | - | - | - | - | - | - | Stalker *et al.*, 1984 |
| *Empoasca fabae* | 53 | 1 | 12 | 1 | 7 | 1 | 2 | 23 | 1 | - | Stalker & Campbell, 1983 |
| *Frankliniella fusca* | 53 | - | 11 | - | 9 | 1 | 2 | 25 | | - | Stalker & Campbell, 1983 |
| *F. schultzei* | ? | - | 1 | - | - | - | - | - | 1 | - | Amin, 1985 |
| *Helicoverpa zea* | 53 | - | 8 | 1 | 6 | 1 | 2 | 12 | 1 | - | Stalker & Campbell, 1983 |
| *Scirtothrips dorsalis* | ? | - | 2 | - | - | - | - | - | - | - | Amin, 1985 |
| *Spodoptera frugiperda* | 14 | - | 4 | - | 1 | - | - | 1 | - | - | Lynch *et al.*, 1981 |
| *S. litura* | 22 | - | 1 | - | - | - | - | 1 | - | 4 | ICRISAT, 1990 |
| *Tetranychus tumidellus* | 54 | - | - | 1 | - | 1 | - | 1 | - | - | Leuck & Hammons, 1968 |
| *T. urticae* | 112 | - | 3 | 1 | 1 | - | - | 19 | - | - | Johnson *et al.*, 1977 |

[a]*Ara.* = *Arachis*, *Cau.* = *Caulorrhizae*, *Ere.* = *Erectoides* [includes both section *Erectoides* and *Procumbentes* (formally sect. *Erectoides* ser. *procumbentes*) species], *Ext.* = *Extranervosae*, *Het.* = *Heteranthae*, *Rhi.* = *Rhizomatosae*, *Tri.* = *Triseminatae*.

for field resistance to *Aspergillus* and several lines with high levels of resistance may have been found (Holbrook *et al.*, 1992). Genetic resources in wild *Arachis* species will not likely be useful for reducing aflatoxin in the cultivated peanut because they support *Aspergillus* spp. growth and toxin production (Mehan *et al.*, 1992).

Except for rosette virus, for which high levels of resistance were found in the 1950s in Africa, screening the peanut germplasm for viruses has only been a relatively recent objective of many peanut breeding programs (Wynne *et al.*, 1991). A large part of the ICRISAT collection has been evaluated for tomato spotted wilt virus (TSWV), and to a lesser extent for peanut mottle virus (PMV) and peanut clump virus—resistant genotypes were found in 23, 2, and 0 genotypes, respectively (Wynne *et* al., 1991; Singh *et al.*, 1992). Melouk *et al.* (1984) evaluated 156 *Arachis* accessions for peanut mottle virus and found five section *Rhizomatosae* genotypes and three section *Arachis* genotypes without symptoms or serological evidence of infection. Unfortunately, the two PMV-resistant genotypes reported by ICRISAT were wild *Arachis* species, *A. chacoensis* coll. GKP 10602 (= *A. diogoi*) and in *A. pusilla* coll. GKP 12922 (= *A. triseminata*), so direct utilization of the resistant sources in conventional breeding programs will be difficult.

A large portion of the USDA *A. hypogaea* collection has been screened for resistance to the root-knot nematode *Meloidogyne arenaria* (Holbrook and Noe, 1992). Moderately high levels of resistance, as measured by numbers of egg masses and eggs, have been identified. Significantly higher levels of resistance have also been found in *Arachis* species (Nelson *et al.*, 1989; Holbrook and Noe, 1990) (Table 5). Two germplasm releases derived from interspecific hybrids have recently been made (Simpson *et al.*, 1993a).

**Resistance to Insect Pests**

Yield loss from insects is caused directly by reductions in plant vigor, pod and seed damage, and indirectly by being a vector for viruses. Host plant resistance to peanut insect pests were reviewed by Lynch (1990) and Lynch and Douce (1992), who indicated that excellent sources of resistance for several insects are found in *A. hypogaea* for potato leafhopper, southern corn rootworm, corn earworm, thrips, and termites. Several magnitudes of higher levels of resistance than found in the cultivated peanut also have been documented for *Arachis* species for several pests (Stalker and Campbell, 1983) (Table 5). Evaluations for insect resistance has lagged behind diseases, in large part because they are believed to be economically less important. However, cv. NC 6 has high levels of southern corn rootworm resistance, and moderate resistance to potato leafhopper and corn earworm, and slight resistance levels to thrips (Lynch and Douce, 1992).

**Multiple Resistances**

Multiple sources of resistance have been identified in cultivated peanuts for several disease and insect pests. The largest screening efforts have been to identify single lines of *A. hypogaea* with combined late leaf spot and rust resistances because these diseases greatly decrease yields across the semi-arid tropics. Of the 10,000 lines evaluated at ICRISAT, 30 were identified with

resistance to both pathogens (Moss *et al.*, 1989). The cultivar ICGV 86590 was recently released from the ICRISAT program as being highly resistant to rust, tolerant to late leaf spot, and with some resistance to bud necrosis; it is also less susceptible than other cultivars grown in India for several other disease and insect pests (Reddy *et al.*, 1993). Several germplasm releases also have multiple sources of disease resistance—for example NC 3033, which is highly resistant to CBR and has moderate resistance to *Sclerotium rolfsii* (Wynne *et al.*, 1991). Simpson *et al.* (1993a) reported multiple resistance to *C. arachidicola* and *C. personatum* and to the nematode species *M. arenaria* in released germplasm lines. A program at ICRISAT to specifically find lines with both disease and insect resistances in single genotypes has resulted in identifying 56 accessions with multiple resistance to pests and diseases (Moss *et al.*, 1989).

Host plant resistance to diseases and insects in many *Arachis* species appears to be much higher than in *A. hypogaea,* and the promise of significant cultivar improvements has resulted in extensive evaluation efforts. Multiple resistances appear to be concentrated in sections *Arachis* and *Rhizomatosae* (Table 5), but this is probably an artifact because most accessions which have been evaluated come from these sections. Regardless of which species in the genus have genes conditioning resistances, taxa in section *Arachis* will be most easily utilized in breeding programs. Because obtaining 40-chromosome hybrid derivatives is difficult and reduced fertility or sterility restricts selection efforts during several hybridization generations, the most important species for crop improvement may be ones with multiple resistances. Advanced generation progenies then have the potential for being resistant to several pathogens or pests. Several diploid species in section *Arachis* have been identified with multiple pest resistances, including *A. chacoensis* (= *A. diogoi*) which is highly resistant to *C. arachidicola*, TSWV, *P. arachidis*, nematode (*M. arenaria*), thrips (*Frankliniella fusca*), corn earworm (*Heliothis zea*), and plant leafhoppers (*Empoasca fabae*). *Arachis cardenasii* is highly resistant to *C. personatum*, TSWV, *P. arachidis*, *Didymella arachidicola*, *M. arenaria*, *F. fusca*, *H. zea*, and *E. fabae*; *A. stenosperma* is highly resistant to *C. arachidicola*, *C. personatum*, *P. arachidis*, *F. fusca*, *E. fabae*, *H. zea*, and *M. arenaria*; and *A. batizocoi* is resistant to *D. arachidicola*, *P. arachidis*, *M. arenaria*, *E. fabae*, and *H. zea*. These four species also have been among the ones most commonly used in crossing programs, and selections should produce improved lines.

### Miscellaneous Traits

Many *Arachis* species and *A. hypogaea* lines have been evaluated for quality characters and reviews presented by Norden *et al.* (1982), Wynne and Coffelt (1982), and Singh *et al.* (1992). Physiological variation in the cultivated peanut is reviewed by Williams and Boote in Chapter 9 of this volume and biological nitrogen fixation is reviewed by Elkan in Chapter 8, also in this volume.

*Arachis hypogaea* ranges between 44 and 56% oil and 25 and 34% protein, whereas *Arachis* species range from 42 to 63% and 21 and 33%, respectively (Cherry, 1977; Stalker *et al.*, 1989). Significant variation also exists among both cultivated and wild peanut species for fatty acid composition (Treadwell *et al.*, 1983; Stalker *et al.*, 1989). However, even though significant differences were

reported by Mozingo *et al.* (1988) for variation in oil, proteins, and fatty acids among 20 virginia-type cultivars released between 1944 and 1985, the extremes were relatively narrow. One mutation of potential importance is a high oleic acid line which is conditioned by two recessive genes in peanut (Moore and Knauft, 1989). Differences have also been found among *Arachis* species for oil and protein profiles (Stalker *et al.*, 1989), but highly desirable traits do not appear to be present in the secondary gene pool for use in crop improvement. The tryptophan content in *A. villosulicarpa* is higher than found in *A. hypogaea* (Amaya *et al.*, 1977), but these species will not hybridize. On the positive side, closely related species to *A. hypogaea* do not have oil or protein profiles which are expected to lower the quality of peanut products once they are introgressed into breeding lines or cultivars (Stalker *et al.*, 1989).

**Forage Utilization**

In tropical and subtropical areas a great need exists for warm-season forages to compliment grass silage. Other legumes, such as the clovers, establish well and produce adequate yields during cool months, but during the hot summers of the South they grow and yield poorly. At least three *Arachis* species have been used for livestock forage or landscape development. *Arachis glabrata* is a diverse species in section *Rhizomatosae* which has good forage potential and several cultivar releases have been made, including cvs. Florigraze (Prine *et al.*, 1986) and Arbrook (Prine *et al.*, 1990). Unfortunately, few seeds are produced even though pollen viability is high (Niles and Quesenberry, 1992), and virtually all of the forage acreage in the U.S. has been planted using rhizomes.

*Arachis pintoi* has been identified as a potentially good forage species for use in Brazil, Colombia (Asakawa and Ramirez-R., 1989), and Australia (Cameron *et al.*, 1989). The species is a perennial, produces large numbers of seeds, and is relatively easy to establish in the field. *Arachis repens* is used extensively in South America as a roadside plant or as a yard or landscape plant.

## CONCLUSIONS

The genus *Arachis* is an old group of unusual plants. The various taxa have evolved in some interesting and inhospitable habitats in Argentina, Bolivia, Brazil, Paraguay, and Uruguay. In many of its native environments, *Arachis* contributes significantly to the perpetuation of the local ecology; that is, *Arachis* produces nitrogen for associated species, pollen for insects of various types, stability for soil particles, forage for animals, and seeds for various bird species if they can find the fruits. It has not been evident that disease and/or insect organisms have co-evolved with *Arachis*, but in time it will surely be demonstrated that such is the case. As man became a foraging and then gathering species, the wild *Arachis* most surely contributed to his survival. Considerable work has been done on man's development of cultigens in *Arachis* but, with the advent of molecular genetics—and now the elucidation of the taxonomy of the genus, the surface has only been scratched. Much future improvement can be expected in the cultivated *A. hypogaea*, and we may even see new man-made species that will become important in the food chain of man and/or animals.

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