JA No. 635

ADVANCES IN AGRONOMY, VOL. 41

SPECIATION, CYTOGENETICS, AND UTILIZATION OF *Arachis* SPECIES[1]

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I. INTRODUCTION

Utilization of wild species for improvement of cultivated forms has been investigated since Faircloth made the first interspecific hybrids in 1717. Many wild species have been of value in crop improvement for a large number of traits (Harlan, 1976; Hawkes, 1977; Stalker, 1980a; Hadley and Openshaw, 1980). However, in leguminous oilseeds, utilization of species germplasm has proven difficult, in large part because of barriers to interspecific hybridization between species (Smartt, 1979). Further, sterility often restricts introgression from wild to cultivated accessions even when initial hybridization is possible. Interspecific hybridization is also difficult among the peanut species in the genus *Arachis*, but breeding populations derived from crossing *A. hypogaea* L. with related species are currently being evaluated for farmer use (Moss, 1985b).

Four species of *Arachis* have been cultivated, including two diploids ($2n = 2x = 20$: *A. villosulicarpa* Hoehne and *A. repens* Handro) and two tetraploids ($2n = 4x = 40$: *A. glabrata* Benth. and *A. hypogaea*). *Arachis villosulicarpa* has only been cultivated by Indians in the northwestern part of the Brazilian state of Mato Grosso (Gregory *et al.*, 1973). *Arachis repens* and *A. glabrata* have been grown in different parts of South America as forages or as ground covers in urban areas. *Arachis glabrata* has also been selected for forage qualities in Florida, where recent cultivar releases have been made (Prine *et al.*, 1981). However, *A. hypogaea* is the only species which is cultivated extensively for commercial production of seeds and oil.

[1]This article is a contribution from paper No. *10726* of the Journal Series of the North Carolina Agricultural Research Service, Raleigh, North Carolina 27695, and Paper No. *635* of the Journal Series of the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, P.O., Andhra Pradesh 502 324, India.

The cultivated peanut, *A. hypogaea,* is a major crop in most tropical and subtropical areas of the world. As compared to other oilseeds, plants are relatively drought resistant, which makes them especially important in semiarid regions where precipitation exceeds evaporation for only 2–7 months per year (Bunting *et al.,* 1985). Although the crop grows best in sandy, well-drained soils, peanuts are cultivated in a wide range of field conditions from clays to sands and from acidic to alkaline soils. In the United States, the seeds are used mainly for confectionary purposes or for peanut butter. However, approximately two-thirds of the total world peanut crop is used for oil, which cumulatively represents 20% of the world market (Woodroof, 1973).

Most peanuts are used as a cash crop and even small farmers may sell their entire harvest. In addition to seeds being of high value, plant residues are extremely important as fodder for cattle in many regions of the world. Shells are also used for fuel, soil conditioners, fodder, chemicals, resin extenders, cork substitutes, and for hardboard (Gibbons, 1980). The peanut is becoming increasingly important as an income source in tree plantations, such as coconut, rubber, or banana, before tree crops mature. In Africa and Asia, many peanuts are intercropped between maize, sorghum, pulses or, in a few areas, between mature coconut trees.

While *A. hypogaea* has the widest distribution of any *Arachis* species, it also has many pests and diseases which attack all parts of the plant. Disease controls are seldom practiced in less developed countries, and one of the major plant breeding objectives is to improve resistances to plant pests (Wynne and Gregory, 1981). In addition, increased stability of yield and adaptation of the peanut to many environments are important breeding objectives. Several *Arachis* species have significantly higher levels of resistance for many important disease and insect pests than are found in cultivated accessions. As in the cases of other crop species, however, attempts to utilize wild species have limitations and obstacles. For example, sterility barriers and genomic incompatibilities restrict utilizing many potentially important genes even after initial interspecific hybids are obtained. However, significant progress has been made toward utilizing germplasm resources of *Arachis*.

Collection, maintenance, and evaluation of peanut germplasm resources have occurred relatively late compared to many other crop species such as tobacco, wheat, or maize. Only during the past 20–25 years have concentrated efforts been undertaken to collect and evaluate the agronomic potential of germplasm resources in the genus. This chapter reviews the current status in the introgression of germplasm from wild to cultivated species of peanut. The successes have been due to a knowledge of the botany, taxonomy, cytogenetics, and genetics of the species related to *A. hypogaea* and to effective screening of the available germplasm. Therefore, summaries of

species variability, genomic and species relationships, and resources of agronomically important characteristics are presented, followed by an account of the methods used and of achievements in *Arachis* germplasm utilization.

II. BOTANY AND TAXONOMY

The genus *Arachis* belongs to the family Leguminosae, tribe Aeschynomeneae, subtribe Stylosanthenae. Species have alternately attached basal and dorsal anthers, flowers in terminal or axillary spikes or small heads, pinnate leaves, and few leaflets without stipules (Taubert, 1894). Most of the *Arachis* species have tetrafoliate leaves, but two species, *A. tuberosa* Benth. and *A. guaranitica* Chod. et Hassl., are trifoliate. *Arachis* species, along with *Trifolium subterraneum* L. and *Vigna subterranea* (L.) Verdc., flower above ground but produce fruit and seeds below the soil level. Species of peanut are self-pollinating, but outcrossing may also occur in up to 2.5% of the flowers (Norden, 1980). A structure called a peg grows geotropically after fertilization and carries the developing embryo into the soil, after which elongation ceases, the pod expands, and the embryo initiates a rapid growth phase. Both annual and perennial members of the genus are found in nature.

The first peanut species described was *A. hypogaea* by Linnaeus in 1753. This species has two subspecies, each of which has two botanical varieties (Table I). Not until 1841 were wild species described, including *A. villosa* Benth., *A. tuberosa, A. glabrata,* and *A. pusilla* Benth. (Bentham, 1841). Taxonomic treatments of the genus were later completed by Chevalier

Table I

Subspecific and Varietal Classification of *A. hypogaea*

Subspecies	Variety	Type	Comments
hypogaea	*hypogaea*	Virginia	No floral axes on main stem; alternating pairs of floral and vegetative axes on branches; branches short, less hairy
	hirsuta	Peruvian runner	No floral axes on main stem; alternating pairs of floral and vegetative axes on branches; branches long, more hairy
fastigiata	*fastigiata*	Valencia	Floral axes on main stem; sequential floral axes on branches; little branched, curved branches
	vulgaris	Spanish	Floral axes on main stem; sequential floral axes on branching; more branched, upright branches

(1933, 1934, 1936), Hoehne (1940), and Hermann (1954). Currently, 22 species diagnoses have been published (excluding *A. nambyquarae* Hoehne, which is a cultivar of *A. hypogaea,* and *A. batizogaea* Krap. et Fern., which originated from a man-made hybrid), with another 12 names commonly used in the literature but not described (Table II). The guidelines outlined by Resslar (1980) will be used in this paper even though proper diagnoses for many of the taxa have not been published.

A complete revision of the taxonomy of the genus is greatly needed, and considering the vast number of new accessions collected within the past 10 years, perhaps 50 or more additional species will eventually be described. Compounding the problem of species names are those designations which have been incorrectly given to taxa in the literature. For example, *A. nambyquarae* Hoehne is not a separate species, but a cultivar of *A. hypogaea.* The name *A. diogoi* Hoehne (a species of section *Arachis*) was incorrectly used for an unnamed section *Erectoides* species by Johansen and Smith (1956), and the names *A. prostrata* Benth. and *A. marginata* Gard. have been used incorrectly for many different accessions (Gregory *et al.,* 1973). Since germplasm is widely distributed with collection numbers and names, and there is no written description of many species, misidentifications are easily made. Peanut researchers have associated collection numbers with taxa to circumvent partially the problem of nomenclature.

Based on morphological comparisons, and to a lesser extent on cross-compatibility and pollen stainability of interspecific hybrids, Krapovickas (1969, 1973) and Gregory *et al.* (1973) proposed sectional classifications for the *Arachis* species. The classification suggested by Gregory *et al.* (1973) is more commonly adopted and will be followed throughout this review (Table II). Although sectional names remain tentative because proper diagnoses have not been published, the groups are useful for defining general crossing relationships of taxa in the genus.

III. PLANT COLLECTION AND MAINTENANCE

Taxa in the genus *Arachis* are widely distributed in South America from the Atlantic Ocean to the foothills of the Andes Mountains and from the mouth of the Amazon River in the North to approximately 34°S in Uruguay. Although the cultivated species usually prefers sandy, well-drained soil, wild species of *Arachis* are found in many habitats, including rocky areas, heavy soils, marshy areas, and even in running water (Valls *et al.,* 1985). While many species proliferate in shaded areas, others prefer open and sunny environments. Plants are most often found in ecotypes such as rock outcroppings, broken forested areas, forest-grassland margins, or

Table II

Taxonomic Subdivision of the Genus *Arachis*[a]

Section *Arachis nom. nud.*
- Series *Annuae* Krap. et Greg. *nom. nud.* (2*n* = 2*x* = 20)
  - *A. batizocoi* Krap. et Greg.
  - *A. duranensis* Krap. et Greg. *nom. nud.*
  - *A. spegazzinii* Greg. et Greg. *nom. nud.*
  - *A. stenosperma* Greg. et Greg. *nom. nud.*
  - *A. ipaensis* Greg. et Greg. *nom. nud.*
  - *A. spinaclava*
- Series *Perennes* Krap. et Greg. *nom. nud.* (2*n* = 2*x* = 20)
  - *A. helodes* Martius ex Krap. et Rig.
  - *A. villosa* Benth. var. *villosa*
  - *A. villosa* var. *correntina* Burkart [*A. correntina* (Burk.) Krap. et Greg. *nom. nud.*]
  - *A. diogoi* Hoehne
  - *A. cardenasii* Krap. et Greg. *nom. nud.*
  - *A. chacoense* Krap. et Greg. *nom. nud.*
- Series *Amphiploides* Krap. et Greg. *nom. nud.* (2*n* = 4*x* = 40)
  - *A. hypogaea* L. (*A. nambyquarae* Horne)
  - *A. monticola* Krap. et Rig.
  - *A.* × *batizogaea* Krap. et Fern. (of experimental hybrid origin)

Section *Erectoides* Krap. et Greg. *nom. nud.* (2*n* = 2*x* = 20)
- Series *Trifoliolatae* Krap. et Greg. *nom. nud.*
  - *A. guaranitica* Chod. et Hassl.
  - *A. tuberosa* Benth.
- Series *Tetrafoliatae* Krap. et Greg. *nom. nud.*
  - *A. benthamii* Handro
  - *A. martii* Handro
  - *A. paraguariensis* Chod. et Hassl.
  - *A. oteroi* Krap. et Greg. *nom. nud.*
- Series *Procumbensae* Krap. et Greg. *nom. nud.*
  - *A. rigonii* Krap. et Greg.
  - *A. lignosa* (Chod. et Hassl.) Krap. et Greg. *nom. nud.*

Section *Caulorhizae* Krap. et Greg. *nom. nud.* (2*n* = 2*x* = 20)
- *A. repens* Handro
- *A. pintoi* Krap. et Greg. *nom. nud.*

Section *Rhizomatosae* Krap. et Greg. *nom. nud.*
- Series *Prorhizomatosae* Krap. et Greg. *nom. nud.* (2*n* = 2*x* = 20)
  - *A. burkartii* Handro
- Series *Eurhizomatosae* Krap. et Greg. *nom. nud.* (2*n* = 4*x* = 40)
  - *A. glabrata* Benth.
  - *A. hagenbeckii* Harms

Section *Extranervosae* Krap. et Greg. *nom. nud.* (2*n* = 2*x* = 20)
- *A. marginata* Gard.
- *A. lutescens* Krap. et Rig.
- *A. villosulicarpa* Hoehne
- *A. macedoi* Krap. et Greg. *nom. nud.*
- *A. prostrata* Benth.

Section *Ambinervosae* Krap. et Greg. *nom. nud.* (2*n* = 2*x* = 20) (no species names, valid or invalid, have been given to forms in this section)

Section *Triseminalae* Krap. et Greg. *nom. nud.* (2*n* = 2*x* = 20)
- *A. pusilla* Benth.

Uncertain sectional affinity
- *A. angustifolia* (Chod. et Hassl.) Killip

[a]After Gregory *et al.* (1973) and Resslar (1980).

in disturbed habitats. They grow from sea level to approximately 1600 m in elevation. The largest number of taxa are found in the west central region of Brazil (Valls *et al.*, 1985), with the second highest concentration found in Bolivia. Extensive genetic diversity exists in the genus for many traits of agronomic importance.

Seeds of the cultivated peanut were among the earliest crops introduced to Europe from the New World and species have been periodically collected in South America since its first discovery. However, not until the late 1950s were concentrated efforts made systematically to collect and preserve variability in *Arachis*. This was largely due to the inaccessibility of many parts of South America and to the wide geographic distributions of peanut species. Twenty-four expeditions were organized between 1958 and 1983, and 639 wild species accessions plus 961 accessions of *A. hypogaea* were collected (Valls *et al.*, 1985). Nearly a hundred wild species accessions have also been collected since 1983. Table III summarizes major germplasm collections of *Arachis* species.

Priorities for future *Arachis* germplasm collection in South America for both cultivated and wild species of the genus have been established (Valls *et al.*, 1985). The highest priority for collecting *Arachis* species is in the Brazilian states of Mato Grosso and Mato Grosso do Sul, and the second priority is for Paraguay. Although Bolivia also represents an important area for future collections, expeditions are currently not planned due to inaccessibility of some areas of the country.

Germplasm resources of wild *Arachis* species are difficult to maintain due to specialized adaptations to many environments. For example, many species are adapted to arid climates, while others are found in wet habitats, and these extremes are difficult to duplicate. Many species accessions do not produce

Table III

Wild *Arachis* Accessions Collected and Conserved between 1936–1983[a]

Section	Collected number	Conserved (1983)	
		USA	Total
Ambinervosae	20	8	15
Arachis	171	150	159
Caulorhizae	17	11	17
Erectoides	345	77	82
Extranervosae	99	45	72
Rhizomatosae	209	93	110
Triseminalae	9	5	9
Totals	870	389	464

[a]After Valls *et al.* (1985)

seeds when grown in the United States and, therefore, must be maintained as live plants. Many other accessions will produce seeds at one location and not another, so multiple germplasm storage facilities are required for seed increase and maintenance. Initiation of reproductive development in peanut species has not been adequately investigated, but many environmental factors probably influence pegging and pod development, such as photoperiod, heat, endogenous hormone levels, and plant stresses. A general trend in section *Arachis* species is profuse flowering in long-day photoperiods with a higher rate of peg formation in short-day photoperiods (Stalker and Wynne, 1983). However, several species [such as *A. chacoense* Krap. et Greg. *nom. nud.*, *A. correntina* (Berk.) Krap. et Greg. *nom. nud.*, and *A. villosa*] produce few to no flowers under short-day conditions. Investigations are urgently needed to find methods to induce seed set because of the expense associated with propagating germplasm collections as vegetative plants plus the required duplications at several locations to ensure long-term survival of accessions under cultivation.

IV. CENTERS OF ORIGIN

The center of orgin for *Arachis* species was most likely in central Brazil (Gregory *et al.*, 1980). The geocarpic habit of the plant suggests that long-distance dispersal has been along water courses. Gregory *et al.* (1973) presented a theory that the most ancient species were found at high elevations and more recent speciation has occurred as seeds were washed down toward the sea and became isolated. To support this view, they noted that many species are adapted to highland conditions by having tuberoid roots, tuberiform hypocotyls, or rhizomes. Further, as seeds moved to lower elevations they became isolated in major river valleys and different sections of the genus evolved in parallel evolution. Although species in different sections of the genus were once believed to be isolated, considerable overlaps in distributions occur, especially for members of the sections *Arachis, Erectoides, Extranervosae,* and *Rhizomatosae* (Valls *et al.*, 1985). Since the major sectional groups of the genus have widespread distributions, species most likely diverged early in the evolutionary history of the genus and subsequently distributed along watersheds.

The cultivated species *A. hypogaea* probably originated from a wild allotetraploid species (Smartt and Gregory, 1967). *Arachis monticola* Krap. et Rig. is the only tetraploid known to be cross-compatible with *A. hypogaea* and the most likely direct progenitor. Since this species is found only in the southern Bolivia–northern Argentina region, this is the region of the presumed center of origin for the cultivated peanut (Krapovickas,

1968). Although the tetraploid progenitor species is generally considered to be *A. monticola,* much speculation has centered around designating the diploid species which gave rise to the allotetraploid. Krapovickas *et al.* (1974) indicated that *A. batizocoi* Krap. et Greg. is one of the diploid progenitors and the species is now considered to be the donor of the B genome of *A. hypogaea* (Smartt *et al.,* 1978a,b; Smartt and Stalker, 1982). The donor of the A genome is more elusive, however, and several species have been suggested, including *A. villosa* (Varisai Muhammad, 1973), *A. duranensis* Krap. et Greg. *nom. nud.* (Seetharam *et al.,* 1973; Gregory and Gregory, 1976) and *A. cardenasii* Krap. et Greg. *nom. nud.* (Gregory and Gregory, 1976; Smartt *et al.,* 1978a). Because of distribution patterns and probable centers of origin of the cultivated peanut, diploid species of section *Arachis,* now found far from the Bolivia–Argentina region, can most likely be eliminated as possible direct ancestors. However, as many unique taxa have been collected in Bolivia, and many more are probably still to be found, the donor of the A genome may await discovery.

In addition to the primary center of origin, five secondary centers of variability exists for the cultivated species in South America (Gregory and Gregory, 1976; Wynne and Coffelt, 1982). Africa represents another center of diversity for the cultivated peanut (Gibbons *et al.,* 1972).

V. CYTOGENETICS OF *Arachis* SPECIES

The chromosome number of $2n = 40$ was first reported by Kawakami (1930) for *A. hypogaea.* Husted (1931, 1933, 1936) confirmed the ploidy level and analyzed the meiotic and somatic chromosomes of seven cultivars. The meiotic chromosomes of *A. hypogaea* pair mostly as 20 bivalents, but a few multivalents have also been observed (Husted, 1936). Hybrids among subspecific accessions have mostly bivalents at metaphase I, but univalents also exist at a low frequency. Husted (1936), Raman (1976), and Stalker (1980b) concluded that chromosome structural differences exist between the subspecies *hypogaea* and *fastigiata.* Further, Gregory *et al.* (1980) observed reduced fertility in hybrids between subspecies, and genetic differences have been reported between the subspecies *hypogaea* and *fastigiata* (Krapovickas, 1973; Wynne, 1974).

The somatic chromosomes of *A. hypogaea* are small and most have a median centromere. Husted (1933, 1936) analyzed somatic chromosomes of several cultivars and distinguished a pair of small chromosomes, which he termed "A" chromosomes, and one pair with a secondary constriction, which he termed "B" chromosomes. Babu (1955) reported several types of secondary constrictions in *A. hypogaea,* and cultivars can be distinguished based on karyotypic differences (D'Cruz and Tankasale, 1961; Stalker and Dalmacio, 1986). At least 15 of the 20 chromosome pairs have been distinguished and, based on arm ratios and chromosome lengths, Stalker and Dalmacio (1986) were able to separate members of different botanical varieties based on somatic chromosome morphology. Analyses of somatic chromosomes support previous investigations with meiotic chromosomes of *A. hypogaea,* which illustrated cytological variation between subspecies.

Aneuploidy was first observed in *A. hypogaea* by Husted (1936), who observed a plant with 41-chromosomes plus a chromosome fragment. Other naturally occurring aneuploids were observed by Spielman *et al.* (1979) and Stalker (1985c) after observing somatic chromosomes of plants propagated from small seeds. Eight different trisomics or double trisomics ($2n + 1 + 1$) were cytologically verified by Stalker (1985c). Chemical treatments (Ashri *et al.,* 1977) or ionizing radiation (Patil and Bora, 1961; Patil, 1968; Madhava Menon *et al.,* 1970) have also produced aneuploid plants. In addition, aneuploids are commonly observed after interspecific *A. hypogaea* hybrids are colchicine-treated (Smartt and Gregory, 1967; Spielman *et al.,* 1979; Company *et al.,* 1982). Davis and Simpson (1976) reported chromosome numbers ranging from 32 to 48 in derivatives of a 6*x* (*A. hypogaea* × *A. cardenasii*) hybrid.

Wild species of *Arachis* were not analyzed cytologically until the late 1940s. A tetraploid ($2n = 40$) species, *A. glabrata,* was reported by Gregory (1946), and Mendes (1947) later observed four diploid species in the genus. Only 26 of 33 named species have chromosome numbers confirmed in the literature (Smartt and Stalker, 1982). Published information on the group is highly inadequate; however, judging from unpublished work in several laboratories and inferences from Gregory and Gregory (1979), most species in the genus are diploid ($2n = 20$). Polyploid ($2n = 40$) species are also found in sections *Arachis* and *Rhizomatosae,* and Smartt and Stalker (1982) concluded that polyploidy evolved independently in the two groups.

Analyses of pollen mother cells (PMCs) indicate that chromosomes of diploid species pair mostly as bivalents (Raman, 1976; Resslar and Gregory, 1979; Smartt *et al.,* 1978a,b; Stalker and Wynne, 1979; Singh and Moss, 1982), but quadrivalents have also been observed at a low frequency in the diploid species *A. villosa* and *A. spegazzinii* Greg. et Greg. *nom. nud.* (Singh and Moss, 1982). In polyploids of a section *Rhizomatosae* species, Raman (1976) reported up to four quadrivalents in PMCs. A second accession reported by Stalker (1985b) averaged 19.92 bivalents and only 0.04 quadrivalents per PMC.

In addition to analyses of chromosome pairing at meiosis, Kirti *et al.,* (1983) and Jahnavi and Murty (1985a,b) analyzed the pachytene chromosomes of species in sections *Arachis, Erectoides, Extranervosae, Rhizomatosae,* and *Triseminalae* and distinguished chromosome pairs. Although chromosomes

did not stain well, Jahnavi and Murty (1985b) concluded that six different chromosomes, three specialized chromosomes, and one nucleolus organizer chromosome are present in species of different groups.

Most karyological analyses in *Arachis* have used species in section *Arachis,* in which nine species have been analyzed (Stalker and Dalmacio, 1981; Singh and Moss, 1982; Stalker, 1985a). Genomes of most species are symmetrical with median chromosomes. Although somatic chromosomes are small, ranging from 1.4 to 3.9 mm in length, species can be identified based on karyological differences. By using arm ratios as variables, species of section *Arachis* can be divided into clusters in which species with an A genome group together and species with chromosomes typical of the species *A. batizocoi* (B genome) separate into a second cluster (Singh and Moss, 1982). Further, *A. spinaclava* has a highly asymmetrical karyotype with subtelocentric chromosomes not found in other species of the group (Stalker, 1985a). Smartt (1964) reported that the distinctively small chromosome pair found in most section *Arachis* species was not present in a section *Erectoides* species, *A. paraguariensis* Chod. et Hassl., which implies that the karyotype of section *Erectoides* species may be differentiated from chromosomes of most section *Arachis* species.

VI. INTERSPECIFIC HYBRIDIZATION IN *Arachis*

Interspecific hybrids in the genus were first attempted by Hull and Carver (1938) when they tried to cross *A. hypogaea* and *A. glabrata,* a species now known to be distantly related to the cultivated peanut. The first successful hybrid reported in the genus was between *A. hypogaea* and the diploid species *A. villosa* var. *correntina* in 1951 (Krapovickas and Rigoni, 1951). The cultivated species has since been hybridized with at least 12 and possibly as many as 18 species of the genus (Kumar *et al.,* 1957; Smartt and Gregory, 1967; Gregory and Gregory, 1979; Singh, 1985; Singh and Moss, 1984b; Pompeu, 1977; Stalker, unpublished data). To date, the only hybrids between the cultivated peanut and wild species have been with members of section *Arachis.* Since many accessions have been introduced recently from South America, this conclusion must be verified using a wide range of variability in the genus, but results thus far have generally coincided with the crossing relationships established by Gregory and Gregory (1979) for sectional groups. Although there are reports of crosses between *A. hypogaea* and members of other sections, these crosses have not been repeated and thus will not be discussed further in this chapter.

Raman and Kesavan (1962) reported the first hybrids among wild species in the genus between *A. duranensis* and *A. villosa* var. *correntina.* Hybrids

were fertile and had regular chromosome pairing during meiosis. Since the first hybrid was reported, hundreds of interspecific crosses have been produced to determine the biosystematic relationships among species or to introgress germplasm to cultivated peanut. The most extensive single hybridization program conducted thus far was by Gregory and Gregory (1979), who reported cross-compatibility relationships among 91 accessions of *Arachis* species. They showed that intrasectional hybrids are much easier to produce than intersectional ones, but low frequencies of success are still observed for many hybrid combinations within groups. Gregory and Gregory (1979) determined relationships among taxa based on both crossability and pollen stainability data. They found that pollen stainability of intrasectional hybrids of section *Arachis* averaged 30.2% when crosses were made among species at the same ploidy level. Intrasectional hybrids among species within other groups ranged from a low of 0.2% in section *Extranervosae* to a high of 86.8% in section *Caulorhizae.* All intersectional hybrids were completely female-sterile and averaged only 1.9% pollen stainability (Gregory and Gregory, 1979).

Since *A. hypogaea* belongs to section *Arachis,* researchers have concentrated efforts within this section. Most interspecific hybrids between species with an A genome have 10 bivalents during meiosis (Resslar and Gregory, 1979; Smartt *et al.,* 1978a,b; Stalker and Wynne, 1979; Singh and Moss, 1984a). Perennial species of the group generally hybridize more easily as male rather than as female parents. Although meiosis is regular, pollen stainability ranges between 20 and 85% and seed production is limited for several hybrid combinations. In contrast to hybrids between A genome species, when crosses are made between *A. batizocoi* (B genome) and other members of section *Arachis,* all hybrids are sterile and have irregular meioses with a range of 4.6–8.6 bivalents per PMC (Gibbons and Turley, 1967; Smartt *et al.,* 1978a,b; Stalker and Wynne, 1979; Singh and Moss, 1984a). When the species *A. spinaclava* (D genome) is hybridized with either A or B genome species, all hybrids are sterile and meiotically irregular (Stalker, 1985a). Many other recently collected taxa must also be analyzed cytologically and, based of fertility data of F_1 hybrids, additional unique genomes may be found in the group.

Because of high levels of sterility in intersectional hybrids between diploid species, crosses have been attempted after raising the ploidy level of species or their hybrids. All attempted crosses between amphidiploids of section *Arachis* species and amphidiploids or natural tetraploids of species in other sections (*Erectoides* or *Rhizomatosae*) have failed. Hybridization at the tetraploid level is more difficult than between diploids and tetraploids for at least some groups of the genus. For example, the two diploid ($2n = 20$) section *Arachis* species *A. duranensis* and *A. stenosperma* have been hybridized with the 40-chromosome amphidiploids (*A. rigonii* × *A.* sp. coll. GKP

9841, PI 262278) of the section *Erectoides* (Stalker, 1981). A high frequency of bivalents was observed and Stalker concluded that chromosome homologies exist among members of sections *Arachis* and *Erectoides.* Complex hybrids between sections *Erectoides* and *Rhizomatosae* have also been cytologically analyzed and chromosome homologies reported for at least one hybrid combination (Stalker, 1985b). Also, plants of one 40-chromosome intersectional *Erectoides* × *Rhizomatosae* hybrid combination were male-fertile and produced selfed seeds. Several triploid hybrids between section *Arachis* (2*x*) and (*Erectoides* × *Rhizomatosae*) (4*x*) have also been made but all hybrids failed to flower even though they had been propagated for several years (Stalker, 1985b).

Based on the cumulative cross-compatibility data of interspecific hybrids by many investigators, a series of genomes for *Arachis* species were proposed by Smartt and Stalker (1982) and Stalker (1985b) as follows:

A: section *Arachis,* perennials and most annuals
B: section *Arachis* (*A. batizocoi*)
D: section *Arachis* (*A. spinaclava*)
Am: section *Ambinervosae*
C: section *Caulorhizae*
E: section *Erectoides*
Ex: section *Extranervosae*
T: section *Triseminalae*
R: section *Rhizomatosae*, series *Prorhizomatosae*

Arachis hypogaea and *A. monticola* have an AB genome, while the genomes of tetraploid species in section *Rhizomatosae* may be similar to the A genome of section *Arachis* and the E genome of section *Erectoides.* Only the A, B, and D genome of section *Arachis* have been studied intensively, and other genomic designations in the genus remain to be verified cytologically. However, even in section *Arachis* there are unanswered questions, such as the real differentiation between designated A and B genomes.

Based on cytological analyses, only two to four chromosome pairs are differentiated between *A. batizocoi* and A genome species (Stalker and Wynne, 1979; Singh and Moss, 1984a). Triploid hybrids between *A. hypogaea* and diploid species have a few trivalents, but hexaploids obtained after colchicine treatment average six or more univalents and may have as many as 20 unpaired chromosomes (Company *et al.,* 1982; Singh, 1985). Pairing mechanisms, or lack thereof, are apparently under genetic control. Further, after backcrossing hexaploids with *A. hypogaea,* pentaploids are produced with the expected 20 bivalent plus 10 univalents, but after one generation of self-pollination, 25 bivalents have been observed in some progenies (Stalker, unpublished data). This indicates that considerable homology exists among the A and B genomes.

Genomic designations outside of section *Arachis* are based mostly on cross-compatibilities. Since incompatibilities may result from single genes, cytoplasmic effects, or other factors, there may be considerable homology among the genomes which have been designated as unique. Several problems also remain unanswered for groups of species. For example, why will diploid *Prorhizomatosae* not hybridize with tetraploid members of the same section when taxa from other sections will hybridize with the tetraploid rhizomatous species? A D genome has been designated for a species which is morphologically identified with members of section *Arachis,* but the taxa may be genomically more similar to species in other sections. Regardless, sectional names are useful for communication concerning groups of species and, from present knowledge, potentials for utilizing species in the genus can be determined. Germplasm pools can be also designated for establishing potentials for introgression to *A. hypogaea.* The primary gene pool comprises *A. hypogaea* accessions and genetic stocks plus the closely related tetraploid species *A. monticola.* Large collections of the cultivated species exist in the United States (*ca.* 4000 accessions) and at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), which has more than 8000 lines (Wynne and Coffelt, 1982). Although several accessions of *A. monticola* have been cataloged in germplasm lists, they all represent collections from at most two sites in South America. *Arachis hypogaea* will hybridize with *A. monticola* and produce fertile hybrids which have normal meiosis (Krapovickas and Rigoni, 1957; Raman, 1958). Analyses of somatic chromosomes have confirmed the close relationship between the species, indicating that they belong to the same biological species.

The secondary gene pool is represented by diploid members of section *Arachis* which have an A or B genome. Hybrids between the diploid and tetraploid species of the group are sterile, but fertility can be restored by manipulating ploidy levels and good evidence exists for homology between the chromosomes of wild and cultivated species (Singh, 1985; Stalker, 1985b). Although *A. batizocoi* is the most likely representative donor of the B genome in *A. hypogaea,* identification of the A genome donor species has not been made. However, enough similarities exist between *A. hypogaea* and most of the A genome species of section *Arachis* that gene transfer can occur from wild taxa to the cultivated peanut.

The tertiary gene pool includes all taxa outside section *Arachis* plus species of section *Arachis* which do not have an A or B genome (for example, *A. spinaclava).* Hybrids between *A. hypogaea* and these species have not been produced and specialized techniques will be required to produce hybrids. However, F_1 generation plants are expected to be completely sterile and methods to introgress small chromosome segments will be necessary for utilization of these germplasm resources.

VII. GERMPLASM EVALUATION

Identification of desirable traits, especially for disease and insect resistances, in *Arachis* species must precede utilization of germplasm resources. Disease and insect resistances have had the highest rates for successful introgression from wild species to many crop plants (Watson, 1970; Knott and Dvorak, 1976). Likewise, the most commonly investigated agronomic traits in wild species are pest resistances. The peanut is plagued by a large number of pests, many of which are now worldwide in distribution. Because of the agronomic importance and impact of diseases and pests on yield and quality, introgression of disease resistance from wild species to cultivars has been a high priority in many breeding programs.

A. Disease Resistances

The three most important diseases of *A. hypogaea* worldwide are *Cercospora arachidicola* Hori (early leafspot), *Cercosporidium personatum* (Berk. et Curt.) Deighton (late leafspot) and *Puccinia arachidis* Speg. (peanut rust). Subrahmanyam *et al.* (1984) estimated that in India, which is one of the largest producers of peanuts, yield losses due to rust and leafspots are approximately 70% annually. Gibbons (1980) estimated that production in locations where fungicides are not used, largely because of high chemical costs, have yield decreases of approximately 50%, and even when chemicals are applied yield may be decreased by 10% (Jackson and Bell, 1969). In addition to actual production losses directly due to the diseases are costs of chemicals, application expenses, and plant damage incurred during applications. Although only one of the leafspots may be common at a particular location during the year, the disease populations may change over years as cultivars are replaced (Smith and Littrell, 1980).

Many *Arachis* species have been evaluated for resistance to the *C. arachidicola* pathogen (Table IV). The three species *A. glabrata, A. hagenbeckii,* and *A. repens* have high levels of resistance to this pathogen (Gibbons and Bailey, 1967). Abdou *et al.* (1974) screened 94 species accessions in the greenhouse and found members of sections *Arachis* (*A. chacoense GKP 10602), Caulorhizae* (*A. repens GKP 10538), Extranervosae* (*A. villosulicarpa,* three accessions), and *Rhizomatosae* (*A.* sp. GKP 10596) to be immune to *C. arachidicola.* Melouk and Banks (1978) confirmed the immune reaction of *A. chacoense,* but Foster *et al.* (1981) and Company *et al.* (1982) observed small lesions on leaves of field-grown plants. Kolawole (1976) reported high levels of resistance in a second section *Arachis* species which Sharief *et al.* (1978) concluded was the *A. stenosperma* Greg. et Greg. *nom. nud.,* collection HLK 410. Because evaluations of both cultivated and wild species at different locations had been done with different techniques and disease pressures, Foster *et al.* (1981) compared 9 section *Arachis* species with 14 reportedly resistant cultivated genotypes. They confirmed a high level of resistance in *A. stenosperma* (HLK 410) and found that *A. chacoense* had significantly fewer lesions per leaf than any other species tested. Sharief *et al.* (1978) reported that resistance in *Arachis* species is multigenic, while Company *et al.* (1982) found triploid interspecific hybrids between *A. hypogaea* and the *Arachis* species *A. cardenasii* and *A. chacoense* to be resistant to early leafspot in the field. This indicated at least partial dominance for resistance. *Cercospora arachidicola* resistance appears to have been introgressed from the wild diploid species *A. cardenasii* to *A. hypogaea* (Stalker, 1984).

Late leafspot (*C. personatum*) is the most severe peanut disease in many production areas. Abdou *et al.* (1974) screened the same 94 accessions mentioned previously for this pathogen in the greenhouse. They reported high levels of resistance in several taxa of sections *Arachis*, *Caulorhizae, Extranervosae,* and *Rhizomatosae. Arachis cardenasii* was the only species in the accessions which is both cross-compatible with *A. hypogaea* and immune; Subrahmanyam *et al.* (1980) confirmed the reactions in separate experiments. Kolawole (1976) reported high levels of resistance in a second species, now believed to be *A. stenosperma.* Resistance has recently been selected in 40-chromosome interspecific hybrid derivatives of *A. hypogaea* × section *Arachis* species (Moss, 1985b).

Because populations of leafspots can change, breeding for only one pathogen and not the other may be futile. Fortunately, high levels of resistance have been found in several genotypes to both early and late leafspots (Abdou *et al.,* 1974; Kolawole, 1976). In addition, *A. cardenasii* (which is reported as resistant to *C. personatum* but susceptible to *C. arachidicola*) has at least moderate levels of resistance to the early leafspot pathogen for lesion number and lesion size, but not for genes conditioning defoliation (Foster *et al.,* 1981).

In addition to fungal pathogens, peanuts are invaded by many viruses. Several of these cause severe damage and yield loss such as bud necrosis and peanut stunt, while others express only mild symptoms which may have little effect on yield. A comprehensive review of peanut diseases was made by Porter *et al.* (1982), who discussed descriptions of causal organisms, symptoms, disease cycles, and controls. This chapter will thus be restricted to reports directly related to wild *Arachis* species.

Groundnut rosette virus is restricted to Africa south of the Sahara and may be the most destructive virus disease of peanut (Porter *et al.,* 1982). While resistance has been found in the *Arachis* species *A. glabrata* and *A. repens* (Gibbons, 1969), the species *A. glabrata* and *A. prostrata* Benth. (identified as *A. hagenbeckii* and *A. repens* by Gibbons, 1969) were reported as being symptomless carriers of the virus by Klesser (1967). Because resistance was found only in species which will not hybridize with *A. hypogaea,* and at about the same time adequate levels of resistance were also found in the cultivated accessions,

Table IV

Pest Resistance in Wild *Arachis* Species[a]

Collection	Collector[b]	PI	Species	C.a	C.p	R	PSV	Th	PHL	CEW	SM	LCSB
Section *Ambinervosae*												
12943	GK	338452	*A.* sp.	—	—	—	—	HR	I	HR	S	S
12946	GK	338454	*A.* sp.	—	—	—	—	HR	HR	HR	—	S
Section *Arachis*												
408	HLK	338279	*A. stenosperma*	—	—	HR	—	R	HR	HR	S	MR
410	HLK	338280	*A. stenosperma*	HR	HR	HR	—	HR	HR	HR	S	MR
7264	K	219824	*A. monticola*	S	S	S	S	—	—	—	S	S
7830	K	261871	*A. correntina*	—	—	—	R	—	—	—	S	—
7897	K	262873	*A. correntina*	—	—	—	R	—	—	—	—	—
7988	K	—	*A. duranensis*	MR	—	I	I	S	I	HR	—	MR
9484	K	298639	*A. batizocoi*	S	—	I	—	I	HR	HR	—	S
9530	GKP	262808	*A. correntina*	—	—	I	R	HR	HR	HR	S	MR
9531	GKP	262809	*A. correntina*	—	—	I	—	—	—	—	—	—
9548	GKP	262839	*A. correntina*	MR	MR	—	R	—	—	—	R	—
9901	GKP	262270	*A.* sp.	S	S	—	—	—	—	—	—	—
10017	GKP	262141	*A. cardenasii*	HR	HR	I	S	HR	HR	HR	—	MR
10038	GKP	262133	*A. spegazzinii*	MR	—	I	R	R	HR	HR	S	MR
10602	GKP	276235	*A. chacoense*	HR	HR	I	S	HR	HR	HR	S	R
22585	Bu	298636	*A. villosa*	R	R	—	I	R	HR	HR	S	R
30006	GK	468150	*A.* sp.	—	—	I	—	—	—	—	—	—
30011	GK	468154	*A.* sp.	—	—	I	—	—	—	—	—	—
30031	GK	—	*A. helodes*	—	—	HR	—	—	—	—	—	—
30035	GK	468168	*A.* sp.	—	—	HR	—	—	—	—	—	—
30063	GKBSPSc	468199	*A.* sp.	—	—	S	—	—	—	—	—	—
30085	GKBSPScZ	468331	*A.* sp.	—	—	I	—	—	—	—	—	—
A. correntina	—	—	*A. correntina*	—	—	I	R	—	—	—	MR	R
Manfredi #5	—	—	*A. correntina-villosa*	—	—	—	I	HR	I	HR	—	R
Manfredi #8	—	—	*A. correntina-villosa*	—	—	—	R	—	—	—	S	—
Manfredi #36	-	-	*A. correntina-villosa*	—	—	—	R	I	HR	HR	MR	MR
A. villosa	—	—	*A. villosa*	R	R	I	S	—	—	—	MR	—

Section *Caulorhizae*												
10538	GKP	276199	*A. repens*	S	S	—	I	I	HR	HR	—	—
12787	GK	338447	*A. pintoi*	—	—	—	S	—	—	—	S	—
Section *Erectoides*												
565-66	—	338297	—	—	—	—	—	HR	R	R	S	MR
9646	GKP	262842	*A. paraguariensis*	R	MR	—	R	—	—	—	S	—
9764	GKP	262859	*A. benthamii*	R	MR	—	I	—	—	—	—	—
9769	GKP	262862	*A. benthamii*	MR	MR	—	R	—	—	—	—	—
9788	GKP	262790	*A.* sp.	R	R	—	—	—	—	—	—	—
9795	GKP	262863	*A.* sp.	MR	MR	—	—	—	—	—	—	—
9812	GKP	—	*A.* sp.	MR	MR	—	—	—	—	—	—	—
9820	GKP	262791	*A.* sp.	S	S	—	—	—	—	—	—	—
9825	GKP	263105	*A.* sp.	—	—	—	S	—	—	—	—	—
9835	GKP	—	*A.* sp.	—	—	—	S	—	—	—	—	—
9837	GKP	—	*A.* sp.	R	R	—	—	—	—	—	—	—
9841	GKP	262278	*A.* sp.	MR	MR	—	R	I	HR	HR	S	R
9990	GKP	261877	*A.* sp.	HR	R	I	R	HR	R	HR	S	R
9993	GKP	261878	*A.* sp.	MR	MR	I	—	HR	HR	HR	S	R
10002	GKP	—	*A.* sp.	MR	MR	I	—	HR	HR	HR	S	—
10034	GKP	262142	*A. rigonii*	—	—	—	S	HR	I	HR	R	S
10541	GKP	276208	*A. oteroi*	S	S	—	—	—	—	—	—	—
10543	GK	276209	*A.* sp.	S	S	—	—	—	—	—	—	—
10573	GK	276225	*A.* sp.	R	MR	—	I	I	HR	HR	MR	MR
10574	GKP	276226	*A.* sp.	R	R	—	R	—	—	—	—	—
10576	GK	276228	*A.* sp.	—	—	—	S	I	I	HR	—	R
10580	GK	276229	*A.* sp.	MR	MR	—	I	—	—	—	MR	—
10582	GK	276230	*A.* sp.	S	S	—	—	—	—	—	—	—
10585	GK	276231	*A. paraguariensis*	—	S	—	R	—	—	—	S	—
10588	GK	276232	*A.* sp.	S	S	—	—	—	—	—	—	—
11462	KFC	—	*A. paraguariensis*	—	—	I	R	—	—	—	—	—
11488	KC	—	*A. paraguariensis*	—	—	—	S	I	HR	HR	S	R
14444	KHe	338320	*A.* sp.	—	—	—	—	I	S	HR	—	

Table IV (Continued)

Collection	Collector[b]	PI	Species	C.a	C.p	R	PSV	Th	PHL	CEW	SM	LCSB
Section *Extranervosae*												
9906	GKP	262272	*A. lutescens*	R	HR	—	—	—	—	—	—	—
10127	GKP	276203	*A. macedoi*	R	—	—	—	I	I	HR	MR	MR
10406	GKP	276198	*A. margenata*	S	S	—	MR	—	—	—	—	—
A. villosulicarpa		336985	*A. villosulicarpa*	HR	HR	I	—	—	—	—	S	—
1960 #3	—	—	*A.* sp.	—	—	—	I	—	—	—	—	—
1968 #100	—	—	*A.* sp.	—	—	I	I	HR	I	HR	—	—
9553	GKP	262801	*A.* sp.	HR	MR	—	I	—	—	—	—	—
9562	GKP	—	*A.* sp.	R	HR	—	—	—	—	—	—	—
9564	GKP	262811	*A.* sp.	S	S	—	I	—	—	—	—	—
9566A	GKP	262812	*A.* sp.	S	S	I	R	—	—	—	—	—
9566B	GKP	262813	*A.* sp.	S	S	—	—	—	—	—		—
9567	GKP	262814	*A.* sp.	HR	HR	I	HR	—	—	—	—	—
9568	GKP	262815	*A.* sp.	HR	HR	—	I	—	—	—	—	—
9569	GKP	262816	*A.* sp.	MR	MR	—	I	—	—	—	—	—
9570	GKP	262817	*A.* sp.	HR	R	—	I	R	HR	R	—	—
9571	GKP	262818	*A.* sp.	MR	MR	—	I	—	—	—	—	—
9572	GKP	262819	*A.* sp.	HR	MR	—	S	—	—	—	—	—
9574	GKP	262820	*A.* sp.	S	S	—	I	—	—	—	—	—
9575	GKP	262821	*A.* sp.	HR	R	—	—	HR	HR	R	—	—
9576	GKP	262822	*A.* sp.	R	HR	—	I	HR	HR	R	—	—
9578	GKP	262824	*A.* sp.	S	S	—	R	—	—	—	—	—
9580	GKP	262825	*A.* sp.	S	S	I	I	—	—	—	—	—
9587	GKP	262826	*A.* sp.	R	MR	I	I	—	—	—	—	—
9591	GKP	262827	*A.* sp.	—	—	I	I	—	—	—	R	—
9592	GKP	262828	*A.* sp.	MR	MR	I	—	HR	I	HR	—	—
9610	GKP	262832	*A.* sp.	HR	MR	I	I	—	—	—	—	—
9610B	GKP	262832	*A.* sp.	HR	MR	—	I	—	—	—	R	—
9618	GKP	—	*A.* sp.	—	—	I	I	—	—	—	R	—
9629	GKP	262834	*A.* sp.	S	S	—	S	—	—	—	R	—
9634	GKP	262836	*A.* sp.	MR	MR	I	I	—	—	—	—	—
9642	GKP	262839	*A.* sp.	MR	R	—	HR	—	—	—	—	—
9644	GKP	262840	*A.* sp.	HR	MR	—	I	—	—	—	—	—
9645	GKP	262841	*A.* sp.	S	MR	I	MR	HR	HR	MR	—	—
9649	GKP	262844	*A.* sp.	HR	R	I	I	HR	HR	HR	—	—
9664	GKP	262847	*A.* sp.	S	S	—	—	—	—	—	—	—
9667	GKP	262848	*A.* sp.	S	MR	I	R	HR	I	HR	—	—
9797	GKP	262807	*A.* sp.	—	—	I	I	—	—	—	—	—
9806	GKP	262792	*A.* sp.	—	—	I	I	—	—	—	—	—
9813	GKP	262793	*A.* sp.	MR	—	I	I	I	I	HR	—	—
9815	GKP	262794	*A.* sp.	HR	MR	—	I	I	I	HR	R	—
9822	GKP	262795	*A.* sp.	S	S	—	I	—	—	—	—	—
9827	GKP	262796	*A. glabrata*	S	S	I	I	—	—	—	R	—
9830	GKP	262797	*A. glabrata*	S	S	I	R	I	HR	HR	—	—
9834	GKP	262798	*A.* sp.	HR	HR	I	S	HR	I	HR	—	—
9882	GKP	262286	*A.* sp.	R	R	I	R	HR	HR	HR	R	—
9893	GKP	262287	*A.* sp.	HR	R	—	S	HR	HR	HR	R	—
9921	GKP	262296	*A.* sp.	HR	MR	—	I	—	—	—	R	—
9922	GKP	262297	*A.* sp.	HR	MR	—	I	—	—	—	R	—
9925	GKP	262299	*A.* sp.	MR	R	—	I	—	—	—	R	—
9935	GKP	262301	*A.* sp.	MR	MR	I	I	HR	HR	R	MR	—
9966	GKP	262306	*A.* sp.	—	—	—	I	HR	I	HR	—	—
10105	GKP	276200	*A.* sp.	S	S	—	I	—	—	—	—	—
10120	GKP	276202	*A.* sp.	MR	MR	—	I	HR	HR	HR	R	—
10550	GK	—	*A.* sp.	—	—	—	I	—	—	—	MR	—
10559	GKP	276217	*A.* sp.	S	S	—	—	—	—	—	—	—
10566	GK	276223	*A.* sp.	S	S	I	I	HR	I	R	—	—
10596	GK	276233	*A.* sp.	HR	HR	I	I	HR	I	HR	—	—
A. glabrata-B_1	—	—	*A. glabrata*	MR	MR	I	I	—	—	—	—	—
Section *Triseminalae*												
12922	GKP	338449	*A. pusilla*	—	—	I	—	I	I	HR	MR	MR

[a]Insect or disease: C.a, *Cercospora arachidicola;* C.p, *Cercosporidium personatum*; R, rust (*Puccinia arachidis*); PSV, peanut stunt virus; Th, thrips (*Frankliniella fusca*); PHL, potato leafhopper (*Empoasca fabae*); CEW, corn earworm (*Heliothis zea*); SM, spider mite (*Tetranychus urticae*); LCSB, lesser cornstalk borer (*Elasmopalpus lignosellus*). Rating: S, susceptible, MR, moderately resistant; R, resistant, HR, highly resistant; I, immunity (based on authors' interpretation of literature cited in text).

[b]Collectors: B, Banks; Bu, Burkart; C, Cristobal; F, Fugarazzo; G, Gregory; H, Hammons; He, Hemsy; K, Krapovickas; L, Langford; P, Pietrarelli; S, Simpson; Sc, Schinini; Z, Zurita.

little screening or attempted utilization of wild species has occurred. High-yielding rosette-resistant cultivars have been released for grower use in Africa (Gillier, 1978).

Tomato spotted wilt virus, the causal organism for bud necrosis disease, is widespread in many peanut production areas and may cause up to 90% yield loss (Saint-Smith *et al.*, 1972). Ghanekar (1980) screened approximately 7000 *A. hypogaea* accessions and did not find field resistance to the disease. Subrahmanyam *et al.* (1985) inoculated 42 *Arachis* species in the greenhouse and field. The species *A. pusilla* GK 12922, *A. correntina GKP 9530, and A. cardenasii* GKP 10017 became infected in the greenhouse but expressed no symptoms in the field. *Arachis chacoense* GKP 10602 showed infection neither after mechanical injection of the virus nor after infection by thrips (although virus was detected after grafting), and this species may represent the best source of resistance to bud necrosis. Since *A. chacoense* has been hybridized with *A. hypogaea*, it should serve as a usable source for resistance in a peanut breeding program.

Peanut stunt virus was reported in Virginia during 1964 (Miller and Troutman, 1966), and epidemics occurred in the following years. Since then, stunt virus has been found in other production regions in the United States, Japan, and Africa (Porter *et al.*, 1982). Hebert and Stalker (1981) screened approximately 4000 cultivated accessions and all were susceptible to the virus. However, after evaluating 90 *Arachis* species accesions, they found high levels of resistance in species of sections *Arachis, Caulorhizae, Erectoides,* and *Rhizomatosae* (Table IV). Again, the most accessible species were the highly resistant sources *A. duranensis* K 7988, *A. villosa* B 22585, and an *A. correntina-villosa* genotype (Manfredi #8), and several others with high tolerance levels [*A. correntina* K 7897 and GKP 9548 and two *A. correntina-villosa* genotypes (Manfredi #5 and #36)] found in section *Arachis.* Hebert and Stalker (1981) also reported that resistance is not conditioned by a single dominant gene, so introgression may be difficult from wild to cultivated species. Because peanut stunt virus has effectively been controlled through cultural practices and incidence has been insignificant during the past 10 years, no concentrated efforts have been made to transfer genes conferring stunt virus resistance from the wild to cultivated species.

Peanut mottle virus is found worldwide and can infect almost every plant in a peanut field. Demski and Sowell (1981) concluded that economic losses due to the virus are second only to leafspots in the southeastern United States. Kuhn *et al.* (1968) screened more than 450 cultivated accessions but did not find usable levels of resistance. Later, Kuhn *et al.* (1978) identified two tolerant *A. hypogaea* accessions. Demski and Sowell (1981) evaluated seven species accessions of section *Rhizomatosae* and six of these were immune to peanut mottle virus. Subrahmanyam *et al.* (1985) screened an additional 50 *Arachis* accessions and found no infection after mechanical or airbrush inoculations in the species *A. pusilla* GK 12922, *A. chacoense* GKP 10602, *A. cardenasii* GKP 10017, and *A. correntina* GKP 9530. In addition, *A. pusilla* and *A. chacoense* were not infected after grafting infected scions onto their stems; therefore, these two species accessions may have true immunity.

Fitzner *et al.* (1985) evaluated 14 species of section *Arachis* for the soil-borne disease Cylindrocladium black rot, caused by *Cylindrocladium crotalariae* (Loos) Bell and Sobers. Resistance was reported only for the species *A. monticola* GKBSPSc 30062. They indicated that a valuable source of resistance for developing cultivars may have been found because *A. monticola* produces fertile hybrids with *A. hypogaea.*

Another soil-borne problem for peanut production in many areas is nematode infestations. In some regions of the world, peanuts cannot be grown without nematode controls (Porter *et al.*, 1982). Nematodes may also be associated with high levels of aflatoxin and with other soil-borne diseases (see Porter *et al.*, 1982). *Meloidogyne hapla* Chitwood (northern root knot nematodes) are the most important species which attack peanut. Of 33 *Arachis* accessions evaluated by Banks (1969), only accession PI 262286 (of section *Rhizomatosae*) had moderate levels of resistance. Castillo *et al.* (1973) evaluated 12 wild species accessions and, in addition to confirming resistance in PI 262286, reported three additional PIs, 262841, 262814, and 262844, as being more resistant than the cultivated controls.

B. Insect Resistances

Insects can cause severe yield losses in peanut by feeding on all plant parts. In addition, insect species have been shown to be vectors for viruses (see Smith and Barfield, 1982). Surveys have not been taken to establish the economically important pests in many production areas, but Smith and Barfield (1982) listed 360 insect species which attack peanuts. The lesser cornstalk borer [*Elasmopalpus lignosellus* (Zeller)] is the most severe subterranean insect pest in the United States, and the southern corn rootworm (*Diabrotica undecimpunctata howardii* Barber) also has a wide distribution. Aboveground foliage insects including tobacco thrips (*Frankliniella fusca* Hinds), potato leafhoppers, (*Empoasca fabae* Harris), corn earworms (*Heliothis zea* Bodie), and fall armyworms (*Spedoptera fragiperda* J. E. Smith) are among the most severe insect pests of peanuts in the United States. Many insects move into peanut fields in successive waves. Thrips arrive early in the growing season, followed by corn earworm invasion at peak bloom and then by potato leafhopper migrations (Campbell and Wynne, 1980). In the semiarid tropics, the predominant species of insect pests include the groundnut aphid (*Aphis craccivora* Koch), thrips [*Scirtothrips dorsalis* Hood, *Caliothrips indicus* Bagnall, *Frankliniella schultzei* (Trybom), *F. fusca,* and *Ennoethrips flavens* Moulton], jassids (*Empoasca* sp.), armyworms (*Spodoptera* sp.), and termites (*Microtermes* sp. and *Odontotermes* sp.) (Amin, 1985).

A large number of *Arachis* accessions have been screened for insect resistances including resistance to thrips, leafhoppers, and corn earworms (Stalker and Campbell, 1983); armyworms (Lynch *et al.,* 1981); lesser cornstalk borers (Stalker *et al.,* 1984); and spider mites (Leuck and Hammons, 1968; Johnson *et al.,* 1977). High levels of resistance have been found for the first four insect pests listed above, whereas lower (but still high) levels of resistance have been reported for the lesser cornstalk borer and spider mites (Table IV). Most importantly, resistances are found in species which will hybridize with *A. hypogaea.* Stalker and Campbell (1983) indicated that the mechanism of resistance to *H. zea* in *Arachis* species was antibiosis. In attempts to utilize the resistances for insect pests, 40-chromosome interspecific hybrid derivatives with *A. hypogaea* were evaluated and high levels of resistance for several insect pests were found (Stalker and Campbell, 1983; ICRISAT, 1985).

C. Other Traits

Arachis species are potentially valuable germplasm resources for traits other than disease and insect resistances. For example, peanut seed protein is usually low in the sulfer-containing amino-acids and tryptophan. *Arachis villosulicarpa* is high in tryptophan (range of 1.44–1.66%) as compared to the highest *A. hypogaea* line (1.41%) tested by Amaya *et al.* (1977). Many of the *Arachis* species are extremely drought resistant and research in the area of physiological traits needs to be conducted.

In addition to seeds and vegetative plants collected on exploration trips in South America since 1976, nodules have also been obtained from many accessions. *Bradyrhizobium* have been isolated and maintained from both cultivated and wild *Arachis* species (Elkan *et al.,* 1981). Many strains have been evaluated for plant–*Bradyrhizobium* interactions; and one strain, NC 92, increased peanut yields under field conditions when applied to the cultivar Robut 33-1 in India (ICRISAT, 1983).

VIII. Utilization of Wild *Arachis* Species

Wild species of *Arachis* are a valuable source of desirable characters for cultivar improvement. Especially when the wild species are the only source of resistance to diseases (for example, to peanut clump virus), attempts need to be made to combine the genomes of cultivated and wild species to develop genotypes with stable resistance. Results from the few studies so far conducted indicate that genes for resistance in wild peanut species may be different from those in cultivated peanut (for example, peanut rust) (Singh *et al.,* 1984). However, difficulties of gene transfer from wild species have precluded widespread use of potential germplasm and have also limited our knowledge of the nature and genetics of resistance in the wild species.

A. Incompatibilities Restricting Gene Transfer

The major restriction for study and use of wild species in *Arachis* is cross-incompatibilities between most species and the cultivated peanut. With the exception of *A. monticola,* all wild species in section *Arachis* that can be hybridized with the cultivated peanut are diploids. Thus, hybrids are sterile. Even among these cross-compatible species the success rate for interspecific hybrid production may be low. Reasons for this include incompatibilities among species, especially when the wild species is used as a female parent; hybrid sterility due to the polyploidy; genomic differences among species; irregular meiosis in colchicine-treated hybrids; and difficulties encountered during backcross generations when sterile aneuploid or pentaploid plants are obtained. Even when hybrids can be obtained, the problem of eliminating undesirable wild species characters still exists. When genomes are common to both cultivated and wild species, this may not be a problem. If there are no chromosome homologies, it may be necessary to induce translocations for gene introgression. Even where genomes are homologous or homoeologous and pairing occurs, linkage may restrict recombination between desired and undesirable genes and prevent the production of *A. hypogaea*-like lines with the desired agronomic characters (Stalker *et al.,* 1979). Before a program can be designed to circumvent interspecific hybridization barriers between *A. hypogaea* and other species, reproductive ontogeny and isolation barriers must be understood.

Approximately 12 hr elapse between pollination and fertilization (Smith, 1956). About a week after fertilization, an intercalary meristem of the peg located in the ovary proximal to the ovules begins a rapid geotropic elongation (Jacobs, 1947). Gibberellic acid has a significant stimulatory effect on peg elongation (Amir, 1969), while auxin inhibits peg elongation and is associated with fruit enlargement (Jacobs, 1951). Several days after elongation initiates, the peg penetrates the soil, ceases to grow, and expands into a pod (Smith, 1950, 1956; Yasuda, 1943). Ziv (1981) reported that light is necessary for peg elongation. When pegs fail to reach the soil, they remain viable for several days and then wither. Moisture in the absence of light appears to be the most important factor governing pod development (Yasuda, 1943). Although the peg follows a sigmoidal growth pattern, the embryo and endosperm initially divide and then become quiescent; the embryo contains between 5 and 27 cells at the time the peg penetrates the soil (Schenk, 1961). After the peg is underground, the embryo then maintains a rapid growth phase. Both the root apex and cotyledons are initiated in the globular embryo stage, and by the heart-shaped embryo stage the cotyledons appear as a projection (Pallai and Raju, 1975). Schenk (1961) reported physiological changes associated with peg development, and Brennan (1969), Gregory *et al.* (1973), and Periasamy and Sampoornam (1984) reviewed in more detail the reproductive development of the cultivated peanut. Halward and Stalker (1985, 1987a) reported differences in development of reproductive tissues of wild and cultivated peanuts.

Although many hybridization failures of interspecific crosses have been attributed to embryo abortion, only a few investigations have been reported detailing mechanisms of incompatibility. Johanson and Smith (1956) attributed the failure of *A. hypogaea* × *A. diogoi* (not true *diogoi* vide Gregory and Gregory, 1979) to slow growth and degeneration of the embryo accompanied by hypertrophy of integuments. In *A. hypogaea* × *A. glabrata* (section *Rhizomatosae*) crosses, Murty *et al.* (1980) observed up to a 48-hr delay in fertilization and early embryo abortion. In *A. monticola* × *A.* sp. (section *Rhizomatosae*) crosses, Sastri and Moss (1982) observed large callus plugs along pollen tubes; however, a few pollen tubes were observed in the ovary. They further reported that gibberellic acid and kinetin treatments stimulated peg production in incompatible crosses. In the more closely related species of section *Arachis* incompatibility among species can be caused by the failure of pollen to germinate on the stigma, restriction in fertilization, and/or embryo abortion (Halward and Stalker, 1984). Further, interspecific hybrids can abort a early as 6 days after pollination (for example, in diploid × hexaploid hybrids) or remain viable but undeveloped until the time of normal maturity (for example, hexaploid × diploid hybrids) (Halward and Stalker, 1985, 1987b). Future recovery of interspecific hybrids will thus depend on developing techniques to initiate peg development, promote embryo growth on the plant, and to recover viable, but small, embryos *in vitro*. Promoting embryo development can either be done through ovule culture or, in the case of peanuts, by applying hormones to developing tissues *in vivo* (Mallikarjuna and Sastri, 1985a). Application of embryo culture techniques will then be necessary to recover small reproductive tissues after embryos have reached the heart-shaped embryo stage of development.

B. Direct Hybridization within Section *Arachis*

1. *Hybrids between Tetraploid Species*

Arachis monticola is a tetraploid in series *Amphiploides* of section *Arachis* and is the only wild *Arachis* taxon which can be readily crossed with *A. hypogaea* to produce fertile progeny. The species has been given specific status, but it is a member of the same biological species as *A. hypogaea* and logically could be considered as a subspecies of the cultivated peanut. *Arachis monticola* was used by Hammons (1970) in the pedigree of Spancross and probably by Simpson and Smith (1974) to develop Tamnut 74. For all practical purposes, *A. monticola* can be considered a wild form of peanut which does not need species manipulations for its utilization in breeding programs.

Table V

Number of Pods Produced per 100 Pollinations in Successive Backcrosses of Hexaploids to *A. hypogaea*[a]

Wild species used in production of hexaploid	Backcross					Number of fertile derivatives selected
	BC_1	BC_2	BC_3	BC_4	BC_5	
A. cardenasii	9	18	12	26	—	9
A. chacoense	6	10	17	7	16	9
A. stenosperma	14	16	8	4	—	2
A. correntina	25	5	—	—	—	—
A. villosa	7	—	—	—	—	—
A. batizocoi	10	—	—	—	—	—
Mean	9	16	11	10	16	

[a]From ICRISAT (1981–1982).

2. *Hybrids between A. hypogae and Diploid Species*

a. Triploids. All attempts at crossing *A. hypogaea* with diploid species with an A or B genome have produced hybrids, although the crossing success varies depending on the species used and the direction of the cross (Table V). The interspecific hybrids are triploids, usually vigorous, flower profusely, and are mostly sterile (Smartt and Gregory, 1967; Raman, 1976; Gregory and Gregory, 1979; Seetharam *et al.*, 1973). There were an average of 8.8 univalents, 9.1 bivalents, and 1.0 trivalents per PMC in the triploids between *A. hypogaea* and eight diploid species (Singh and Moss, 1984b). Segregation was irregular and the percentage of stainable pollen grains varied in size. Sterility has been overcome by colchicine treatment to produce hexaploids for many hybrid combinations (Smartt and Gregory, 1967; Spielman *et al.*, 1979; Spielman and Moss, 1976; Company *et al.*, 1982).

Although tripolids are usually sterile, seeds were produced on several hybrids of different cross-combinations of interspecific *A. hypogaea* hybrids (Simpson and Davis, 1983; Singh and Moss, 1984b). Eighty-two percent of the progeny derived from selfing triploids were hexaploid, indicating the formation of competent unreduced gametes (Singh and Moss, 1984b). Progenies other than hexaploids had chromosome numbers ranging from $2n = 20$ to 59, indicating that gametes with fewer than 30 chromosomes can be functional. The hexaploids are of special interest as they have been obtained without the need for colchicine treatment, and, unlike colchiploids they have arisen from postmeiotic cells and thus pairing between wild and cultivated chromosomes has occurred. This is also true for the tetraploids; although produced at lower frequencies (8%) than the hexaploids (82%), they have the advantage of being at the same ploidy level as

the cultivated peanut. Whereas colchiploids have identical homologies and chromosomes will not segregate (except as a result of homologous pairing), the progenies arising from selfed triploids will be unique because chromosome segregation has occurred.

b. Hexaploids. Hexaploids, whether produced by colchicine treatment or from selfing of partially fertile triploids, have many undesirable characters associated with wild species, and none have been seriously considered suitable as the basis for developing the hexaploid peanut as a crop. Hexaploids are, therefore, an intermediate stage in a hybridization and selection process. The chromosome number must be reduced to the teraploid level and then undesireable wild characters eliminated. Tetraploidy can theoretically be achieved in one step by crossing hexaploids with diploid wild species. Although this will achieve the desired ploidy level and provide an opportunity to incorporate additional characters to *A. hypogaea* if a nonparental wild species is used, it also reduces the proportion of cultivated chromosomes in tetraploid derivatives. Hybrids between hexaploids and diploids have been difficult to produce due to embryo abortion (Halward and Stalker, 1984), and no tetraploid populations have been developed from these crosses.

Hexaploids vary in meiotic regularity and in fertility but can be crossed with *A. hypogaea*. Pods per 100 pollinations of these crosses varies from 7 to 25 (Table VI). From three different hexaploids backcrossed to BC_4 or to BC_5 generation, 6775 pollinations produced 894 pods (13%), but only 20 fertile plants with regular meiosis were selected from pregenies (ICRISAT, 1982).

c. Alteration of Ploidy Levels. Other ploidy manipulations are available to bypass the sterility of triploids and difficulties of backcrossing hexaploids. These all involve producing tetraploid derivatives of the wild species which can then be crossed with *A. hypogaea*. Further, the crosses

Table VI

Number of Pods Produced per 100 Pollinations in Successive Backcrosses of *A.* sp. Autotetraploids to *A. hypogaea*[a]

Autotetraploid	BC_1	BC_2	BC_3	Fertile stable derivatives
A. batizocoi	6	7	13	3
A. villosa	5	6	—	1
A. correntina	2	20	—	1
A. stenosperma	3	14	4	
A. spegazzinii	11	—	—	1
Mean	5	8	12	6 (Total)

[a]From ICRISAT (1981–1982).

have the advantage of producing wild × cultivated hybrids with a range of genome formulas (AABB, AAAB, or ABBB) which encourage intergenomic AB pairing, which Smartt *et al.* (1978a,b) predicted would be a problem in transferring wild species characters into *A. hypogaea*. The known genomes in section *Arachis* are the A and B of *A. hypogaea*: the B genome in wild *A. batizocoi* and the A genome of all other wild species except *A. spinaclava,* which has a D genome (Stalker, 1985a). There are differences in chromosome morphology and degree of pairing in hybrids between the wild A genome species (Singh and Moss, 1984a). Thus, the possible ploidy manipulations are to produce autotetraploids of the A, B, and D genomes and AB, AD, and BD amphiploids. In addition, amphiploids can be produced by crossing two different A genome species and doubling the chromosome number of the hybrid (ICRISAT, 1981; Gardner and Stalker, 1983). A wild range of crosses have been made and tetraploid derivatives produced.

i. Autotetraploids. Autotetraploids of *A. villosa, A correntina, A. stenosperma, A. duranensis, A. spegazzinii, A. chacoense, A. cardenasii,* and *A. batizocoi* have been produced (Singh, 1986a). Multivalents are frequent in autotetraploids; mean quadrivalent number in different autotetraploids ranges from 2.4 to 4.8 per PMC (Singh, 1986a), and pollen stainability ranges from 8 to 16%, except for autotetraploid *A. batizocoi,* which has 37% stainable pollen. Although vegetatively vigorous, autotetraploids are difficult to maintain due to reduced seed fertility; when crossed with *A. hypogaea,* from 2 to 11 pods per hundred pollinations (mean 5%) were produced, but with successive backcrosses to *A. hypogaea* the crossability increased as hybrids became more fertile (Table VI).

The first cross of an autotetraploid to *A. hypogaea* results in plants with genomic constitution AAAB or ABBB, and the absence of homologs for one genome could lead to increased homoeologous (A–B) pairing, which would increase the range of recombinants produced. Forty-chromosome, meiotically regular, and fertile plants can be obtained from autotetraploids within three generations of crossing to *A. hypogaea* (ICRISAT, 1982). For example, of five autotetraploids backcrossed to *A. hypogaea*, 3368 pollinations produced 249 pods (7.4%), from which six fertile derivatives were obtained. Fertile, stable derivatives can be obtained after one cross. Thus, although autotetraploids provide opportunity for homoeologous pairing when backcrossed with *A. hypogaea,* the number of resulting desirable recombinants is low.

ii. Amphidiploids. Presently there are 12 named diploid species in section *Arachis,* although as recent collections are studied this number will likely increase to 15–20 species in the group. Currently, there are only three genomes known, so only the genome combinations AABB, AADD, and BBDD can be produced. A sum of 10 AABB, 10 AADD, and 1 BBDD

Species combinations are thus possible among named species. However, amphiploids can also be produced from two A genome species, so the total number of amphiploids which can be produced among all described taxa is 132; this number includes reciprocal hybrids to account for possible differences in cytoplasmic effects. The amphidiploids represent an important gene pool for peanut improvement, and each one potentially incorporates genes from two species at the same ploidy level as cultivated peanuts. Further, each amphidiploid has at least one genome in common with *A. hypogaea*, which should promote gene transfer.

Many diploid interspecific hybrids have been produced between section *Arachis* species. Pairing and fertility in AA hybrids are reasonably good, with 8.96–9.8 bivalents per PMC and 40–85% pollen stainability. However, in AB, AD, and BD hybrids, paring and fertility are reduced to a mean number of 4.7–8.6 bivalents per PMC and pollen stainability ranging from 3 to 7% for AB, AD, and BD hybrids (Stalker and Wynne, 1979; Singh and Moss, 1982, 1984a; Stalker, 1985a). Comparisons of AA and AB hybrids with the corresponding amphiploids show that pairing is more regular and pollen stainability higher in the AABB amphiploids, but the reverse is true for the AAAA amphiploids (Table VII). When *A. hypogaea* was hybridized with the four amphiploid genotypes, little difference in frequencies of trivalents (mean = 0.34) or quadrivalents (mean = 0.07) per PMC are observed (Gardner and Stalker, 1983). AABB (*A. hypogaea* × amphidiploid) hybrids form fewer bivalents (mean = 14) and have more univalents (mean = 6) than would be expected from their genomic formula (ICRISAT, 1982; Singh, 1986b). Ten univalents in the AAAB hybrids were also observed which could easily be assigned to the B genome, but this assumption is not justified, due to the high univalent frequency in AABB hybrids. This indicates that in *A. hypogaea* × amphidiploid hybrids, both AB and A (wild)–A (Cultivated) pairing is highly probable. Pollen stainability and plant fertility in amphiploids and their hybrids with *A. hypogaea* is high enough to conduct a backcrossing program. Three fertile and stable derivatives were obtained from a total of 321 pods obtained after backcrossing *A. hypogaea* with AABB wild species amphiploids, and seven were obtained from 527 pods for AAAA amphiploids (ICRISAT, 1982). These frequencies of about 1% show that both types of amphiploids are a practical means of introgressing genes from wild species to *A. hypogaea*.

C. Intersectional Hybridization for Gene Introgression

Successful intersectional hybridization is rare in *Arachis*. Of 42 possible combinations, including reciprocals, attempted by Gregory and Gregory (1979), only eight hybrids were produced and none of these involved *A.*

Table VII

Frequency of Chromosome Pairing and Pollen Stainability in Diploid Hybrids, Amphiploids, and *A. hypogaea* × Amphiploids[a]

	I		II		III		IV		Pollen stainability[b]		
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	n[c]
AB hybrid	9.1	7.2–10.6	5.2	4.7–5.5	0.1	0–0.4	0	—	4	3–4	4
AABB amphiploid	3.7	1.5–6.3	16.6	14.9–18.2	0.4	0.3–0.5	0.4	0.2–0.7	(32)	8–60	4
AABB *A. hypogaea* × amphiploid	6.2	4.5–7.9	14.1	13.3–14.9	1.1	0.7–1.5	0.6	0.3–0.9	(63)	—	2
AA hybrid	0.3	0–0.8	9.6	9.4–9.7	0	—	0.1	0–0.2	77	74–81	4
AAAA amphiploid	2.4	0.9–3.5	13.6	13.0–14.5	0.4	0.2–0.8	2.2	1.4–3.0	(41)	—	4
AAAB *A. hypogaea* × amphiploid	10.6	9.7–11.8	11.1	7.2–13.0	1.1	0–2.4	1.0	0.3–1.4	(41)	35–51	7

[a]From ICRISAT (1981).

[b]Figures in parentheses indicate that data were not available for all hybrids or amphiploids.

[c]AB-AABB and AA-AAAA comparisons are for the same species combinations, but comparisons of amphiploids and hybrids with *A. hypogaea* involve different species combinations.

hypogaea. Direct intersectional hybridization with *A. hypogaea* is currently not a possible means of introgression from wild to the cultivated species. Either hormone treatment and/or embryo rescue will be necessary to produce hybrids, or highly crossable genotypes of *Arachis* must be found before germplasm from most species of the genus can be transferred to *A. hypogaea*.

Hybrids have been produced between annual diploids (with either an A or B genome) of section *Arachis* and a number of section *Rhizomatosae* accessions, and between section *Arachis* species and two accessions of section *Erectoides* (Gregory and Gregory, 1979). This suggests that diploid section *Arachis* species may be useful for introgressing genes from species distantly related to the cultivated peanut. Gregory and Gregory (1979) suggested elements in common between sections on the basis of crossability, even though the hybrids were all highly sterile. Stalker (1985b) studied a number of intersectional crosses including a 40-chromosome (*Erectoides* × *Erectoides*) × (*Erectoides* × *Rhizomatosae*) hybrid. The mean number of univalents was less than three, indicating a considerable degree of pairing between members of sections *Erectoides* and *Rhizomatosae* chromosomes. A common genome to taxa of both these sections is likely to exist. The intersectional hybrids have potential for making additional crosses and for ploidy manipulation to introgress genes into *A. hypogaea,* but there have not been concentrated efforts to do this.

D. *In Vitro* Techniques for Interspecific Hybridization

1. *Cell and Protoplast Culture*

Callus is generally easy to produce in *Arachis* but plant regeneration is difficult. Peanut cotyledons have been used to define biochemical parameters for callus growth in cultivars (Verma and van Huystee, 1971; Verma and Marcus, 1974; Russo and Varnell, 1978; Guy *et al.,* 1978). However, regeneration of plants from cotyledon callus of peanuts has not been obtained. Plants were recovered from tissue segments obtained by freeze-shattering cotyledons and growing the segments on moist filter paper (Illingworth, 1968). Mroginski *et al.* (1981) and Pittman *et al.* (1983) were able to regenerate plants *in vitro* from 3- to 5-day-old immature leaves.

Isolation of protoplasts in peanuts was first obtained by Jullian (1970), who mechanically broke the cells. Verma and van Huystee (1971) observed that the cell suspension cultures were heterogenous in size and balanced growth was unlikely. They then developed a method to obtain large numbers of uniform cells in suspension. By using mannitol solutions of different molarity, Holden and Hildebrandt (1972) were able to obtain pro- [illegible] the cells. Callus and roots have

subsequently been produced from single cells of peanuts (Yung-ru and Yu-Hung, 1978).

In summary, callus and protoplast culture techniques could greatly facilitate introgression to *A. hypogaea* for producing both initial F_1 hybrids and for manipulating polyploid levels to recover 40-chromosome hybrid derivatives. However, in *Arachis* the basic work to regenerate plants from single cells or callus is needed before techniques will be useful as a plant breeding tool.

2. *Ovule and Embryo Culture*

In vitro culture of ovules or embryos has successfully been used to produce interspecific hybrids is many genera (Narayanaswami and Norstog, 1964; Raghavan, 1980; Collins *et al.,* 1984). Numerous reviews have also been published describing media requirements and technical aspects of tissue preparation (North, 1976; Raghavan, 1977, 1980; Williams *et al.,* 1982; Collins *et al.,* 1984).

Embryo rescue in peanuts has had a long but sporadic history. Harvey and Schulz (1943) and then Nuchowiz (1955) initiated studies on regenerating peanut embryos. Martin (1970) regenerated peanut ovules only 0.3 mm in length to produce viable plants. However, in an attempt to duplicate Martin's results, Sastri *et al.* (1980), using the same media, could only produce callus, which became necrotic. Further, Johnson (1981) concluded that *in vitro* culture of small embryos required a two-step process in which ovules could be cultured until they became large enough to dissect embryos, and then embryos could be cultured to generate plants. Embryo culture in peanuts is difficult for some genotypes, while easy for others. Ziv and Zamski (1975) produced callus and mature seeds from pegs grown on the plant which were allowed to elongate into media until the pod enlarged and embryos reached the heart stage. They then cultured the heart stage embryo *in vitro*. Ziv and Sager (1984) further found that embryos would develop into young seedlings under red, blue, or far-red subsaturated flux densities, but pod formation was inhibited. Moss *et al.* (1985) cultured 1- to 4-day-old peg tips of *A. hypogaea* and reported ovule growth in many of the cultures.

Reports of rescuing interspecific hybrid embryos are less frequent than reports of *in vitro* culture of *A. hypogaea*. Bajaj *et al.* (1982) cultured 30-day-old F_1 embryos of *A. hypogaea* × *A. villosa*. However, this is a hybrid combination which can relatively easily be obtained without the aid of *in vitro* techniques. Bajaj (1984) reviewed the tissue culture literature and concluded that peanut self and hybrid embryos can be cultured *in vitro,* but application of techniques are yet to be realized. A series of media varying in auxins, cytokinins, and gibberellic acid produced no significant breakthroughs in ovule culture (Sastri *et al.,* 1982). Mallikarjuna and Sastri (1985b) and Stalker *et al.*

(1985) found genotypic differences for responses to gibberellic acid treatments to stimulate peg elongation in the interspecific crosses. Pod and seed development have further been stimulated by applying hormones to peg tissues 10 days after pollination (Sastri and Moss, 1982; Mallikarjuna and Sastri, 1985a). Although hybrid ovules have been stimulated to expand and shoots and roots to develop, fewer than five intersectional hybrids have been recovered (Sastri and Moss, 1982). A major obstacle to hybrid recovery is establishing cultured plants in the greenhouse.

IX. SUCCESSES AND POTENTIALS FOR UTILIZING *Arachis* GERMPLASM

Thousands of interspecific hybrids have been produced in many genera between wild species or between wild species and cultivars, but introgression of genes from wild species to genotypes with agronomic potential and subsequent cultivar release are rare. The major constraint to efficient utilization of interspecific hybrids is low fertility, which results in small populations and the inability to select desirable recombinants. Not only must the desirable genetic material be transferred into the cultivated genome, but yield and quality standards must also be met before wild species can be utilized by the grower.

Arachis monticola has been used for two cultivar releases. This situation is analagous to the use of *Avena sterilis* L. for improvement of *A. sativa* L. (Frey, 1976) or *Hordeum spontaneum* C. Kosch for improving *H. vulgare* L. (Rodgers, 1982), in which cases wild species which are completely cross-compatible with the cultigen were hybridized and selected.

Reports of utilization of species germplasm from taxa in which the first generation hybrids are sterile are much more difficult to find in the literature (Stalker, 1980a). Whole genomes may be added to a cultivar (such as in the case of sugarcane), or, when haploidy techniques are available (such as in the Solanaceae genera *Solanum*), diploids can readily be produced to select progenies with desired traits and tetraploids then be regenerated. However, few wild species in legume genera have been utilized for crop improvement.

In peanut, Stalker *et al.* (1979) described a highly variable interspecific hybrid population derived from an *A. hypogaea* × *A. cardenasii* cross which was self-ed for at least eight generations and hybrid derivatives having 40 chromosomes recovered. Selections were made from the population for *C. arachidicola* (Stalker, 1984), *C. personatum* (ICRISAT, 1984), and *P. arachidis* resistances (ICRISAT, 1984) and for resistance to several insects (Stalker and Campbell, 1983). Several interspecific hybrid populations are in the final stages of testing for release as general breeding materials, and some are already being used in [illegible] breeding programs. Making selections for high yields is as important as [illegible] and a recurrent selection

program has resulted in high-yielding lines from the same *A. hypogaea* × *A. cardenasii* population which have potential for cultivar release (Guok *et al.*, 1986). Several of the lines are now being tested in advanced yield trials in North Carolina and Virginia. Lines with high yields and *C. personatum* and *P. arachidis* resistances are also being tested in the national Indian yield trial. Not only are seed yields high in these lines, but there is little defoliation making the vegetative material an extremely valuable source for cattle feed.

Efforts to utilize species other than *A. cardenasii* are also being made to improve peanut production. Many fertile interspecific hybrid populations resulting from triploids or amphidiploids of *Arachis* species are currently being evaluated in several peanut breeding programs. Several of these hybrid derivatives have potential as cultivar releases.

In most crop species many cultivars have been released which have disease and insect resistances. However, in peanut only the cultivar NC 6 has been released for insect (southern corn rootworm) resistance (Wynne *et al.*, 1977). In addition, several cultivar releases have been made for disease resistances, including NC 8C, selected for Cylindrocladium black rot resistance (Wynne and Beute, 1983); Va 81B, selected for resistance to Sclerotina blight (Coffelt *et al.*, 1984); Southern Runner, resistant to late leafspot (Gorbet *et al.*, 1986); and several rosette-resistant cultivars in Africa (Gillier, 1978). Obviously missing from this list are cultivars resistant to the important diseases caused by early leafspot (*C. arachidicola*) and peanut rust (*P. arachidis*). Further, cultivars used in the United States have been selected for rather narrow environments and only one genotype for each disease has been released. This is the result of several interrelated factors. First, during the early days of peanut production relatively few diseases were economically important. In the United States, diseases have been controlled with chemicals, and there has been the common belief until recently that no variability was available in cultivated accessions. This last point concerning lack of variability resulted in large efforts by botanists, cytogeneticists, and plant breeders in cooperation with pathologists and entomologists to collect, evaluate, and attempt to utilize the wild species of the genus. In many other crop species the plant breeder has been responsible for acquiring, evaluating, and utilizing germplasm resources of related wild species along with those of the crop species. In *Arachis,* efforts have been more diversified, with teams of cytogeneticists working with plant breeders to identify and manipulate useful germplasm. Fortunately, many of the most important traits are found in species which are cross-compatible with the cultivated peanut. In the future, selection for leafspot and rust resistances have a high probability of making a significant contribution to peanut production, especially in tropical and semitropical areas where chemicals are infrequently used by the grower.

Significant progress toward exploiting the variability in the genus *Arachis* is being made. However, the most productive pathway to obtain 40-chromosome hybrid derivatives has not been determined, and perhaps

no one method will prove to be the best for all traits. Interspecific hybrid derivatives which are cross-compatible with *A. hypogaea* have been selected for fertility. Most desired traits in *Arachis* are multigenic and large populations must be derived to utilize the germplasm resources. Like other crop species, hybridization and fertility restoration processes are not easily accomplished, but significant progress is being made toward utilizing wild species of *Arachis*.

X. CONCLUSIONS

Utilization of wild species requires a collective effort by botanists, geneticists, cytogeneticists, and plant breeders. In *Arachis* there exists a large reservoir of germplasm with agronomic potential in numerous taxa. A taxonomic treatment of the genus is urgently needed to avoid confusion and to open communication channels among scientists. However, efforts have been made to evaluate available accessions for the economically important disease and insect pests of peanuts.

Arachis hypogaea is an allotetraploid species and will only hybridize with members of section *Arachis*. In this group are 15–20 species which have genomic similarities to the cultivated peanut. In addition, species accessions have been identified which are highly resistant to the most severe pests of cultivated peanuts. Utilization of these germplasm resources is hindered by sterility of interspecific hybrids due to ploidy and, to a lesser extent, genomic incompatibilities. Attempts to introgress genes conferring resistances to different diseases and insects have proceeded through direct hybridization and through ploidy manipulations. Traits can be transferred to the *A. hypogaea* genome using either pathway, but eliminating undesirable traits is a major problem which must be solved before growers will actually use the available germplasm.

The methodology to utilize species outside section *Arachis* is proceeding in the area of embryo rescue and recovery of hybrids via growth regulator applications to reproductive structures. However, the cytogenetic similarities among genomes of taxa in different sections remain unclear. Because hybrid embryos can be obtained for wide crosses in the genus, specialized techniques such as protoplast fusion may be unnecessary to utilize the germplasm resources. Regardless, efforts to utilize distantly related species should only be conducted when desired traits are not found in the cultivated species or in species closely related to *A. hypogaea*.

[illegible] have been used to create highly variable plant [illegible] and insect

crossing an unadapted *A. hypogaea* accession with a small-seeded diploid species. High yields were unexpected, but results of introgression greatly enhanced the potential exploitation of *Arachis* species germplasm. Perhaps the most valuable use of these hybrid derivatives will be in tropical and semitropical areas where chemicals are infrequently used, but even small increases in disease resistance will result in significant yield increases. In addition, fodder production is an important consideration in many production areas outside the United States. Yield and disease trials are now being conducted with advanced breeding lines derived from wild diploid species of *Arachis*.

REFERENCES

Abdou, Y. A. M., Gregory, W. C., and Cooper, W. E. 1974. *Peanut Sci.* **1**, 6–11.

Amaya, J. F., Young, C. T., and Hammons, R. O. 1977. *Oleagineux* **32**, 225–229.

Amin, P. W. 1985. *In* "Proceedings of an International Workshop on Cytogenetics of *Arachis*," pp. 57–60. ICRISAT Center, Patancheru, A.P., India.

Amir, J. 1969. *Ann. Bot.* **33**, 33–338.

Ashri, A. Offenbach, R., Cahaner, A., and Levy, A. 1977. *Z. Pflanzenzuecht.* **79**, 220–228.

Babu, C. N. 1955. *Indian J. Agric. Sci.* **25**, 41–46.

Bajaj, Y. A. S. 1984. *In* "Handbook of Plant Cell Culture" (P. V. Ammirato, D. A. Evans, W. R. Sharp, and Y. Yamada, eds.), Vol. 3, pp. 193–225. Macmillan, New York.

Bajaj, Y. A. S., Kumar, P., Singh, M. M., and Labana, K. S. 1982. *Euphytica* **31**, 370–375.

Banks, D. J. 1969. *J. Am. Peanut Res. Educ. Assoc.* **1**, 23–28.

Bentham, G. 1841. *Trans. Linn. Soc. (London)* **18**, 155–162.

Brennan, J. R. 1969. *Biologists* **51**, 71–82.

Bunting, A. H., Gibbons, R. W., and Wynne, J. C. 1985. *In* "Grain Legume Crops" (R. J. Summerfield and E. H. Roberts, eds.), pp. 747–800. Collins, London.

Campbell, W. V., and Wynne, J. C. 1980. *In* "Proceedings of the International Workshop on Groundnuts," pp. 149–157. ICRISAT, Patancheru, A.P., India.

Castillo, M. B., Morrison, T. S., Russel, C. C., and Banks, D. J. 1973. *J. Nematol.* **5**, 281–285.

Chevalier, A. 1933. *Rev. Bot. Appl. Agric. Trop.* **13**, 689–789.

Chevalier, A. 1934. *Rev. Bot. Appl. Agric. Trop.* **14**, 565–632, 709–755, 833–864.

Chevalier, A. 1936. *Rev. Bot. Appl. Agric. Trop.* **16**, 673–871.

Coffelt, T. A., Mozingo, R. W., Porter, D. M., and Allison, A. H. 1984. *Va. Agric. Exp. Sta. Bull.* **84**–1.

Collins, G. B., Taylor, N. L., and De Verna, J. W. 1984. *In* "Gene Manipulation in Plant Improvement" (J. P. Gustafson, ed.), pp. 323–383. Plenum, New York.

Company, M., Stalker, H. T., and Wynne, J. C. 1982. *Euphytica* **31**, 885–893.

Davis, K. S., and Simpson, C. E. 1976. *Proc. Am. Peanut Res. Educ. Soc.* **8**, 93 (Abstr.).

D'Cruz, R., and Tankasale, M. P. 1961. *Indian Oilseeds J.* **5**, 58–59.

Demski, J. W., and Sowell, G., Jr. 1981. *Peanut Sci.* **8**, 43–44.

Elkan, G. H., Wynne, J. C., and Schneeweis, T. J. 1981. *Trop. Agric. (Trinidad)* **58**, 297–305.

Fitzner, M. S., Alderman, S. C., and Stalker, H. T. 1985. *Proc. Am. Peanut Res. Educ. Soc.* **17**, 28 (Abstr.).

Foster, D. J., Stalker, H. T., Wynne, J. C., and Beute, M. K. 1981. *Oleagineux* **36**, 139–143.

[illegible] 1976. *Egypt. J. Genet. Cytol.* **5**, 460–482.

Gardner, M. E. B., and Stalker, H. T. 1983. *Crop Sci.* **23**, 1069–1074.
Ghanekar, A. M. 1980. *In* "Proc. International Workshop on Groundnuts," pp. 211–216. ICRISAT, Patancheru, A.P., India.
Gibbons, R. W. 1969. *In* "Third East African Cereals Conf.," Zambia and Malawi. Mimeo report.
Gibbons, R. W. 1980. *In* "Advances in Legume Science" (R. J. Summerfield and A. H. Bunting, eds.), pp. 483–493. Royal Botanic Gardens, Kew.
Gibbons, R. W., and Bailey, B. E. 1967. *J. Agric. Res.* **5**, 57–59.
Gibbons, R. W., and Turley, A. C. 1967. *Annu. Rep. Agric. Res. Council Cent. Afr.* pp. 66–90.
Gibbons, R. W., Bunting, A. H., and Smartt, J. 1972. *Euphytica* **21**, 78–85.
Gillier, P. 1978. *Oleagineux* **33**, 25.
Gorbet, D. W., Norden, A. J., Scokes, F. M., and Knauft, D. A. 1986. *Fla. Agric. Exp. Circue.* **S-324**, 13.
Gregory, M. P., and Gregory, W. C. 1979. *J. Hered.* **70**, 185–193.
Gregory, W. C. 1946. *Res. Farm., 69th Annu. Rep., N.C. Agric. Exp. Sta.* pp. 42–44.
Gregory, W. C., and Gregory, M. P. 1976. *In* "Evolution of Crop Plants" (N. W. Simmonds, ed.), pp. 151–154. Longman, London.
Gregory, W. C., and Gregory, M. P., Krapovickas, A., Smith, B. W., and Yarbrough, J. A. 1973. *In* "Peanuts: Culture and Uses," Chap. 3. Am. Peanut Res. Educ. Assoc., Stillwater, OK.
Gregory, W. C., Krapovickas, A., and Gregory, M. P. 1980. *In* "Advances in Legume Science" (R. J. Summerfield and A. H. Bunting, eds.), Vol. 1. International Legume Conference, Royal Botanic Gardens, Kew.
Guok, H. P., Wynne, J. C., and Stalker, H. T. 1986. *Crop Sci.* **26**, 249–253.
Guy, A. L., Heinis, J. L., and Pancholy, S. K. 1978. *Peanut Sci.* **5**, 78–82.
Hadley, H. H., and Openshaw, S. J. 1980. *In* "Hybridization of Crop Plants" (W. R. Fehr and H. H. Hadley, eds.), pp. 133–159. Am. Soc. Agron., Madison, WI.
Halward, T. M., and Stalker, H. T. 1984. *Agron. Abstr.* 69 (Abstr.).
Halward, T. M., and Stalker, H. T. 1985. *Agron. Abstr.* 56 (Abstr.).
Halward, T. M., and Stalker, H. T. 1987a. *Ann. Bot.*, **59**, 9–14.
Halward, T. M., and Stalker, H. T. 1987b. *Crop Sci.*, **27**, 456–460.
Hammons, R. O. 1970. *Crop Sci.* **10**, 459.
Harlan, J. R. 1976. *Crop Sci.* **16**, 329–333.
Harvey, R. H., and Schulz, E. F. 1943. *J. Am. Soc. Agron.* **35**, 631.
Hawkes, J. G. 1977. *Euphytica* **26**, 615–621.
Hebert, T. T., and Stalker, H. T. 1981. *Peanut Sci.* **8**, 45–47.
Hermann. F. J. 1954. *Agr. Monogr. U.S.D.A.* (19).
Hoehne, F. C. 1940. *Flora Bras.* **25(II)** 122, 1–20.
Holden, D. J., and Hildebrandt, A. C. 1972 *Phyton* **29**, 47–54.
Hull, F. H., and Carver, W. A. 1938. *Fla. Agric. Exp. Sta. Annu. Rep.* pp. 39–40.
Husted, L. 1931. *Am. Nat.* **65**, 476–477.
Husted, L. 1933. *Cytologia* **5**, 109–117.
Husted, L. 1936. *Cytologia* **7**, 396–423.
ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1981–1985. "Annual Reports." Patancheru, A.P., India.
Illingworth, J. E. 1968. *Hortic. Sci.* **3**, 274–276.
Jackson, C. R., and Bell, D. K. 1969. *Ga. Agric. Exp. Sta. Res. Bull.* **56**.
Jacobs, W. P. 1947. *Am. J. Bot.* **34**, 361–370.
Jacobs, W. P. 1951. *Am. J. Bot.* **38**, 307–310.
Jahnavi, M. R., and Murty, U. R. 1985a. *Cytologia* **50**, 747–758.

Jahnavi, M. R., and Murty, U. R. 1985b. *Theor. Appl. Genet.* **70**, 157–165.
Johansen, E. L., and Smith, B. W. 1956. *Am. J. Bot.* **43**, 250–258.
Johnson, B. B. 1981. *Environ. Exp. Bot.* **21**, 439 (Abstr.).
Johnson, D. R., Wynne, J. C., and Campbell, W. V. 1977. *Peanut Sci.* **4**, 9–11.
Jullian, M. 1970. *C.R. Hebd. Acad. Sci. Paris* **270**, 3051–3054.
Kawakami, J. 1930. *Bot. Mag. (Tokyo)* **44**, 319–328.
Kirti, P. B., Bharathi, M., Murty, U. R., and Rao, N. G. P. 1983. *Cytologia* **48**, 139–151.
Klesser, P. J. 1967. *S. Afr. J. Agric. Sci.* **10**, 919–927.
Knott, D. R., and Dvorak, J. 1976. *Annu. Rev. Phytopathol.* **14**, 211–235.
Kolawole, K. B. 1976. *Samaru Agric. Newslett.* **18**, 40–43.
Krapovickas, A. 1968. *In* "The Domestication and Exploitation of Plants and Animals" (P. J. Ucko and I. S. Falk, eds.), pp. 424–441. Duckworth, London.
Krapovickas, A. 1969. *Semin. Adv. Genet. Agric. Am. Lat., Maracay, Venezuela* **SAGA/B(d)**, 1–4.
Krapovickas, A. 1973. *In* "Agriculture Genetics. Selected Topics" (R. Moav, ed.), pp. 135–151. Wiley, New York.
Krapovickas, A., and Rigoni, V. A. 1951. *Rev. Invest. Agric. (Buenos Aires)* **5**, 289–293.
Krapovickas, A., and Rigoni, V. A. 1957. *Darwiniana* **11**, 431–455.
Krapovickas, A., Fernandez, A., and Seeligman, P. 1974. *Bonplandia* **3**, 129–142.
Kuhn, C. W., Sowell, G., Jr., Chalkley, J. H., and Stubbs, H. F. 1968. *Plant Dis. Rep.* **52**, 467–468.
Kuhn, C. W., Paquio, O. R., and Adams, D. B. 1978. *Plant Dis. Rep.* **62**, 365–368.
Kumar, L. S. S., D'Cruz, R., and Oke, J. G. 1957. *Curr. Sci.* **4**, 121–122.
Leuck, D. B., and Hammons, R. O. 1968. *J. Econ. Entomol.* **61**, 687–688.
Lynch, R. E., Branch, W. D., and Garner, J. W. 1981. *Peanut Sci.* **8**, 106–109.
Madhava, Menon, P., Raman, V. S., and Krishnaswami, S. 1970. *Madras Agric. J.* **57**, 80–82.
Mallikarjuna, N., and Sastri, D. C. 1985a. *In* "Proceedings of an International Workshop on Cytogenetics of *Arachis*," pp. 147–151. ICRISAT, Patancheru, A.P., India.
Mallikarjuna, N., and Sastri, D. C. 1985b. *In* "Proceedings of an International Workshop on Cytogenetics of *Arachis* ," pp. 153–158. ICRISAT, Patancheru, A.P., India.
Martin, J. P. 1970. *Oleagineux* **25**, 155–156.
Melouk, H. A., and Banks, D. J. 1978. *Peanut Sci.* **5**, 112–114.
Mendes, A. J. T. 1947. *Bragantia* **7**, 257–267.
Miller, L. I., and Troutman, J. L. 1966. *Plant Dis. Rep.* **50**, 139–143.
Moss, J. P. 1985a. *In* "Proceedings of an International Center Seminar on IARC's and Biotechnology." Int. Rice Res. Inst., Los Banos, Laguna, Philippines.
Moss, J. P. 1985b. *In* "Proceedings of an International Workshop on Cytogenetics of *Arachis*," pp. 93–99. ICRISAT, Patancheru, A.P., India.
Moss, J. P., Stalker, H. T., and Pattee, H. E. 1985. *Proc. Am. Peanut Res. Educ. Soc.* **17**, 22 (Abstr).
Mroginski, L. A., Kartha, K. K., and Shylok, J. P. 1981. *Can. J. Bot.* **59**, 826–830.
Murty, U. R., Rao, N. G. P., Kirti, P. B., and Bharathi, M. 1980. *"IARI Reg. Sta. Rep.*, Hyderbad, India.
Narayanswami, S., and Norstog, K. 1964. *Bot. Rev.* **30**, 587–628.
Norden, A. J. 1980. *In* "Hybridization of Crop Plants," (W. R. Fehr and H. H. Hadley, eds.), pp. 443–456. Am. Soc. Agron., Crop Sci. Soc. Am., Madison, WI.
North, C. 1976. *Acta Hortic.* **63**, 67–74.
Nuchowicz, A. 1955. *L. Agric. Louvain* **3**, 3–37.

Pallai, S. K., and Raju, E. C. 1975. *Flora Bd.* **164S**, 487–496.
Patil, S. H. 1968. *Can. J. Gen. Cytol.* **10**, 545-550.
Patil, S. H., and Bora, K. C. 1961. *Indian J. Genet.* **21**, 59–74.
Periasamy, K., and Sampoornam, C. 1984. *Ann. Bot.* **53**, 399–411.
Pittman, R. N., Banks, D. J., Kirby, J. S., Mitchell, E. D., and Richardson, P. E. 1983. *Peanut Sci.* **10**, 21–25.
Pompeu, A. S. 1977. *Ci. Cult.* **29**, 319–321.
Porter, D. M., Smith, D. H., and Rodriguez-Kabana, R. 1982. *In* "Peanut Science and Technology" (H. E. Pattee and C. T. Young, eds.), pp. 326–410. Am. Peanut Res. Educ. Soc., Yoakum, TX.
Prine, G. M., Dunavin, L. S., Moore, J. E., and Roush, R. D. 1981. *Fla. Agric. Exp. Sta. Bull.* S-275.
Raghavan, V. 1977. *In* "Plant Cell, Tissue and Organ Culture" (J. Reinert and Y. P. S. Bajaj, eds.), pp. 375–397. Springer-Verlag, Berlin.
Raghavan, V. 1980. *Int. Rev. Cytol. Suppl.* **11B**, 209–240.
Raman, V. S. 1958. *Indian Oilseeds J.* **2**, 20–23.
Raman, V. S. 1976. "Cytogenetics and Breeding in *Arachis*." Today and Tomorrow's Printers and Publishers, New Delhi.
Raman, V. S., and Kesavan, P. C. 1962. *Nucleus (Calcutta)* **5**, 123–126.
Resslar, P. M., 1980. *Euphytica* **29**, 813–817.
Resslar, P. M., and Gregory, W. C. 1979. *J. Hered.* **70**, 13–33 16.
Rodgers, D. M. 1982. *Diss. Abstr. Int.* **43**, 4, 937B–938B.
Russo, S. L., and Varnell, R. J. 1978. *Soil Crop Sci. Soc. Fla. Proc.* **37**, 34–36.
Saint-Smith, J. H., McCarthy, G. J. P., Rawson, J. E., Langford, S., and Colbran, R. C. 1972. "Peanut Growers Advisory, Leaflet No. 1178," p. 18. Div. Plant Industry, Dept. Plant Industry, Dept. of Primary Industries, Australia.
Sastri, D. C., and Moss, J. P. 1982. *J. Exp. Bot.* **33**, 1293–1301.
Sastri, D. C., Nalini, M. S., and Moss, J. P. 1980. *Proc. Symp. Plant Tissue Cult., Genet. Manip. Somat. Hybrid.* pp. 366–373. Bhabha At. Res. Center, Trombay, India.
Sastri, D. C., Nalini, M. S., and Moss, J. P. 1982. *In* "Tissue Culture of Economically Important Plants: Proceedings of an International Syposium"(A. N. Rao, ed.), pp. 42–57. Committee on Science and Technology in Developing Countries and Asian Network for Biological Sciences, National University of Singapore, Singapore.
Schenk, R. U. 1961. *Ga. Agric. Exp. Sta. Tech. Bull.* **22**, 5–53.
Seetharam, A., Nayar, K. M. D., Sreekantaradhya, R., and Achar, D. K. T. 1973. *Cytologia* **38**, 277–280.
Sharief, Y., Rawlings, J. O., and Gregory, W. C. 1978. *Euphytica* **27**, 741–751.
Simpson, C. E., and Davis, K. S. 1983. *Crop Sci.* **25**, 581–584.
Simpson, C. E., and Smith, O. D. 1974. *Tex. Agric. Exp. Sta. Bull.* L-1348.
Singh, A. K. 1985. *In* "Proceedings of an International Workshop on Cytogenetics of *Arachis*," pp. 107–117. ICRISAT, Patancheru, A.P., India.
Singh, A. K. 1986a. *Theor. Appl. Genet.* **72**, 164–169.
Singh, A. K. 1986b. *Theor. Appl. Genet.*, **72**, 433–439.
Singh, A. K., and Moss, J. P. 1982. *Theor. Appl. Genet.* **61**, 305–314.
Singh, A. K., and Moss, J. P. 1984a. *Theor. Appl. Genet.* **68**, 355–365.
Singh, A. K., and Moss, J. P. 1984b. *Peanut Sci.* **11**, 17–21.
Singh, A. K., Subrahmanyam, P., and Moss, J. P. 1984. *Oleagineux* **39**, 535–537.
Smartt, J. 1964. *Proc. Nat. Peanut Res. Conf. 3rd,* Auburn, AL. pp. 53–56.
Smartt, J. 1979. *Econ. Bot.* **33**, 329–337.
Smartt, J., and Gregory, W. C. 1967. *Oleagineux* **22**, 455–459.
Smartt, J., and Stalker, H. T. 1982. *In* "Peanut Science and Technology" (H. E. Pattee and C. T. Young, eds.), pp. 21–49. Am. Peanut Res. Educ. Soc., Yoakum, TX.

Smartt, J., Gregory, W. C., and Gregory, M. P. 1978a. *Euphytica* **27**, 665–675.
Smartt, J., Gregory, W. C., and Gregory, M. P. 1978b. *Euphytica* **27**, 677–680.
Smith, B. W. 1950. *Am. J. Bot.* **37**, 802–815.
Smith, B. W. 1956. *Am. J. Bot.* **43**, 81–89, 233–240.
Smith, D. H., and Littrell, R. H. 1980. *Plant Dis. Rep.* **64**, 356–361.
Smith, J. W., Jr., and Barfield, C. S. 1982. *In* "Peanut Science and Technology" (H. E. Pattee and C. T. Young, eds.), pp. 250–325. Am. Peanut Res. Educ. Soc., Yoakum, TX.
Spielman, I. V., and Moss, J. P. 1976. *Oleagineux* **31**, 491–494.
Spielman, I. V., Burge, A. P., and Moss, J. P. 1979. *Z. Pflanzenzuecht.* **83**, 236–250.
Stalker, H. T. 1980a. *Adv. Agron.* **33**, 111–147.
Stalker, H. T. 1980b. *In* "Proceedings of an International Workshop on Groundnuts," pp. 73–81. ICRISAT, Patancheru, A.P., India.
Stalker, H. T. 1981. *Crop Sci.* **21**, 359–362.
Stalker, H. T. 1984. *Euphytica* **33**, 529–538.
Stalker, H. T. 1985a. *Proc. Am. Peanut Res. Educ. Soc.* **17**, 23 (Abstr.).
Stalker, H. T. 1985b. *In* "Proceedings of an International Workshop on Cytogenetics of *Arachis*," pp. 65–79. ICRISAT, Patancheru, A.P., India.
Stalker, H. T. 1985c. *In* "Proceedings of an International Workshop on Cytogenetics of *Arachis*," pp. 119–123. ICRISAT, Patancheru, A.P., India.
Stalker, H. T., and Campbell, W. V. 1983. *Peanut Sci.* **10**, 30–33.
Stalker, H. T., and Dalmacio, R. D. 1981. *J. Hered.* **72**, 403–408.
Stalker, H. T., and Dalmacio, R. D. 1986. *Caryologia,* **51**, 617–629.
Stalker, H. T., and Wynne, J. C. 1979. *Peanut Sci.* **6**, 110–114.
Stalker, H. T., and Wynne, J. C. 1983. *Peanut Sci.* **10**, 59–62.
Stalker, H. T., Wynne, J. C., and Company, M. 1979. *Euphytica* **28**, 675–684.
Stalker, H. T., Campbell, W. V., and Wynne, J. C. 1984. *J. Econ. Ent.*. **7**, 53–57.
Stalker, H. T., Moss, J. P., and Seitz, M. H. 1985. *Agron. Abstr.* 1985, **72**, (Abstr.).
Subrahmanyam, P., Mehan, V. K., Nevill, D. J., and McDonald, D. 1980. *In* "Proceedings of an International Workshop on Groundnuts," pp. 193–198. ICRISAT, Patancheru, A.P., India.
Subrahmanyam, P., Williams, J. H., McDonald, D., and Gibbons, R. W. 1984. *Ann. Appl. Biol.* **104**, 467–476.
Sunrahmanyam, P., Ghanekar, A. M., Knolt, B. L., Reddy, C. V. R., and McDonald, D. 1985. *In* "Proceedings of an International Workshop on Cytogenetics of *Arachis*," pp. 49–55. ICRISAT, Patancheru, A.P., India.
Taubert, P. 1894. *In* "Die natuerlichen Pflanzenfamilien III Tiel" (A. Engler and K. Prantl, eds.), pp. 322, 324–325, Part 3.
Valls, J. F. M., Rao, V. R., Simpson, C. E., and Krapovickas, A. 1985. *In* "Proceedings of an International Workshop on Cytogenetics of *Arachis*," pp. 15–33. ICRISAT, Patancheru, A.P., India.
Varisai Muhammad, S. 1973. *Madras Agric. J.* **60**, 1428–1432.
Verma, D. P. S., and Marcus, A. 1974. *J. Cell Sci.* **41**, 331–337.
Verma, D. P. S., and van Huystee, R. B. 1971. *Exp. Cell Res.* **69**, 402–408.
Watson, I. A. 1970. *In* "Genetic Resources in Plants—Their Exploration and Conservation" (O. H. Frankel and E. Bennett, eds.), pp. 441–457. Davis, Philadelphia.
Williams, E. G., Verry, I. M., and Williams, W. M. 1982. *In* "Plant Improvement and Somatic Cell Genetics" (I. K. Vasil, W. R. Scowcroft, and K. J. Frey, eds.), pp. 119–128. Academic Press, New York.
Woodroof, J. G. 1973. *In* "Peanuts—Production, Processing, Products," 2nd Ed. Westport, CT.
Wynne, J. C. 1974. Ph.D. thesis, N.C. State Univ., Raleigh.
Wynne, J. C., and Beute, M. K. 1983. *Crop Sci.* **23**, 184.

Wynne, J. C., and Coffelt, T. A. 1982. *In* "Peanut Science and Technology" (H. E. Pattee and C. T. Young, eds.), pp. 50–94. Am. Peanut Res. Educ. Soc., Yoakum, TX.
Wynne, J. C., and Gregory, W. C. 1981. *Adv. Agron.* **34**, 39–72.
Wynne, J. C., Campbell, W. V., Emery, D. A., and Mozingo, R. W. 1977. *N.C. Agric. Exp. Sta. Bull.* 458.
Yasuda, S. 1943. *Jpn. J. Bot.* **13**, 243–253.
Yung-ru, S., and Yu-hung, L. 1978. *Proc. Symp. Plant Tissue Cult., Peking* p. 529.
Ziv, M. 1981. *Ann. Bot.* **48**, 353–359.
Ziv, M., and Sagar, J. C. 1984. *Plant Sci. Lett.* **34**, 211–218.
Ziv, M., and Zamski, E. 1975. *Ann. Bot.* **39**, 579–583.

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CEREAL–LEGUME INTERCROPPING SYSTEMS

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I. INTRODUCTION

In terms of land use, growing crops in mixed stands is regarded as more productive than growing them separately (Andrew and Kassam, 1976; Willey, 1979). Mixed cropping is practiced traditionally in many parts of Africa, Asia, and Latin America (Ahmed *et al.*, 1979) and interest in cereal–legume intercropping is developing in some temperate regions with warm climates such as Australia and the United States (Searle *et al.*, 1981; McCollum, 1982; Allen and Obura, 1983; Chui and Shibles, 1984). This may be due to some of the established and speculated advantages for intercropping systems such as higher grain yields, greater land use efficiency per unit land area, and improvement of soil fertility through the addition of nitrogen by fixation and excretion from the component legume (Agboola and Fayemi, 1972; Willey, 1979; Eaglesham *et al.*, 1981).

It seems worthwhile to develop cropping systems that have the capacity to maximize crop yields per unit land area while keeping the fertilizer nitrogen requirement to a minimum. The intercropping of legumes with cereals offers scope for developing energy-efficient and sustainable agriculture (Papendick *et al.*, 1976; IAEA, 1980).

Since the reviews by Willey (1979) on intercropping and by Trenbath (1974) on mixed cropping, many papers have been published from both temperate and tropical areas that emphasize general agronomic principles and research needs of intercropping systems. The recent book on multiple cropping systems (Francis 1986) summarizes some of that work and also develops some new ideas. The major emphasis in this chapter is on cereal–legume intercrop systems and we review the available information on various crop combinations. We examine cultural factors such as choice of compatible component crops with diverse morphology, crop geometry and