Chapter 3

GENETICS OF *ARACHIS HYPOGAEA* L.

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Both discontinuous and continuous variation is observed in agronomically important traits of the peanut (*Arachis hypogaea* L.). Most of these traits show inheritance patterns indicative of nuclear control, but some traits have been found to exhibit cytoplasmic inheritance as well. Knowledge of the genetics of traits is required for intelligent selection of the best breeding schemes by the plant breeder to attain the desired agronomic objective. This review summarizes recent research in peanut genetics and does not attempt to cover all the research reviewed previously by Gregory et al. (1951), Seshadri (1962), Gillier and Silvestre (1969), Hammons (1973a), and Shorter (1978).

The qualitative section is primarily restricted to traits for which a factorial model of inheritance has been proposed. It is essentially an update of the excellent review by Hammons (1973a).

Although several reports of the genetics of quantitative traits have been published since Hammons' (1973a) review, knowledge of the quantitative genetics of the peanut is still limited. An attempt is made to present the quantitative studies in terms of appropriate genetic theory and in relationship to plant improvement. The few traits of peanuts shown to be under non-nuclear control are also discussed.

GENETIC VARIABILITY

Although early literature contains reports to the contrary, there is considerable genetic variability in *A. hypogaea*. It is difficult to classify the intraspecific variation of a self-pollinated crop species such as the peanut. The infrequent cross-pollinations that occur give rise to intermediate types which confuse the classification. A number of papers have been published since 1950 that clarify the classification of *A. hypogaea*.

Gregory et al. (1951) distinguished 3 groups of peanuts based primarily on branching pattern: virginia, spanish, and valencia. This classification system was unsatisfactory for the intermediate forms found in the Guarani region of Paraguay and northeast Argentina (Krapovickas and Rigoni, 1960). Bunting (1955) named 2 basic types of branching as "alternative" and "sequential" and suggested that the 2 branching pattern groups should be considered as subspecies.

Krapovickas and Rigoni (1960) proposed the subdivision of *A. hypogaea* L. into 2 subspecies: *A. hypogaea* L. ssp. *hypogaea* and *A. hypogaea* ssp. *fastigiata* Waldron. Subspecies *hypogaea* has a central axis which never bears inflorescences (Stockton-Petit, 1895) and has lateral branches in which 2 vegetative branches alternate regularly with 2 inflorescences or reproductive branches (Bigi, 1950; Gregory et al., 1951; Bunting, 1955). The inflorescences are

simple; seeds show dormancy and plants are late maturing. In general, plants of subspecies *hypogaea* are prostrate but some erect cultivars are known. All the cultivars of this subspecies disseminated in Africa, Asia and the USA have 2 and sometimes 3 seeds per fruit but there exist in Peru and Mexico some forms with 4 seeds per fruit (Krapovickas and Rigoni, 1960).

A. hypogaea ssp. *fastigiata* is composed of plants that are always erect, with inflorescences in the central axis and without a regular pattern in the sequence of reproductive and vegetative branches. Inflorescences can be simple (var. *fastigiata*) or compound (var. *vulgaris*). Fruits are concentrated around the central axis; seeds do not show dormancy and the plants are early maturing.

Krapovickas (1968, 1973) further clarified the classification of peanuts and also related the variability to 5 geographic regions: Guaranian, Bolivian, Peruvian, Amazonian and the region of Goiás and Minas Gerais. Gregory and-Gregory (1976) extended the number of regions to 6 to include the northeast region of Brazil. The subspecific nomenclature was related to geographical regions as follows (Gregory et al., 1980):

A. hypogaea
- ssp. *hypogaea*
  - var. *hypogaea* - Bolivian, Amazonian
  - var. *hirsuta* - Peruvian
- ssp. *fastigiata* Waldron
  - var. *fastigiata* - Guaranian, Goiás and Minas Gerais, Peruvian, northeast Brazil
  - var. *vulgaris* Harz-Guaranian, Goiás and Minas Gerais, northeast Brazil

The Bolivian region was identified as the center of origin of the cultivated peanut, with the remaining regions as secondary centers of diversity (Figure 1).

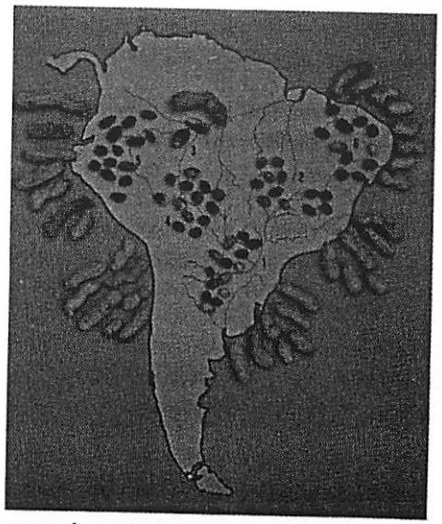

Fig. 1. Fruit and seed types characteristic of gene centers of *A. hypogaea* L. Geographic areas are (1) Guarani region (Paraguay-Paraná); (2) Goiás and Mina Gerais region (Tocantins, São Francisco); (3) Rondonia and northwest Mato Grosso (south Amazon); (4) Bolivian region (southwest Amazon); (5) Peruvian region (upper Amazon and west coast); and (6) northeastern Brazil

Gibbons et al. (1972) classified the variability that had been introduced or evolved in Africa during the last 5 centuries. They emphasized that each of the botanical varieties of Krapovickas' classification contained a large array of local cultivars. Gibbons et al. (1972) suggested that the variation in the African collection had arisen by hybridization and subsequent selection in Africa, making it an important secondary center of variation of both the Guarani and Bolivian peanuts of South America. Gregory et al. (1973) cautioned that additional exploration of the Bolivian center of origin is needed to resolve the relationship between South American and African variability.

QUALITATIVE CHARACTERS

Hammons (1973a) reviewed the literature on qualitative inheritance in peanuts prior to 1973. Increasing evidence indicates that qualitatively inherited traits are probably controlled by at least duplicate genes. This is largely due to the alloploid nature of the peanut and tends to confirm the theory of 2 genomes in *A. hypogaea*. Early reports of mono- and digenic models are as likely to be di-, tri-, or tetragenic, but population sizes were too small to distinguish between the simpler and more complex models. The number of genes may vary greatly among the parental lines used in an inheritance study. Obviously fewer genes will be detected to control a trait in closely related parents, while the number of different genes or alleles found controlling a trait will increase among more divergent parents. Cytoplasmic and/or maternal effects further complicate qualitative inheritance studies. The phenotypic expression of nuclear genes may be modified by the presence, absence, or interaction of different plasmons.

Plant Characters

Growth Habit. Growth habit has been studied extensively in peanuts. There are at least 2 distinct growth habits, erect (bunch or upright) and spreading (runner or trailing), and several intermediate forms. The spreading type was found dominant to erect by Badami (1928), Hayes (1933), Patel et al. (1936), Dalal (1962), Katayama and Nagatomo (1963), Tahir (1965), Coffelt (1974), Resslar and Emery (1978), and Jadhav and Shinde (1979), but Hassan and Srivastava (1966) concluded that erect was dominant to spreading. Balaiah et al. (1977) concluded that virginia bunch (semi-spreading) was dominant to both virginia runner (spreading) and spanish (erect). Ashri and coworkers (Ashri, 1964, 1968b, 1976a,b; Ashri and Goldin, 1963; Ashri and Levy, 1976) feel that when 2 or more genes are involved with complementary action, dominance applies to the allelic relationship and not to the trait.

Monofactorial control of growth habit was indicated in studies by Hassan and Srivastava (1966), Shchori and Ashri (1970), Balaiah et al. (1977), Jadhav and Shinde (1979), but others (Badami, 1928; Hayes, 1933; Patel et al., 1936; Higgins, 1938; John et al., 1954; Dalal, 1962; Ashri and Goldin, 1963; Ashri, 1964, 1968b; Coffelt, 1974; Resslar and Emery, 1978) found bifactorial and trifactorial (Ashri, 1976a,b; Ashri and Levy, 1976) control. The reported differences appear to depend upon the parental materials studied. In some cases, cytoplasmic influence has been indicated (Husted, 1934; Ashri and Goldin, 1963; Katayama and Nagatomo, 1963; Ashri, 1964, 1968b, 1976a,b; Ashri and Levy, 1976; Resslar and Emery, 1978). Ashri and coworkers (Ashri and Goldin, 1963; Ashri, 1964, 1968b, 1976a,b; Ashri and Levy, 1976) have proposed true plasmon inheritance of growth habit with at least 4 different plasmons involved. Resslar and Emery (1978), in repeating Ashri's early work (Ashri and Goldin, 1963; Ashri, 1964, 1968b), found that plasmon differences did not persist past the F_2 generation in North Carolina. Thus, Resslar and Emery (1978) proposed that maternal rather than cytoplasmic inheritance *per se* accounted for the reciprocal cross differences.

Several genotypes, parental phenotypes, and genetic models have been proposed for growth habit (Table 1). The differences reported in these studies are probably due to the natural variability that exists in the germplasm used. Three chemically induced mutants affecting growth habit-open-habit-1 (ob_1), open-habit-2 (ob_2), and spherical (sp) - were reported to be recessive and monogenically controlled (Shchori and Ashri, 1970). Levy and Ashri (1978) induced chemical and radiation mutants in both nuclear and plasmon loci affecting growth habit. Some mutants were heteroplasmic for growth habit and others had chromosomal aberrations.

Halevy et al. (1969) found that spreading plants contained a higher concentration of gibberellic acid antagonists and a particular gibberellic acid inhibitor not found in erect plants. Ziv et al. (1973) reported that the spreading habit was light-induced, requiring blue plus far-red light of a certain minimum intensity. Thus, the genic and cytoplasmic factors interact with light environments for the expression of growth habit. Therefore, differences in light could alter growth habit expression. Coffelt (unpublished) could not explain the genetic control of growth habit for plants grown in the greenhouse; however, when plants from the same crosses were grown in the field, a satisfactory F_2 ratio was observed (Coffelt, 1974).

The intermediate types in segregating generations complicate the determination of the inheritance of growth habit. Except for Ashri, the intermediate types have been classified as either erect or spreading. The misclassification of these intermediates could easily explain differences in the proposed bifactorial models. The genetic and environment interaction indicates that the experimental conditions need to be consistent between experiments or carefully monitored to understand interactions between experiments.

Plant Type. Hull (1937) classified 3 plant types in crosses between spanish and runner (virginia) types. He proposed that 2 duplicate loci controlled plant type. The valencia type is a double recessive, $va_1\ va_1\ va_2\ va_2$; spanish, $Va_1\ Va_1\ va_2\ va_2$; and runner (virginia), $va_1\ va_1\ Va_2\ Va_2$.

Branching Pattern. Branching pattern or the number and arrangement of reproductive and vegetative branches serve as a basis for varietal classification in peanuts (Gregory et al., 1973). Patel et al. (1936) reported branched (*BB*) dominant to nonbranched (*bb*). Similar results have been obtained by Tahir (1965), Patil and Mouli (1975a), and Balaiah et al. (1977), while Wynne (1975) proposed quantitative inheritance. Patil and Mouli (1975a) suggested that cytoplasmic factors may be present in a dwarf mutant that suppresses the normally dominant branched condition.

Mouli and Patil (1976) found a radiation-induced mutant with suppressed primary branches and no secondary or tertiary branches. They proposed that

Table 1. The genetic basis of growth habit inheritance in peanuts (*Arachis hypogaea* L.).

Genotype Female x Male	Phenotype[a] Female x Male	F_2 ratio	Author(s)
$S_1 S_1 S_2 S_2 \times s_1 s_1 S_2 S_2$	B x R	15 R:1 B	Hayes (1933)
	B x R	1 R:2 I:1 B	Higgins (1938)
	R x B	3 R:1 B	Patel et al. (1936); Dalal (1962); Jadhav & Shinde (1979)
[V,] Hb_1 Hb_1 Hb_2 Hb_2 x [V_4] Hb_1 Hb_1 hb_2 hb_2	R x B	3 R:1 B	Ashri (1968B)
$s_1 s_1 S_2 S_2 \times S_1 S_1 s_2 s_2$	B x B	9 R:7 B	Patel et al. (1936); Dalal (1962)
[V,] Hb_1 Hb_1 hb_2 hb_2 x	B x B	9 R:7 B	Ashri & Goldin (1963); Ashri (1964, 1968b); Resslar & Emery (1978)
[0] hb_1 hb_1 Hb_2 Hb_2			
[V_4 Hb_1 Hb_1 hb_2 hb_2 hb_5 hb_5 x	B x B	9 R:7 B	Ashri (1976a)
[G] hb_1 hb_1 hb_2 hb_2 Hb_5 Hb_5			
[G] hb_1 hb_1 hb_2 hb_2 Hb_5 Hb_5 x	B x B	9 R:7 B	Ashri (1976a)
[0] hb_1 hb_1 Hb_2 Hb_2 hb_5 hb_5			
[0] Hb_1 Hb_1 hb_2 hb_2 x	B x B	6 R:7 B	Ashri & Goldin (1963)
[V,] Hb_1 Hb_1 hb_2 hb_2			
[0] Hb_1 Hb_1 hb_2 hb_2 x	B x B	5 R:11 B	Ashri (1964, 1968b); Resslar & Emery (1978)
[V,] Hb_1 Hb_1 hb_2 hb_2			
[G] hb_1 hb_1 hb_2 hb_2 Hb_5 Hb_5 x	B x B	5 R:11 B	Ashri (1976a)
[V,] Hb_1 Hb_1 hb_2 hb_2 hb_5 hb_5			
[V,] Hb_1 Hb_1 Hb_2 Hb_2 x	R x R	All R	Ashri (1968b)
[0] Hb_1 Hb_1 Hb_2 Hb_2			
[0] hb_1 hb_1 Hb_2 Hb_2 x	B x R	3 R:1 B	Ashri (1968b)
[V,] Hb_1 Hb_1 Hb_2 Hb_2			
ohoh x OhOh	OH x B	3 B:1 OH	Shchori & Ashri (1970)
hb_3 hb_3 hb_4 hb_4 x Hb_3 Hb_3 Hb_4 Hb_4	B x R	11 R:5 B	Coffelt (1974)
Hb_3 Hb_3 Hb_4 Hb_4 x hb_3 hb_3 hb_4 hb_4	R x B	11 R:5 B	Coffelt (1974)
[0] hb_1 hb_1 Hb_2 Hb_2 hb_5 hb_5 x	B x B	7 R:9 B	Ashri (1976a)
[G] hb_1 hb_1 hb_2 hb_2 Hb_5 Hb_5			
[V,] Hb_1 Hb_1 hb_2 hb_2 hb_5 hb_5 x	B x B	3 R:1 B	Ashri & Levy (1976)
[M,] Hb_1 Hb_1 Hb_2 Hb_2 hb_5 hb_5			
$S_1 S_1 S_2 S_2 \times s_1 s_1 S_2 S_2$	R x B	3 B:1 R	Hassan & Srivastava (1966); Balaiah et al. (1977)
$S_1 S_1 s_2 s_2 \times s_1 s_1 S_2 S_2$	Sp B x Va B	3 Va B:1 Sp B	Balaiah et al. (1977)

[a]B = Bunch, R = runner, I = Intermediate, OH = pen Habit, Sp = spanish and Va = virginia.

the mutant was recessive to normal branching and monogenically inherited. The gene symbols *Bsp bsp* were designated to represent suppressed branching. They suggested that the use of the gene symbol *B* for both branching and brachytic should be resolved. Since brachytic also reflects a form of reduced branching, *B* could be used as a gene symbol for both, with the subscripts *sp* and *s* distinguishing the loci. Additional studies are needed to determine if these genes are allelic.

Perry (1968), working with 2 radiation-induced mutants (vegetative and reproductive) and 2 natural varieties, *hypogaea* (vegetative) and *fastigiata* (reproductive), concluded from F_1 hybrid behavior that (1) the radiation-induced reproductive form differed from the natural reproductive form, (2) the natural vegetative form was dominant to the 3 other forms, (3) the locus controlling the radiation-induced vegetative form was the same in 4 independent M_2 families, and (4) at least some of the loci controlling the radiation-induced reproductive form were the same in independent M_2 families.

Ashri et al. (1977) isolated 3 chemically induced mutants with reduced branching from the cultivar Congo. The presence of only 4 primary branches and no secondary or tertiary branches was due to a trisomic which was transmitted through either male or female gametes.

Main Stem Inflorescence. Hammons (1971) reported that the presence of inflorescences in main stem leaf axils was controlled by 2 sets of duplicate loci designated J_1-J_2-K_1-K_2, with epistasis between sets of loci. When both *J* loci or both *K* loci or all 4 loci are homozygous recessive, flowering in the main stem leaf axils occurs, giving an F_2 ratio of 225 vegetative:31 reproductive branches on the main stem. A range in the number of flowering axils was noted on the main stems of the plants. This may be due to the presence of 2, 3, or 4 sets of homozygous recessive loci or to modifying factors (Coffelt, unpublished). Wynne (1975) confirmed the model proposed by Hammons (1971) in a different set of intersubspecific crosses.

Plant Maturity. Both annual and perennial species of *Arachis* occur. Seshadri (1962) reported that perennial growth habit was dominant to the annual growth habit.

Within the annual species, various durations of the growing season are required for maturity. The length of the growing season is important for production in areas where environmental conditions such as rainfall and frost are limiting. Badami (1923, 1928) reported earliness (*e*) recessive to late (*E*). However, Patel et al. (1936) and Hassan (1964) reported incomplete dominance and assigned the symbols *L*, *l* for late and early maturity, respectively.

Dwarfism. Several dwarf mutants have been reported in peanuts. The most common form of dwarfism is the sterile brachytic. They have significantly shorter internodes, leaf rachises and petioles, and are sterile. They usually occur in the F_2 generation of intersubspecific crosses. Hull (1937) reported monogenic inheritance, while most other investigators (Hayes, 1933; Husted, 1934; Patel et al., 1936; Varisai Mohammad et al., 1966; Balaiah et al., 1977) have proposed a 15:1 ratio with 2 complementary factors. Ashri (1968a) found a third gene affecting the trait.

Coffelt and Hammons (1972) proposed tetragenic inheritance with an F_2 phenotypic ratio of 243 normal:13 sterile brachytic plants. This ratio was confirmed in the analysis of additional F_2 material (Coffelt and Hammons, 1973).

Analysis of other reports (Hayes, 1933; Husted, 1934; Patel et al., 1936; Varisai Mohammad et al., 1966; Ashri, 1968a; Balaiah et al., 1977) for goodness-of-fit to the 243:13 F_2 ratio indicated that the tetragenic model is more probable than the digenic model in most cases (Coffelt and Hammons, 1972).

Thus, sterile brachytic appears to be controlled by 4 unlinked loci. Gene symbols Bs_1 bs_1, Bs_2 bs_2, Bs_3 bs_3, and Bs_4 bs_4 have been proposed to represent the 2 sets of factors with complementary-duplicate action (Coffelt and Hammons, 1972). They suggested the *Bs* gene symbol to replace the *X*, *Y*, and *N* symbols proposed in earlier reports (Husted, 1934; Patel et al., 1936; Ashri, 1968a). *B* symbolizes the brachytic or dwarfing factor and the subscript *s* represents the sterile factor. Two or more dominant alleles, 1 each at any 2 loci, result in normal plants. The double recessive at any 3 or all 4 loci results in brachytic plants. Coffelt and Hammons (1973) reported that sterile brachytic was not associated with seed size, even though 40% more brachytics than expected were observed in the smaller seed size classes (<2.38 x 1.90 cm).

Patil and Mouli (1975a) reported on a fertile dwarf (Gujarat Dwarf) that spontaneously mutated from the valencia cultivar, Kopergaon-3. Crosses between Gujarat Dwarf and Kopergaon-3 indicated monogenic control of plant height with normal dominant to dwarf. However, in crosses of these 2 cultivars with other cultivars of normal height, they found that normal (♀) x normal (♂) and normal (♀) x dwarf (♂) crosses showed overdominance in the F_1, but dwarf (♀) x normal (♂) crosses exhibited no overdominance. They concluded that a cytoplasmic modifier was present in the Gujarat Dwarf or possibly more than 1 gene was involved in plant height determination and suggested the gene symbols *Dv dv* to represent dwarfism in valencia types.

Patil and Mouli (1977, 1978) isolated two X-ray-induced sterile dwarfs from Spanish Improved. The first (Patil and Mouli, 1977) was associated with asynaptic chromosome behavior. They proposed monogenic inheritance (*Dasy dasy*) with an F_2 phenotypic ratio of 3 normal:1 asynaptic dwarf. The second (Patil and Mouli, 1978) mutant had normal-appearing leaflets at the 2 basal nodes. However, subsequent leaflets and nodes were greatly reduced in size. The mutant was designated "bunchy top." Segregation indicated monogenic inheritance (*Dstu dstu*).

Shchori and Ashri (1970) chemically induced 3 dwarf mutants: dwarf-1 (dw_1), dwarf-2(dw_2), and dwarf-3 (dw_3). The dwarfs were all recessive to normal plant height and appeared to be monogenically controlled although dwarf-3 gave irregular segregations.

Ashri (1970a) reported a dominant chemically induced mutant with variable penetrance and expressivity in the M_1 of Dixie Anak. Heterozygous plants were extremely diminutive, dwarfed, and leafletless or intermediate or grew initially as diminutive and then produced some normal branches. The mutation was pleiotropic, also affecting the gibberellin levels in the plant. Diminutive plants produced normal growth when sprayed with gibberellic acid. The mutant allele is dominant with a lethal double recessive.

Nodulation. Gorbet and Burton (1979) reported the occurrence of nonnodulating plants in the progeny of a cross between a Florida breeding line 487A-4-1-2 and PI 262090. Their field results indicated that the nonnodulating trait was probably not inherited as a simple recessive, since nodulated progeny were obtained from selections classified as nonnodulated. The inheritance of this trait or the mode of action inhibiting the nodulation process has not been reported.

Nigam et al. (1980) found nonnodulating plants from crosses of a rust-resistant Peruvian cultivar, PI 259747, with 2 virginia cultivars, NC 17 and NC Ac 2731. Segregation of the F_2 and F_3 generations of the cross of PI 259747 and NC 17 indicated that a pair of independent duplicate genes control nodulation. The genetic constitution of the nonnodulating plants was inferred to be n_1 n_2 n_1 n_2.

Floral Characters

Flowers of *A. hypogaea* are aerial and papilionate. The color of the standard petal ranges from white to yellow to orange to a deep burnt orange or amber (Hammons, 1973a).

Corolla Color. Five distinct corolla colors have been reported by Hayes (1933) and John et al. (1954). Most reports (Hayes, 1933; Patil, 1965; Bilquez and Lecomte, 1969; Jadhav and Shinde, 1979) indicated the dark color dominant to light, but Kumar and Joshi (1943) reported incomplete dominance of orange to white. Kumar and Joshi (1943) reported that when Poona White was crossed to Poona Local from which it was selected a monogenic F_2 ratio of 1 orange:2 intermediate:1 white was obtained. The F_1 was also intermediate in color, indicating incomplete dominance or codominance of white and orange. Patil (1965) and Jadhav and Shinde (1979), using Poona White in crosses with yellow-flowered plants, reported F_2 ratios of 15 yellow:1 white, indicating duplicate loci. Patil (1965) proposed the gene symbols $Y_{fl\,1}$ $y_{fl\,1}$ and $Y_{fl\,2}$ $y_{fl\,2}$ to represent the loci.

Bilquez and Lecomte (1969) also reported digenic inheritance for corolla color. However, they assigned the gene symbols *Aa* to represent the control of red pigment (anthocyanin) production and *Yy* to represent the control of yellow pigment (probably flavone) production. They assigned the genotypes *AAYY* to Senegal 61-13, *aaYY* to Senegal 28-204, and *aayy* to Senegal 64-02, a mutant isolated from Senegal 28-204 following radiation. Bilquez and Lecomte (1969) explained a deficiency in the *yy* genotype as due to certation. Hammons (1973a) proposed that a recessive suppressor was active, giving a 13:3 F_2 ratio for the cross Senegal 28-204 x Senegal 64-02. He also suggested a trigenic ratio of 39:13:9:3 for the cross between Senegal 61-13 and Senegal 64-02.

Standard Crescent. The standard petal of the peanut flower has a purple crescent at the base from which purple lines radiate, ranging in intensity from absence to prominence (Hammons, 1973a). Three expressions involving the standard crescent have been studied: (1) presence vs. absence, (2) compact vs. loose, and (3) bright vs. no color.

Most reports have indicated purple crescent dominant to no crescent, with duplicate genes involved (Srinivasalu and Loganathan, 1959; Varisai Mohammad et al., 1966; Srivastava, 1968). It was also noted that these factors were closely related to those determining white testa and stem pigmentation (Srinivasalu and Loganathan, 1959; Seshadri, 1962; Varisai Mohammad et al., 1966; Srivastava, 1968). Srivastava (1968) proposed that the genes designated by Higgins (1940) as D_1 d_1 D_2 d_2 necessary for testa coloration also control the

presence of the standard crescent, with D_1 D_2 responsible for its presence. Srivastava (1968) felt that these factors were so critical for crescent formation that they be renamed as "crescent factors." However, Hammons (1973a) felt that evidence supporting their role in testa coloration (Higgins, 1940; Hammons, 1963; Yona, 1964; Harvey, 1967; Ashri, 1969) precluded this change.

Srivastava (1968) also classified crescents as absent, loose, or compact. Absent x compact crosses gave an F_2 ratio of 11 compact:4 loose:1 absent, while compact x loose crosses gave an F_2 ratio of 15 compact:1 loose. This was attributed to a cumulative effect of duplicate factors. Thus, a second pair of nonallelic factors appears to effect both testa color and the standard crescent. The second set of alleles which affect pigmentation of stem, peg, and crescent may be attributed to the duplicate factors R_1 r_1 R_2 r_2 proposed by Patel et al. (1936) and corresponding to the F_1 f_1 F_2 f_2 factors of Higgins (1940). Srivastava (1968) suggested designating these as pigment factors.

Srivastava (1968) also reported that variation in intensity of standard crescent color is under genetic control. When loose x absent crescent was crossed, the normal bright colored crescent of the F_1 segregated in a tetragenic ratio of 225 bright:15 feeble:16 absent crescents in the F_2, indicating that 2 sets of duplicate factors control bright crescent.

The control of 3 separate traits (standard crescent, stem pigmentation, and testa color) by the same 2 sets of duplicate factors requires additional study to determine if the same factors control all 3 traits. Some evidence for tight linkage of several factors was reported by Seshadri (1962). He reported that Philippine White has the factor for crescent formation but not stem pigmentation, and Nambiquara has stem pigmentation but not crescent formation. Srinivasalu and Loganathan (1959) and Varisai Mohammad et al. (1966) also reported variable relationships among pigmentation of stems, pegs, and seed testa.

Fading Time. Critical studies of fading time of flowers in peanuts are lacking. However, Hayes (1933) reported that early fading of flowers was dominant to late fading, while Seshadri (1962) reported the F_1 and F_2 to be intermediate in crosses between late fading (erect) and early fading (spreading) types.

Wing Petal Shape. Srivastava (1968) reported that boat shape was dominant to broad or scoop shape of the wing petal, with monogenic control in crosses between the 2 types. A cross between 2 broadshaped parents produced an F_1 with chinned or projected shaped wing petals. The F_2 segregated 9 chinned:7 broad, indicating that 2 factors (*ch* and *w*) that separately produce broad wing complementary combine to produce chinned.

Sterility. Coffelt and Hammons (1972) reviewed the literature for reports of sterility and found that most male-sterile plants were also female-sterile or unable to support embryo development. Hammons (1957-1972) has investigated the genetic behavior of a female-sterile but male-fertile plant. Although the trait is recessive, F_2 data indicate either mono- or trigenic inheritance, depending upon the parents.

Leaf Color. The subspecies *hypogaea* (virginia) and *fastigiata* (spanish-valencia) normally differ in leaf color. Badami (1923) and Dalal (1962) reported the dark green color of *hypogaea* dominant to the light green of *fastigiata*, with monogenic inheritance. Badami (1923) proposed the gene symbols *Gg*, while Dalal (1962) proposed the gene symbols G_1 g_1. In contrast, Patil (1966, 1969) reported a radiation-induced mutant, darker green, to be recessive with duplicate genes (Dr_1 dr_1 Dr_2 dr_2). Balaiah et al. (1977) reported incomplete dominance of leaf color with an F_2 ratio of 1 dark green:2 intermediate:1 light green.

Albinism. Yellow to white chlorophyll-deficient seedlings which die before flowering occur frequently in intersubspecific crosses. Badami (1928) suggested a trigenic model for inheritance of this character, with dark green the triplicate dominant and albino the triplicate recessive. Most others (Patel et al., 1936; Hull, 1937; Katayama and Nagatomo, 1963; Patil, 1965; Syakudo and Kawabata, 1965; Balaiah et al., 1977) report duplicate gene control with a 15:1 F_2 ratio. Several gene symbols were proposed (Table 2). However, Coffelt and Hammons (1971) found that their data were not compatible with either digenic or trigenic models. They proposed a trigenic model with duplicate loci controlling chlorophyll development epistatic to a third locus conditioning a zygotic lethal giving an F_2 ratio of 60 green:3 albinos:1 zygotic lethal. Re-evaluation of other data (Patel et al., 1936; Hull, 1937; Katayama and Nagatomo, 1963; Syakudo and Kawabata, 1965; Balaiah et al., 1977) indicated that they were not incompatible with the proposed trigenic model (Coffelt and Hammons, 1971; Hammons, 1973a). Coffelt and Hammons (1973) later confirmed the trigenic model with additional F_2 families. They also found that albinism was associated with small seed size. They suggested that the 2 most likely explanations were (1) that some metabolite necessary for chlorophyll formation is present in mature seed and absent in immature seed, thus the smaller sizes which are mostly immature seed have more albinos than the larger, mostly mature seed; or (2) that since albinism represents deranged seedling metabolism, a pleiotropic effect of genes controlling albinism could be smaller seed size. Other possibilities proposed were linkage or the presence of a small chromosomal deletion. Coffelt and Hammons (1973) pointed out that breeders could eliminate several undesirable plants from selection nurseries by sizing seed in the F_2 prior to planting. Conversely, geneticists could recover a higher proportion of mutants from the smaller seed size classes. This also appears to be true in induced mutants (Gregory et al., 1968).

Miryuta (1962) postulated a tetrasomic ratio of 1:35 for albinism. His model requires a self-regulating system of selective pairing of homologous sister chromosomes. Present knowledge of cytogenetic behavior and inheritance of other qualitative traits in peanuts rules out such preferential pairing (Hammons, 1973a).

Other Chlorophyll Deficiencies. Other chlorophyll-deficient mutants have been studied in peanuts in addition to albinism. Gillier and Silvestre (1969) reported a dominant yellow leaf mutant, but did not propose a genetic model for inheritance. Hammons (1973a) found a spontaneous recessive mutant to a rusty-leaf phenotype, but has not proposed a genetic model for inheritance.

Tripp (1968) reported monogenic inheritance of a naturally occurring virescent mutant that could be maintained only in restricted light. Tai and coworkers (1970, 1972, 1977) renamed the mutant krinkle lutescens and studied its relationship to other chlorophyll-deficient mutants (aureus, lutescens 0018, lutescens 0026, and virescent) and the dominant leaf mutant krinkle

Table 2. The genetic basis of the inheritance of albinism in peanuts (*Arachis hypogaea* L.).

Genotypes*	Phenotype	F_2 ratio	Author(s)
$G_1G_1g_2g_2 \times g_1g_1G_2G_2$ (Va) (Sp)	green x green	15 green: 1 albino	Patel et al. (1936); Balaiah et al. (1977)
$L_1L_1l_2l_2 \times l_1l_1L_2L_2$ (Sp) (Va)	green x green	15 green: 1 albino	Hull (1937)
$L_1L_1L_2L_2 \times l_1l_1L_2L_2$ (Val) (Va)	green x green	All green	Hull (1937)
$L_1L_1L_2L_2 \times L_1L_1l_2l_2$ (Val) (Sp)	green x green	All green	Hull (1937)
AAll x aaLL	green x green	15 green: 1 albino	Katayama & Nagatomo (1963)
$Clpl_1\ Clpl_1\ clpl_2\ clpl_2 \times$ $clpl_1\ clpl_1\ Clpl_2\ Clpl_2$	green x green	15 green: 1 albino	Patil (1965)
$C_1C_1c_2c_2LL \times c_1c_1C_2C_2$ (Sp) (Va)	green x green	60 green: 3 albino: 1 zygotic lethal	Coffelt & Hammons (1971,73)

*Va = virginia, Sp = spanish and Val = valencia.

(Hammons, 1964). The aureus, lutescens, and krinkle mutants were spontaneous, whereas the virescent (Patil, 1969) mutant was induced by radiation. Aureus and lutescens mutants are each determined by duplicate homozygous recessive loci, with duplicate dominant epistasis for normal green (Tai et al., 1970, 1977). They proposed the gene symbols $Au_1\ au_1\ Au_2\ au_2$ for aureus and $Lu_1\ lu_1\ Lu_2\ lu_2$ for lutescens. The F_1 plants were normal green in all crosses, a result which was attributed to complementary gene action.

Patil (1966, 1969) reported monogenic control of virescent in crosses between the mutant virescent and Spanish Improved, darker green mutant, and imparipinnate mutant. The studies by Shchori and Ashri (1970) and Tai et al. (1977) confirm monogenic inheritance. However, Patil (1966, 1969) reported a trigenic model when virescent was crossed with the induced mutant large-pod, leading him to conclude that a second locus was present to control virescent.

In crosses between aureus (*au*) and virescent (*v*), Tai et al. (1977) reported an F_2 ratio of 675 green:225 v:45 au:15 v-au:64 seedling lethals. In crosses between lutescens (*lu*) and virescent (*v*), they reported an F_2 ratio of 45 green:15 v: 3 lu: 1 seedling lethal. In crosses between lutescens (*lu*) and aureus (*au*), Tai et al. (1970) reported an F_2 ratio of 225 green:15 au:15 lu:1 seedling lethal.

Patil (1973) isolated persistent chlorophyll-deficient mutants in crosses between an X-ray-induced virescent (Patil, 1969) and the krinkleleaf mutant (Hammons, 1964) and in crosses between krinkle and Spanish Improved, which he designated as chlorina (*cl*). The F_2 of both crosses segregated 15 green:1 cl, indicating duplicate loci with 1 pair of recessive alleles each from krinkel and either Spanish Improved or virescent. The triple recessive virescent-chlorina produced a seedling lethal.

Genotypes for the mutants lutescens, aureus, virescent, krinkle, chlorina, krinkle-chlorina, darker green, imparipinnate, and large pod and the cultivar Spanish Improved are given in Table 3.

Patil and Mouli (1975b) found a dominant mutant with variegated leaves and standard petals in an irradiated population. They proposed that the mutant was allelic to the recessive virescent mutant (*v*) and suggested the gene symbol V_m. The mutant was not pollen-transmissible and not plasmon-controlled. Therefore, they proposed that another mutation occurred simultaneously in a closely linked gametophyte factor which prevented pollen transmission of V_m.

Table 3. Genotypes of chlorophyll-deficient mutants.

Mutant	Genotype
Lutescens	$VVAu_1\ Au_1\ Au_2\ Au_2\ lu_1\ lu_1$ $lu_2\ lu_2\ L_1\ L_1\ L_2\ L_2$
Aureus	$VVau_1\ au_1\ au_2\ au_2\ Lu_1\ Lu_1$ $Lu_2\ Lu_2\ L_1\ L_1\ l_2\ l_2$
Virescent	$w_1\ w_1\ W_2\ W_2\ v_1\ v_1\ v_2$ $v_2\ Au_1\ Au_1\ Au_2\ Au_2\ lu_1$ $lu_1\ Lu_2\ Lu_2\ l_1\ l_1\ L_2\ L_2$ $krkrcl_1\ cl_1\ Cl_2\ Cl_2\ Dr_1$ $Dr_1Dr_2\ Dr_2\ Imp_1\ Imp_1$
Krinkle	$VVCl_1\ Cl_1\ cl_2\ cl_2\ KrKr$
Spanish Improved	$VVcl_1\ cl_1\ Cl_2\ Cl_2\ krkr$
Chlorina	$VVcl_1\ cl_1\ cl_2\ cl_2\ krkr$
Krinkle-Chlorina	$VVcl_1\ cl_1\ cl_2\ cl_2\ KrKr$
Darker green	$V_1\ V_1\ dr_1\ dr_1\ dr_2\ dr_2$
Imparipinnate	$V_1\ V_1\ imp_1\ imp_1$
Large pod	$V_1\ V_1\ V_2\ V_2\ W_1\ W_1\ w_2\ w_2$

Shchori and Ashri (1970) reported recessive, monogenic inheritance of a chemically induced mutant, xanthamaculata (X_m) which has leaves speckled with yellow spots. Patil (1966, 1969) reported that the radiation-induced mutants xantha and albina were inherited as recessive lethals.

Physiological Relationships. Tai and Todd (1972) reported the concentrations of chlorophylls a and b, neoxanthin, violaxanthin, lutein, and carotenes in normal and mutant (aureus, krinkle lutescens, lutescens 0018, and lutescens 0026) plants. Carotenoids, especially xanthophylls, were greatly reduced in the lutescens mutants. Aureus did not retain chlorophyll as long as normal plants, while lutescens failed to accumulate the chlorophylls (especially b) to normal levels. The F_1 plants from crosses between normal and lutescens plants and between aureus and lutescens plants appeared normal both phenotypically and chemically. The chlorophyll a to b ratio in all lutescens mutants and aureus mutants was approximately twice the ratio of normal plants. From these results, Tai and Todd (1972) concluded that the aureus and lutescens mutants belong to Wettstein's second group of chlorophyll-deficient mutants, i.e., the mutants develop a normal chloroplast structure that is destroyed secondarily.

Benedict and Ketring (1972) and Benedict et al. (1974) reported the physiological effects of the induced mutant virescent. They concluded that the nuclear gene affects the early stages of plastid development, coding for the regulation of the synthesis of a cytoplasmic component that is essential for the development of mesophyll cells and plastids. Some of the pleiotropic effects are slower development of fructose-1,6-diP,NADP-glyceraldehyde-3-P-dehy-

drogenase, and NAD-malate dehydrogenase. Dark respiration, leaf expansion, enzyme activity in the reductive pentose phosphate pathway, plastid fine structure, soluble proteins, and rate of chloroplast development were also lower. They found these effects could be negated by placing plants in continuous darkness for 72-96 hours before being exposed to light. They proposed that although the chloroplast is a semi-autonomous organelle, nuclear gene control of chloroplast differentiation may not be independent of cellular growth.

The reports by Benedict and Ketring (1972), Tai and Todd (1972), and Benedict et al. (1974) with chlorophyll-deficient mutants, Yona (1964) and Halevy and Ashri (1971) with testa color, and Halevy et al. (1969) with growth habit are the only studies which have related the effect of genes to the physiology of peanuts. An understanding of the physiological pathways and their corresponding genetic control mechanisms may be helpful for future improvements in peanut breeding and ultimately peanut production.

Leaf Shape. Hayes (1933) reported valencia leaf shape recessive to Sine cultivars leaf shape. Hassan (1964) concluded that elliptical shape was recessive to elliptical-oblong shape. Badami (1928) noted that the F_1 was intermediate in leaf size and a wide range of sizes occurred in the F_2. These reports suggest that the inheritance of the normal leaf sizes observed in the subspecies is complex and may be quantitatively controlled. However, several natural and induced mutants have been found which indicate that qualitative inheritance is also involved in the control of leaf size.

Balaiah et al. (1977) studied the mutant Gujarat narrow leaf. Narrow leaf was conditioned by a single gene dominant to normal leaf size. Kansara (1967) and Matlock et al. (1970) reported partial dominance of narrow leaf mutants, with monogenic inheritance. Matlock et al. (1970) proposed the gene symbols *Nl nl* to represent narrow leaf. Coffelt (unpublished) has also observed dominance or at least partial dominance of the Gujarat narrow leaf trait; however, F_2 segregation patterns were inconsistent with a monogenic model.

Hayes (1933) reported a krinkled leaf mutant recessive to normal leaf, while Hammons (1964) found a dominant krinkle leaf mutant. Hammons (1964) proposed monogenic inheritance and the gene symbols *Kr kr* for the krinkle leaf mutant.

Srivastava (1970) reported a monogenic dominant mottled leaf mutant which also resulted in reduced yield and plant size.

Bhide and Desale (1970) studied a spear-shaped small leaflet mutant isolated from Kopergaon-1, with reduced internodal and calyx tube lengths. Backcrossing of the true-breeding mutant to the Kopergaon-1 parent indicated recessive, monogenic inheritance. Ashri (1970b) also found a small leaflet mutant. He concluded that inheritance was controlled by 2 duplicate genes, which he designated as Sl_1 sl_1 and Sl_2 sl_2.

Hammons (1953) described a radiation-induced change in leaflet shape called cup. It is characterized by ventrally involute leaflets, reduced plant and pod size, and sinuous succulent stems which snap under slight tension. It is controlled by a single recessive gene (*cu cu*) which has pleiotropic action.

Loesch (1961) and Loesch and Hammons (1968) reported the inheritance of 5 recessive radiation-induced mutants. The mutants flop, ilex, and $ilex_{50}$ were monogenically inherited, while the mutants hedera and corduroy were controlled by duplicate factors.

Branch and Hammons (1981) reported a second gene for the flop trait. In intersubspecific crosses between the mutant flop and normal leaf parents, they found digenic inheritance and an F_2 phenotypic ratio of 15 normal:1 flop. The gene symbols Fl_1 fl_1 Fl_2 fl_2 were proposed.

Other Foliage Characteristics: Bilquez et al. (1965) found an apetiolated leaf mutant that was inherited as a monogenic recessive. Hayes (1933) proposed that red color of leaf vein was dominant to the absence of color.

Balaiah et al. (1977) studied the inheritance of stomata number in crosses between Gujarat narrow leaf mutant and 4 spanish cultivars. Low stomate number ($<55/mm^2$) was recessive to high stomate number ($>55/mm^2$). Monogenic inheritance was observed in the cross with J-11, while digenic inheritance was observed in the crosses with AK12-24, S206, and TMV7. The following genotypes were proposed:

Gujarat narrow leaf: ls_1 ls_1 ls_2 ls_2

J-11: Ls_1 Ls_1 ls_2 ls_2

AK12-24, S206, TMV7: Ls_1 Ls_1 Ls_2 Ls_2

Reports of drought resistance in the Gujarat narrow leaf mutant may be due to the reduced stomate number ($<55/mm^2$) and not to leaf shape *per se*.

Mouli and Patil (1975) found a modified stipule shape in an irradiated population. Normal stipules are sickle-shaped and adnate. The mutant formed foliaceous stipules in the first 3 formed leaves and occasionally the fourth. Crosses with Trombay groundnuts (TG-3, 6, 8, and 9) indicated that paternal inheritance was involved. They proposed monogenic inheritance in the cross with TG-8 and an F_2 phenotypic ratio of 1:1. Digenic inheritance was observed in the crosses with TG3, TG6, and TG9 with an F_2 phenotypic ratio of 12:4. The mutant behaved as a recessive in all F_2 generations. Nagarajan and Aiyadurai (1958) reported the occurrence of a tricotyledonary mutant, but did not report a genetic model.

Stem Pigmentation. Reports by Badami (1928), Hayes (1933), Patel et al. (1936), Patil (1965), Prasad and Srivastava (1967), Balaiah et al. (1977), and Jadhav and Shinde (1979) indicated that dark or purple stem color is dominant to light or green stem color, but Culp et al. (1968) reported incomplete dominance. Monogenic inheritance has been reported in most studies with an F_2 phenotypic ratio of 3 dark:1 light (Hayes, 1933; Patil, 1965; Balaiah et al., 1977; Jadhav and Shinde, 1979). But 3 studies have indicated digenic inheritance with either a 9:7 F_2 ratio (Patil, 1965; Prasad and Srivastava, 1967) or a 15:1 F_2 ratio (Patel et al., 1936). Patel et al. (1936) proposed that the genes R_1 and R_2 controlling rose seed coat color also controlled stem pigmentation. Patil (1965) proposed the gene symbols *Pst pst Pstl pstl* for stem pigmentation.

Stem Pubescence. Stem pubescence has been reported as either dominant (Badami, 1928; Patil, 1965; Jadhav and Shinde, 1979) or incompletely dominant (Patel et al., 1936; Balaiah et al., 1977) to the absence of pubescence. Monogenic F_2 ratios of 3:1 or 1:2:1 have been suggested, depending upon whether complete or incomplete dominance was proposed. Patel et al. (1936) proposed the gene symbols *HH* and *hh* for hairy and sparsely hairy, respectively. Patil (1965) proposed the gene symbols *Hst* for hairy. Patil (1965) also reported that the gene for stem pubescence was linked to the gene *Rp* for reticulated pod, with a crossover value of 31.5%.

Pod and Seed Characters

Pod (shell) and seed testa are both maternal tissues in peanuts. Thus, F_1 embryos are surrounded by the maternal parent type pod and testa, and F_2 embryos by the F_1 pod and testa. The first genetic work on peanuts was initiated by van der Stok (1910) who studied pod size and testa color. Subsequent work has shown these to be among the most complexly inherited characteristics in peanuts (Hammons, 1973a).

Pod Size. All reports (van der Stok, 1910; Badami, 1928; Hassan, 1964; Balaiah et al., 1977) have indicated large pod size dominant to small pod size. Badami (1928) suggested that 3 factors controlled pod size, while Balaiah et al. (1977) reported monogenic inheritance with a good fit to an F_2 ratio of 3 large:1 small pods. Other reports have suggested quantitative inheritance.

Pod Constriction. Contrasting reports occur on the inheritance of pod constriction. Badami (1928) and Hassan (1964) proposed the absence of pod constriction was dominant to its presence. Badami (1928) proposed that 2 factors were involved, while Hassan (1964) suggested a trigenic complementary model. Badami (1928) classified 4 groups based on depth of constriction with the cylindrical type being the double dominant. Hassan (1964) proposed an F_2 phenotypic ratio of 45:19. He assumed that *A* is a basic gene for pod constriction with *B* and *C* being complementary to *A*, but not to each other. Accordingly, shallow constriction appears when *A* is present together with *B* or *C* or both. Unpublished data of Mauboussin (Gillier and Silvestre, 1969) and Ashri (Coffelt and Hammons, 1974b) indicated the presence of pod constriction dominant to the absence of pod constriction.

Coffelt and Hammons (1974b) also reported that pod constriction was dominant to the absence of pod constriction. Working with reciprocal crosses between Argentine (unconstricted) and Early Runner (constricted), they proposed F_2 ratios of 27 constricted: 37 unconstricted pods when Argentine was the female parent and 54 constricted: 10 unconstricted pods when Early Runner was the female parent. They suggested that 3 unlinked nuclear loci and 1 cytoplasmic factor interact with complementary duplicate action to condition pod constriction. The gene symbols $Pc_1\ pc_1$, $Pc_2\ pc_2$, and $Pc_3\ pc_3$ were proposed to represent the nuclear genes and *Aa* the cytoplasmic factor. One dominant allele at each of any 3 of the 4 loci conditions the presence of pod constriction. The Argentine cytoplasmic factor was recessive, while the Early Runner cytoplasmic factor was dominant. The genotypic formulae for Argentine and Early Runner were reported as $pc_1\ pc_1\ pc_2\ pc_2\ pc_3\ \ pc_3\ a$ and $Pc_1\ Pc_1\ Pc_2\ Pc_2\ Pc_3\ Pc_3$A, respectively. Other nuclear and cytoplasmic factors may be present to control the depth of constriction (Coffelt and Hammons, 1974b).

Other Pod Characteristics. Seshadri (1962) reported that in Badami's (1928) material thin pericarp was dominant to thick pericarp and was controlled by 5 factors. He also stated that thin pericarp was linked to pigmy seed, but neither linkage values nor the method used to determine linkage was reported.

Tan and Norden (1972) studied the inheritance of pod pubescence in crosses between 2 tomentose (very hairy) lines (F458-4-9-2 and F458-4-1-9 and 4 glabrous lines (F416-2-8-1, F431A-13-1-4, GA119-20, and PI 279956). All F_1 pods were tomentose. The F_2 pods from crosses involving F416-2-8-1 and F413A-13-1-4 segregated in a ratio of 5 tomentose:6 pubescent:4 puberulent:1 glabrous, while those from crosses involving GA119-20 segregated in a ratio of 5 tomentose:6 pubescent:5 glabrous. Crosses involving PI 279956 did not segregate into ratios that fit simple genetic models. From these results and the data from the F_3 generation, they postulated that pod pubescence was determined by 2 loci with additive gene action.

All reports (Badami, 1928; Patil, 1965; Mauboussin from Gillier and Silvestre, 1969; Jadhav and Shinde, 1979) have indicated that prominent or deep pod reticulation is dominant to shallow pod reticulation. Three studies (Patil, 1965; Mauboussin from Gillier and Silvestre, 1969; Jadhav and Shinde, 1979) with at least 1 parent in common (Poona White) have suggested monogenic inheritance, with an F_2 phenotypic ratio of 3 deeply reticulated pods:1 shallow reticulated pod. Patil (1965) proposed the gene symbol *Rp rp*. In contrast, Badami (1928) reported that at least 4 factors were involved.

Balaiah et al. (1977) proposed that the nonbeaked pod type was dominant to the beaked pod type. A monogenic F_2 ratio of 3 nonbeaked:1 beaked pod was observed.

Most researchers (Badami, 1928; Tahir, 1965; Balaiah et al., 1977) have indicated that 3 or more seeds per pod is dominant to fewer than 3 seeds per pod. However, Seshadri (1962) reported that fewer than 3 seeds per pod was dominant to 3 or more seeds per pod. Balaiah et al. (1977) proposed monogenic control, while Badami (1928) reported that 3 factors were involved.

Garet (1976) found shelling percentages to be quantitatively inherited. In contrast, Martin (1967) reported shelling percentage to be controlled by 1 pair of genes without dominance.

Seed Size and Shape. Hassan (1964) and Balaiah et al. (1977) reported large seed size dominant to small seed size. Balaiah et al. (1977) proposed monogenic control with an F_2 phenotypic ratio of 3:1. They also observed transgressive segregation and suggested the existence of an important complex of modifier genes. Martin (1967) reported 5 pairs of genes control seed size with 4 pairs having isodirectional effects.

Hayes (1933) and Balaiah et al. (1977) reported long seed shape dominant to short or round. Hayes (1933) proposed bigenic control with an F_2 ratio of 15 long:1 short, while Balaiah et al. (1977) proposed monogenic control with an F_2 ratio of 3 long:1 short. In contrast, Hull (1937) concluded that length was controlled by the maternal parent rather than by the embryo genotype.

Seed Dormancy. Seed dormancy is an inherent property of the peanut seed and is not related to the properties of the seed coat (Hammons, 1973a). Stokes and Hull (1930) reported that dormancy was incompletely dominant. Later, Hull (1937) proposed multigenic control since he observed a normal frequency distribution. However, 4 crosses had marked transgressive segregation over the dominant parent. In contrast, Lin and Lin (1971) reported monogenic behavior in the F_2 and F_3 generations. They proposed the gene symbol *Dd* for seed dormancy.

Rough Testa. Tripp (1968) proposed that rough or reticulated testa was controlled by duplicate genes with recessive epistasis. He observed an F_2 phenotypic ratio of 9 rough:7 smooth testa.

Testa Color. Testa color has been extensively studied in peanuts since van der Stok reported on testa color in 1910. Testa color can range from white to a

deep purple that appears almost black. Five classes of testa color are readily distinguished - white, tan, red, purple, and wine. Environmental factors and maturity can influence the intensity of each color. At least 3 loci have been identified for determining testa color. Their interaction with each other in controlling testa color has led to reports of several phenotypes, genotypes, and F_2 phenotypic ratios (Table 4).

Higgins (1940) proposed that pigment production is governed by duplicate genes $D_1\,d_1\,D_2\,d_2$, and that the testa color flesh (rose, pink, russet or tan) is also governed by duplicate genes $F_1 f_1\, F_2 f_2$. The latter are equivalent to the $R_1\,r_1\,R_2\,r_2$ genes proposed by Patel et al. (1936). The double recessive $d_1\,d_1\,d_2\,d_2$ is epistatic to the F loci and results in white testa. One dominant allele at either F locus plus 1 dominant allele at either D locus conditions flesh testa color. These loci also may interact with genes for red (R_1), wine (Wn), and purple (P) testa colors. These results were confirmed by Hammons (1963), Harvey (1967), Prasad and Srivastava (1967), and Balaiah et al. (1977). However, Hammons (1973a) proposed that although abundant evidence establishes the necessity of D for color and F for red testa, additional research is needed to determine if both are duplicate genes.

The relationship of the loci governing purple testa color (P) with the F and R loci is not clear. Patel et al. (1936) reported complete dominance of P and F_2 ratios indicating digenic epistatic inheritance (12 purple:3 red:1 rose) and trigenic inheritance (45 purple:15 rose:4 white). In contrast, Krapovickas and Rigoni (1952), Harvey (1967), and Srivastava (1968) reported that purple was incompletely dominant to flesh. Krapovickas and Rigoni (1952) felt that dark purple was determined by at least 2 gene pairs with cumulative effects, while Harvey (1967) found that although the R loci were not necessary for purple

Table 4. The genetic basis of testa color inheritance in peanuts (*Arachis hypogaea* L). Genetic symbols and F_2 ratios reported by the authors cited.[a].

Genotypes	Parental phenotypes[b]	F_2 ratio[b]	Author(s)
- x -	Red x light red	3:1	van der Stok (1910)
R x r	Red x rosy (brown)	3:1	Badami (1928)
- x -	Brick red x light tan	3:1	Stokes & Hull (1930)
- x -	Red x tan	3:1	Hayes (1933)
- x -	Brick red x russet	3:1	Husted (1934)
$pRd\,R_1\,R_2$ x $p\,rd\,R_1\,R_2$	Red x rose	3:1	Patel et al. (1936)
$P\,rd\,R_1\,R_2$ x $p\,rd\,R_1\,R_2$	Purple x rose	3:1	"
$p\,rd\,R_1\,R_2$ x $p\,rd\,r_1\,r_2$	Rose x white	15:1	"
$P\,rd\,R_1\,R_2$ x $p\,rd\,r_1\,r_2$	Purple x white	45P:15Rs:4W	"
$pRd\,R_1\,R_2$ x $p\,rd\,r_1\,r_2$	Red x white	45R:15Rs:4W	"
$P\,rd\,R_1\,R_2$ x $p\,Rd\,R_1\,R_2$	Purple x red	12P:3R:1Rs	"
- x -	Russet x tan	3:1	Hull (1937)
$F_1\,F_2$ x $f_1\,f_2$	Flesh x white	15F:1W	Higgins (1940)
$R\,F_1\,F_2$ x $r\,F_1\,F_2$	Red x flesh	3R:1F	"
$R\,F_1\,F_2\,d_1\,d_2$ x $r\,f_1\,f_2\,D_1\,D_2$	White x white	675R:225F:124W	"
$R\,F_1\,F_2\,d_1\,d_2$ x $r\,F_1\,F_2\,D_1\,D_2$	White x flesh	45R:15F:4W	"
$R\,F_1\,F_2\,d_1\,d_2$ x $R\,F_1\,F_2\,D_1\,D_2$	White x red	15R:1W	"
$R\,F_1\,F_2\,d_1\,d_2$ x $R\,F_1\,F_2\,D_1\,d_2$	White x red	3R:1W	"
R x r	Flesh x creme	3:1	Ilieff (1942)
V x v	Dark lilac x creme	1:2:1	"
$r\,F_1\,F_2\,D_1\,D_2$ x $r\,f_1\,f_2\,D_1\,D_2$	Pink x white	15pk:1W	Hammons (1957-72)
$R\,f_1\,f_2\,D_1\,D_2$ x $R\,F_1\,F_2\,d_1\,d_2$	White x white	225R:31W	Hammons (1963)
$R\,f_1\,f_2\,D_1\,D_2$ x $r\,F_1\,F_2\,D_1\,D_2$	White x flesh	45R:15F:4W	"
$R\,f_1\,f_2\,D_1\,D_2$ x $r\,F_1\,F_2\,d_1\,d_2$	White x white	All white	"
$r\,F_1\,F_2\,d_1\,d_2$ x $r\,f_1\,f_2\,D_1\,D_2$	White x white	225F:31W	"
$r\,F_1\,F_2\,d_1\,d_2$ x $r\,F_1\,F_2\,D_1\,D_2$	White x flesh	15F:1W	"
$r\,f_1\,f_2\,D_1\,D_2$ x $r\,F_1\,F_2\,D_1\,D_2$	White x flesh	15R:1W	Hammons (1964)
$R\,F_1\,F_2\,D_1\,D_2$ x $r\,F_1\,F_2\,D_1\,D_2$	Red x flesh	3R:1F	"

Table 4 (Continued)

Genotypes	Parental phenotypes[b]	F_2 ratio[b]	Author(s)
$R\,F_1\,F_2\,d_1\,d_2$ x $r\,F_1\,F_2\,D_1\,D_2$	White x flesh	45R:15F:4W	"
Rkr x rkr	Red x light rose	3:1	Patil (1965)
$Rk_1\,Rk_2$ x $rk_1\,rk_2$	Lt. rose x white	15:1	"
$Rk_1\,Rk_2$ x (?)	Lt rose x purple	45P:19	"
$Rd\,r_1\,r_2$ x $rd\,R_1\,R_2$	White x rose	45R:15Rs:4W	Varisai Muhammad et al. (1966)
$r\,F_1\,F_2\,d_1\,d_2$ x $r\,f_1\,f_2\,D_1\,D_2$	White x white	225F:31W	Harvey (1967)
$R\,F_1\,F_2\,d_1\,d_2$ x $R\,f_1\,f_2\,D_1\,D_2$	White x white	225R:31W	"
$R\,f_1\,f_2\,D_1\,D_2$ x $R\,F_1\,F_2\,D_1\,D_2$	White x red	15R:1W	"
$r\,F_1\,F_2\,d_1\,d_2$ x $R\,F_1\,F_2\,D_1\,D_2$	White x red	45R:15F:4W	"
$r\,f_1\,f_2\,D_1\,D_2$ x $r\,F_1\,F_2\,D_1\,d_2$	White x flesh	15F:1W	"
$r\,F_1\,F_2\,D_1\,d_2$ x $R\,f_1\,f_2\,D_1\,D_2$	Flesh x white	45R:15F:4W	"
$r\,F_1\,F_2\,D_1\,d_2$ x $r\,F_1\,F_2\,d_1\,d_2$	Flesh x white	3F:1W	"
$R\,F_1\,F_2\,D_1\,D_2$ x $r\,F_1\,F_2\,D_1\,d_1$	Red x flesh	3R:1F	"
$Pr\,F_1\,F_2\,D_1\,D_2$ x $p\,R\,F_1\,F_2\,D_1\,D_2$	Purple x red	12P:3R:1F	"
$Pr\,F_1\,F_2\,D_1\,D_2$ x $p\,r\,F_1\,F_2\,D_1\,D_2$	Purple x flesh	3P:1F	"
$r\,F_1\,F_2\,w\,D_1\,D_2$ x $r\,F_1\,F_2\,W\,d_1\,d_2$	Wine x white	45F:15Wn:4W	"
$r\,F_1\,F_2\,W\,D_1\,d_2$ x $r\,F_1\,F_2\,w\,D_1\,D_2$	Flesh x wine	3F;1Wn	"
$P_1\,P_2\,R_1\,R_2$ x $p_1\,p_2\,R_1\,R_2$	Purple x rose	15P:1Rs	Prasad & Srivastava (1967)
$p_1\,p_2\,R_1\,R_2$ x $p_1\,p_2\,r_1\,r_2$	Rose x lt. rose	15Rs:1	"
$p_1\,p_2\,R_1\,R_2$ x $p_1\,p_2\,r_1\,r_2$	Purple x lt. rose	255:1	"
- x -	Red x rose	13R:3Rs	Srivastava (1968)
- x -	White x red	39R:9Rs:16W	"
- x -	Rose x red	3Rs:1R	"
- x -	Rose x purple	1P:2:1Rs	"
- x -	Purple x white	105:45:30:45:15:16	"
$R\,T\,d_1\,d_2$ x -	White x red	9R:3Rs:4W	"
$R\,T\,d_1\,d_2$ x $R\,T\,D_1\,D_2$	White x red	11R:4W/R:1W	"
- x -	Purple (P/V) x red (NV)	36:12:9:3:3:1	"
- x -	Rose (NV) x R/V	3:1:2:1	"
- x -	Red x tan	1R:2Pk:1T	Gibbons (Hammons, 1973)
$r_1\,r_2$ - $D_1\,D_2$ x $R_1\,R_2$			
$F_1\,F_2\,d_1\,d_2$	R/V x white	15 color:1W	Ashri (1969)
$r_1\,R_2$ x $R_1\,r_2$	Flesh x R/W	13R:3F	Ashri (1970c)
$r_2\,v$ x $r_2\,V$	R x R/W	1:2:1	Branch & Hammons (1979)
R_2v x r_2v	PK x R	1:2:1	Branch & Hammons (1980)
R_2v x r_2V	PK x R/W	1:2:1:2:4:2:1:2:1	Branch & Hammons (1980)

[a]Table reproduced in part from Hammons (1973a) with author's permission.

[b]Abbreviations for F_2 ratios and parental phenotypes are: F = flesh, P = purple, Pk = pink, R = red, Rs = rose, T = tan, W = white, Wn = wine, R/W = red-and-white variegated, W/R = white-and-red variegated, P/V = purple variegated, NV = nonvariegated solid or self-color and R/V = red variegated.

testa color, they did modify the color. In crossing purple and white testa-colored cultivars, Srivastava (1968) observed a greyish red testa color in the F_1 and an F_2 phenotypic ratio of 105 greyish red:45 deep purple:30 light purple:45 deep red:15 rose:16 white. He proposed that purple testa color was not expressed when either the red or rose factors were heterozygous.

The inheritance of red testa color is also more complex than originally proposed. Most reports (Patel et al., 1936; Higgins, 1940; Hammons, 1963; Harvey, 1967; Srivastava, 1968, 1973; Jadhav and Shinde, 1979) indicate red dominant to flesh (pink or rose), with the factor for red testa interacting with the F loci to produce red testa. However, Krapovickas and Rigoni (1950) reported the occurrence of red testa in the F_2 and F_3 of crosses between 2 flesh (pink or rose) testa-colored lines. They suspected an epistatic factor in 1 of the flesh testa lines (Guaycuru) for red inhibition. Furthermore, Srivastava (1968, 1972) observed that flesh (rose) was dominant to red in 1 cross with monogenic inheritance. Ashri (1969, 1970c) observed similar results for inheritance of the red portion of the testa of a variegated seed coat. The red testa parent used by Srivastava (1968, 1972) was selected from a variegated testa line. Sri-

(1968, 1972) also proposed that a single factor *T* controlled flesh (rose) testa color instead of 2 factors (F_1 F_2) and was not necessary for the expression of red or purple testa color. In another study, Yona (1964) suggested that *R* was partially dominant to *r* in some crosses. Branch and Hammons (1980) also reported incomplete dominance of red testa in crosses of 9 flesh-colored lines with the red testa-colored line, Makulu Red. It is evident from these studies that at least 2 loci (R_1 r_1 R_2 r_2) are involved in controlling red testa. The first (R_1 r_1) is dominant to flesh and interacts with the *F* alleles. The second (R_2 r_2) is recessive to flesh and does not interact with the *F* alleles. It is not clear how these loci interact with each other and the other loci controlling testa color.

Harvey (1967) investigated the inheritance of wine testa color which he designated *Ww*. Wine testa color is apparently a double recessive which is independent of alleles at the *F* locus, but not the *D* locus.

Yona (1964) postulated that the precursor controlled by the *D* locus is chromogene, whose conversion to tannin is controlled by the *F* locus. The pigment phlobophene produces the flesh (pink, rose) testa color, and *R* produces a rose pigment that does not dissolve in ethanol. Yona (1964) further postulated that in the presence of *P*, the activity of some of the other controlling genes is altered or its products converted to other pigments. Halevy and Ashri (1971) isolated 2 pigments from the cultivar Congo, a cyanidin and a pelargonidin. They also isolated 3 pigments from the cultivar Pearl Black, 2 of which were cyanidins and 1 of which was peonidin. Glucose was found in all of the pigments. Further research is needed for complete understanding of the genetics of testa pigment biosynthesis.

No evidence for linkage was reported among the 7 loci for testa color studied by Hammons (1963) and Harvey (1967) or with krinkle (Hammons, 1964). Patel et al. (1936) proposed that the factors for rose-colored testa also produced purple stem color.

Variegated Testa. Variegated testa in peanuts has been reported as being due to splitting or rupturing of the outer epidermis caused by a disharmony in growth rates of seed coat and the embryo (Stokes and Hull, 1930; Ashri and Yona, 1965) and to inhibition of full development of the outer epidermal layer of the testa in certain regions (Branch and Hammons, 1979). Branch and Hammons (1979) proposed that since the testa is maternal tissue, disruptive growth of the outer testa and not the inner cell layers is triggered prior to fertilization during differentiation of the megasporangium and subsequent megasporogenesis. Therefore, it is unlikely that variegation is due to rupturing or splitting from uneven growth of the embryo and testa as proposed earlier (Stokes and Hull, 1930; Ashri and Yona, 1965).

Variegated testa has been reported as dominant (Stokes and Hull, 1930; Srivastava, 1968; Mauboussin cited from Gillier and Silvestre, 1969), partially dominant (Krapovickas and Rigoni, 1950; Srivastava, 1968; Gupta, 1974; Branch and Hammons, 1979, 1980), and recessive (Ashri and Yona, 1965) to nonvariegated testa. Monogenic (Srivastava, 1968; Gupta, 1974; Branch and Hammons, 1979, 1980) and digenic (Srivastava, 1968; Mauboussin cited from Gillier and Silvestre, 1969) inheritance has been proposed.

Hammons (1973a) stated that a white spot on the seed coat on the end opposite the micropyle may appear in some crosses involving 1 parent with white testa. Srivastava (1968) reported observing this in a cross between white (RT d_1 d_2) and red (RT D_1 D_2) seed coated peanuts. He observed red testas in the F_1 and an F_2 phenotypic ratio of 11 plain red:4 white spotted red:1 white, indicating digenic differences with cumulative effects.

In a cross between a purple variegated testa line and a red nonvariegated line, Srivastava (1968) observed that variegation was dominant with monogenic control. The epistatic effect of purple over red and the interaction between loci gave an F_2 ratio of 36 purple variegated:12 purple nonvariegated:9 red variegated:3 red nonvariegated:3 rose variegated:1 rose nonvariegated.

In another cross between a rose nonvariegated line and a red variegated line, Srivastava (1968) observed an F_2 ratio of 3 rose nonvariegated:1 red much variegated:2 red little variegated:1 red nonvariegated, indicating incomplete dominance of variegation. Branch and Hammons (1979, 1980) also reported incomplete dominance of variegation in a cross between a red variegated line and a red nonvariegated line, with an F_2 ratio of 1 variegated:2 slightly variegated:1 nonvariegated. Additional crosses of 9 lines with pink testa color and a red variegated line gave an F_2 phenotypic ratio of 1 pink variegated:2 pink partially variegated:1 pink:2 dark pink variegated:4 dark pink patially variegated:2 dark pink:1 red variegated:2 red partially variegated:1 red nonvariegated, the distribution expected from 2 independent loci with incomplete dominance for each gene pair (Branch and Hammons, 1980).

It appears that differences in testa variegation inheritance are due to interactions with parental materials studied. The white spot type of variegation is dependent upon digenic differences with cumulative effects (Srivastava, 1968; Hammons, 1973a). The purple and red variegated patterns are under monogenic control, with the purple completely dominant and red incompletely dominant (Srivastava, 1968; Branch and Hammons, 1979, 1980).

Srivastava (1968) first proposed the gene symbols *Vv* to represent variegated testa. These gene symbols are used by other researchers (Gupta, 1974; Branch and Hammons, 1979, 1980). These gene symbols should not be confused with the gene symbols *Vv* proposed by Patil (1966) to represent the induced mutant virescent.

Inner Testa Color. Rodriguez and Norden (1970) proposed that at least 4 loci control inner testa (seed coat) color. Depending upon the cross, they observed F_2 ratios suggesting monogenic, digenic, trigenic, or tetragenic inheritance. Based on their results, they suggested that 2 dominant complementary factors (*L* and *M*) produce a dark pigment. Two other factors (*N* and *S*) dilute the dark pigment to a lighter form or to white, respectively.

Arginine Content. Tai and Young (1977) concluded from their studies of 9 F_2 families from crosses among 6 peanut lines that free arginine level was controlled by 2 major genes with partial dominance for low arginine.

Induced Mutagenic Changes

Irradiation Induced. Irradiation mutation programs have been conducted in North Carolina (Gregory, 1968), India (Patil, 1966, 1969), Senegal (Bilquez et al., 1965), Israel (Ashri and Levy, 1974b), and South Africa (Tuchlenski, 1958). A description of the macromutants and their genetic control has been reviewed (Bilquez et al., 1965; Patil, 1966, 1969; Gregory,

1968; Hammons, 1973a) and is discussed in other sections of this chapter. Though of little economic value to the grower, some of the macromutants have contributed greatly to a better understanding of the basic genetics of the peanut.

Gregory (1965) demonstrated that as the magnitude of phenotypic effect of the mutation decreased, the frequency of mutant plants increased exponentially. Further, the more completely these large phenotypic changes are eliminated from the population, the more symmetrical the very small changes in the genome become. Stucker et al. (1968) derived the quantitative genetic expectations for estimating induced polygenic variance in mutant populations following elimination of macromutants, and demonstrated that the distribution of plus and minus mutations supported the hypothesis that these mutations occurred with about equal frequency (Gregory, 1968). The effects of these small changes on yield and seed size were also noted. Emery et al. (1972) gave further evidence for this hypothesis by showing that the mutated backgrounds of 9 macromutant families of cup appear to be randomly associated with the macromutant *cu* locus. The magnitude of the range of hybrid means and variances within 3 specific cup backgrounds, together with the differential environmental response of specific hybrids indicated the diverse nature of the mutated backgrounds.

Patil (1966, 1969) has reported isolating trisomic and tetrasomic mutations following irradiation. Based upon experiences with other crops, these mutants should be of value in cytogenetic research on peanuts (Hammons, 1973a).

Chemically Induced. Ashri and co-workers (Ashri and Goldin, 1965; Ashri, 1970a, 1972; Shchori and Ashri, 1970; Ashri and Levy, 1974a,b; Levy et al., 1979) conducted extensive research with chemical mutagens in Israel and found that the chemicals diethyl sulfate (DES), ethidium bromide (EB), sodium azide (SA), ethyl methane sulphonate (EMS), N-methyl-N'-nitro-N-nitrosoguanidine (MNNG), hydroxylamine (HA), nitrous acid (NA), 5-BU, ICR-170, acriflavine, chloramphenicol and erythromycin are mutagenic to peanuts. Ashri (1970a, 1972) and Shchori and Ashri (1970) observed polygenic mutants as well as macromutants, in agreement with the results of Gregory (1956, 1965, 1968) following irradiation.

Ashri (1972) proposed a scheme for identifying plasmon and nuclear gene mutations controlling growth habit following prolonged chemical mutagenesis since the peanut system is particularly well suited for detecting plasmon mutations for growth habit. The chemically induced macromutants and genetic models proposed for their inheritance are discussed in previous sections of this chapter.

Sensitivity. Gregory (1956) recognized differences in sensitivity among cultivars to irradiation early in his work. He felt that selection could be made among genetically similar stocks for greater or lesser sensitivity. Bilquez and Martin (1961) and Bilquez et al. (1965) also observed differences in sensitivity to irradiation in their mutagenic studies in Senegal. Emery et al. (1970) reported that sensitivity in peanut embryos to irradiation depended on moisture content.

Ashri and co-workers (Ashri and Goldin, 1965; Ashri, 1972; Ashri and Levy, 1974a,b; Levy et al., 1979) reported differences in physiological sensitivity among cultivars to chemical mutagenic agents similar to those observed for radiation. Using DES, Ashri (1970a, 1972) and Shchori and Ashri (1970) found both single trait and pleiotropic mutations with a higher induction rate in the cultivar least physiologically sensitive to DES. Ashri and Levy (1974a) reported several factors affecting sensitivity. Embryos in early developmental stages were more sensitive than in latter stages. Alkylating agents were more injurious than acridines. The concentration of the mutagen was the most important factor in treatments longer than 24 hours, while time of exposure was equally important in treatments less than 24 hours.

In comparing radiation (gamma-rays) and chemically (EMS) induced mutations, Ashri and Levy (1974b) found that gamma-rays gave a higher mutation rate. Dixie Anak was the cultivar most sensitive to both gamma-rays and EMS, with TBR [V_4] and Congo less sensitive. The types of mutants observed varied for mutagen and cultivar. All mutations were recessive.

Pest Resistance

Groundnut Rosette Virus. Berchoux (1960) reported that resistance to groundnut rosette virus (GRV) is governed by 2 recessive genes with duplicate action. An F_2 phenotypic ratio of 15 susceptible:1 resistant plant was observed. The gene symbols *Aa Bb* were proposed. Berchoux (1960) and Daniel and Berchoux (1965) reported that resistance is due to the production of an antivirus substance by resistant plants. This genetic information, plus the development of suitable artificial infection techniques for field screening of segregating populations for resistance to GRV, led to the successful transfer of GRV resistance to a commercial cultivar (28-20R.R.) using the backcross method of breeding (Mauboussin et al., 1970).

Cercospora Leafspots. Smartt (1964), Sharief (1972), and Sharief et al. (1978) concluded from triploid F_1 hybrids of crosses between resistant wild species and susceptible *hypogaea* lines that leafspot [*Cercospora arachidicola* Hori and *Cercosporidium personatum* (Berk. & Curt.)] resistance is recessive since all hybrids were susceptible. Abdou (1966), Sharief (1972), and Sharief et al. (1978) concluded resistance to early leafspot was independent of resistance to late leafspot. Kornegay et al. (1980) observed differences in resistance in F_1 but not in F_2 reciprocal crosses. They concluded that maternal, but not cytoplasmic factors, influenced leafspot resistance. In contrast, Coffelt and Porter (1982) observed significant differences in susceptibility to early leafspot between advanced progenies of reciprocal crosses of Chico and Florigiant. They concluded that cytoplasmic factors may be involved in determining resistance to leafspot. Sharief (1972) reported that 2 or more nuclear genes controlled resistance to leafspot, while Sharief et al. (1978) and Kornegay et al. (1980) proposed quantitative inheritance.

Peanut Rust. Bromfield and Bailey (1972) reported digenic control of rust (*Puccinia arachidis* Speg.) resistance, with resistance recessive to susceptibility.

Verticillium Wilt. Khan et al. (1973) found resistance to Verticillium wilt (*Verticillium dahliae* Kleb.) was controlled by a single recessive gene.

Necrotic-Etch Disease. Hammons (1973b, 1980) reported the occurrence of a necrotic-etch disease in peanuts with no known causal organism. The necrotic-etch character is recessive to the normal condition. Hammons (1973b) observed monogenic, digenic, and trigenic inheritance of resistance, depend-

ing upon the parental lines used. However, in a later report (Hammons, 1980), only digenic inheritance was observed, with an F_2 phenotypic ratio of 15 nondiseased:1 diseased plant. The gene symbols Ne_1 ne_1 Ne_2 ne_2 were proposed.

Sclerotinia Blight. Coffelt and Porter (1982), in studying advanced generation selections between Chico and Florigiant, observed significant differences between progeny of the reciprocal crosses in susceptibility to Sclerotinia blight (*Sclerotinia minor* Jagger). When Chico, a resistant line, was used as the female parent, the progeny were more resistant than when Florigiant, a susceptible line, was used as the female parent. This led them to conclude that cytoplasmic factors may be involved in determining resistance to Sclerotinia blight.

Other Pests. No genetic models have been reported for inheritance of resistance to any of the other major disease, insect, or nematode pests of peanuts. Hammons (1972) stated that the lack of this information hampers selection for pest resistance in commercially accepted cultivars.

Linkage

Only 3 linkage mapping experiments have been reported. Patel et al. (1936) observed nonrandom assortment of growth habit and branching type in a cross between Philippine White (spreading, branched) and Corientes-3 (bunch, nonbranched). They found about 30% crossing-over between genes for spreading and branched. Patil (1965) reported 40.4% crossing-over between genes for growth habit and pod reticulation and 31.5% crossing-over between genes for stem hairiness and pod reticulation.

Three other possible linkages have been observed. Badami (1928) observed an association between violet color and hardiness in stems and of thin pericarp with small seed. Coffelt and Hammons (1973) found an association between small seed size and the occurrence of albino seedlings. Stalker et al. (1979) proposed that a linkage group for several undesirable characters (late maturity, small seeds, separated pod cells, and low yield) was associated with leafspot resistance in crosses between *A. hypogaea* (PI 261942 or PI 261943) and the wild species GKP 10017 (*A. cardenasii* Krap. et Greg. *nom. nud.*). Their conclusions were based on the fact that high yielding lines with acceptable characteristics tended to be more susceptible to leafspot than plants with low yield and undesirable characters.

No effort has been made to assign linkage groups for these few instances of qualitative character linkage. With the increased study of inheritance of qualitative traits, more cases of linkage should be found, especially since many traits involve genes on 2 or more chromosomes.

QUANTITATIVE CHARACTERS

Many important traits of the peanut, such as yield, are quantitatively inherited. The exploitation of the genetic variability of quantitative traits through hybridization, inbreeding, and selection is an important feature of a peanut breeding program.

This section will review the quantitative genetic research most significant to peanut breeders such as (1) nature of genetic variability, (2) type of gene action, (3) heritability, (4) correlation among traits, and (5) the implications of results from quantitative genetic studies on breeding procedures.

Diversity in the Germplasm Pool

Several surveys of genetic variation have been made for characters of economic importance. These investigations have not always recognized that populations including subspecific groups are more variable than a collection of cultivars of a single botanical variety (Hammons, 1973a).

Many researchers have reported means, variances, and associations among quantitative traits for collections of peanut cultivars. Several purported broad-sense estimates of heritability have also been obtained from groups of unrelated cultivars. An extensive review of these studies from the first report by Emery (1899) until 1973 was made by Hammons (1973a).

Character Associations. Rachie and Roberts (1975) suggest that groups of characters are associated and passed on to their progeny after crossing in peanuts. This makes it difficult to develop new cultivars with desired characteristics, especially if the parents are from different subspecific groups. Several studies have been conducted which contribute information on character interrelationships. Traits indicative of yield such as number and weight of pods per plant, number and weight of seed per plant, and pod and seed size were reported to be positively associated in peanut cultivars (Sun, 1932; Hayes, 1933; Maralihalli, 1933; Humphrey, 1942; Lin, 1954; Dorairaj, 1962; Jaswal and Gupta, 1966, 1967; Chandra Mohan et al., 1967; Badwal and Gupta, 1968; Gopani et al., 1970; Sangha and Sandhu, 1970; Coffelt and Hammons, 1973). Significant negative associations were observed between number of pods per plant and seed size measured as g per 100 seed. Inconsistent results have been found for pod weight per plant and g per 100 seed (Lin, 1954; Badwal and Gupta, 1968; Sangha and Sandhu, 1970; Dholaria et al., 1972; Coffelt and Hammons, 1973).

Mital and Mehta (1954) recognized that associations among traits varied with botanical variety. Differences in the correlation of traits among cultivars of a botanical variety, although obvious considering that character association is used to place cultivars into botanical varieties, have now been well established (Mishra, 1958; Dorairaj, 1962; Badwal and Gupta, 1968; Dholaria et al., 1972).

Jaswal and Gupta (1966) found that pod yield was correlated with 4 yield components but regression analysis indicated that only the number of mature pods and the number of pegs influenced yield in 73 virginia peanut (spreading) cultivars. In a similar study using 59 spanish (erect) cultivars, Jaswal and Gupta (1967) found that the number of mature pods and branch length influenced yield. Sangha and Sandhu (1970) and Khangura and Sandhu (1972) reported that pod yield in 30 virginia cultivars was strongly associated with the number of primary and secondary branches, the length of primary and secondary branches, the number of mature pods and shelling percentage. Using path coefficient analysis, Khangura and Sandhu (1972) showed the length of the primary branch had the greatest direct effect on pod yield. Almost all other characters affected pod yield through the length of the primary branch. Path coefficient analysis was used by Lin and Chen (1969) and Lin et al. (1969) to

determine the relationship of yield components to yield in a series of studies conducted in Taiwan. For 173 cultivars, including virginia runner, virginia bunch and spanish types, intertype differences for several traits were significant. In a second study, seasonal differences significantly influenced the components that affected yield.

Diversity in the peanut germplasm pool has also been demonstrated by several studies involving peanut cultivars in which the researcher estimates genotypic variance, genetic advance and heritability values for a group of unrelated genotypes. In a collection of 60 cultivars, including 20 each of spreading (virginia), semispreading and erect (spanish) growth habits, Badwal et al. (1967) estimated genotypic variance (GV) expressed as a percentage of the phenotypic variance. They also estimated genetic advance (GA) as a percentage of the mean. They reported that GV and expected GA were higher for 100 seed weight than for yield and several other traits. Several other workers have used similar techniques and have also estimated such additional parameters as broad-sense heritability (H = genotypic variance/phenotypic variance), genotypic coefficient of variability (GCV = genotypic variance/mean x 100) and phenotypic coefficient of variation (PCV = phenotypic variance/mean x 100).

Basu and Asoka Raj (1969) obtained high heritabilities for days to flowering, pods per plant, and 100 pod weight. The GCV was high for pods per plant. Majumdar et al. (1969) obtained a wide range for PCV for several characters measured in 45 cultivars collected from different growing areas of India. All traits had a high H except for the number of pods and pod yield. Sangha and Sandhu (1970) studied the components of yield in 27 cultivars each of the virginia and spanish type. GCV and GA were high for 4 yield components within each group but only for pod number in both types. A large amount of genetic variability was found for several traits such as number and weight of pods per plant for 108 cultivars investigated by Dixit et al. (1970). Most traits had high H, especially 100-pod and 100-seed weight. Variation in yield and yield-contributory traits at high and low fertility levels using 20 bunch and 20 spreading cultivars was studied by Dholaria and Joshi (1972). High estimates of H for number of pods, number of branches, and 100-seed weight were found. Expected GA was greatest for pods per plant and 100-seed weight at high fertility. Varisai Mohammad et al. (1973) found that PCV was greatest for 100-pod weight for virginia runner cultivars when the trait was measured for 337 bunch, 191 semispreading, and 191 spreading cultivars. In a study repeated 4 times in 3 years using 27 cultivars, Sangha (1973) found PCV, GCV, H and GA to be high for 100-seed weight and number of pods but only moderately high for pod yield. Kushwaha and Tawar (1973), using 40 cultivars from India and Africa, observed high H for 100-pod weight and 100-seed weight and high GA for yield, 100-seed weight and several other components of yield. Sivasubramanian et al. (1977) found high GCV, H, and GA values for height of main stem and pods per plant but estimates for the same parameters were low for pod yield.

These studies demonstrate that considerable variation exists among peanut cultivars for yield, components of yield, and several other traits. These estimates of genotypic variance, heritability, genetic advance, and other associated parameters from groups of unrelated peanut cultivars are not useful to the breeder in predicting the genetic consequences of manipulating the variability. Since it is well established that sufficient variability exists for yield and yield components in cultivated peanuts, additional estimates of genotypic variance, heritability, and genetic advance for yield and its associated components in small groups of unrelated cultivars are not necessary.

Heritability and Correlation in Segregating Generations

Genetic variability, heritability, and correlations have been estimated less frequently in segregating generations than in collections of cultivars. These estimates from segregating populations are useful in understanding the genetic consequences of hybridization, inbreeding and selection in the peanut. Bernard (1960) estimated the genetic and environmental variability for 10 traits, including seed yield, number of pods, weight per seed and leafspot scores in the F_1 -F_4 generations of 4 crosses between 8 diverse cultivars and 15 crosses between 6 F_4 selections from the first group of crosses. All traits had sufficient genetic variability for progress to be made through selection. The weight of seed had a higher estimate of heritability than seed yield. Although several traits were correlated with yield, selection using an index including yield and any or all of the remaining 9 characters was not superior to selection for yield alone.

For 15 characters in the F_2 generation of a diallel made among a virginia, valencia, and spanish line, Syakudo and Kawabata (1965) found that genotypic correlations were higher than phenotypic correlations, although both types were generally low. Estimates of broad-sense heritability were low for all traits except height of the main stem (0.82) and a plant type index (0.89). Oil content was not correlated with the other traits in these crosses.

Lin (1966) found that the major portion of genetic variance among F_2 and F_3 progenies of a spanish x virginia cross was due to dominance effects for number of pods and yield (weight of pods), while additive effects were most important for main stem length and length of branches. Estimates of heritability for number of pods and yield were relatively small. Lin et al. (1971) found that planting densities affected estimates of heritability in an F_5 bulk population. Estimates of broad-sense heritability were higher for yield and number of pods in wide than in narrow spacings.

Martin (1967) studied hybrid and backcross progenies between 2 cultivars with contrasting oil content, shelling outturn, and seed weight and obtained heritability estimates of about 70% for each trait. He determined that cultivar differences were due to 2, 1, and 5 pairs of alleles for oil content, shelling outturn, and seed weight, respectively. Oil content was not correlated with seed weight.

Correlation coefficients and heritability estimates for 9 components of yield in an F_2 population between Argentine (spanish type) and Early Runner (virginia type) were obtained by Coffelt and Hammons (1974a). The characters measured were the number of pods and seeds per plant, pod and seed weight per plant, g per 100 seeds, length and breadth of 10 pods, number of seeds per pod, and pod length/pod breadth ratio. Highly significant positive correlations were found between number of pods and pod weight, number of seeds and seed weight, pod weight and number of seeds per pod and seed weight,

and number of seeds and seed weight. Selection for increases in any of the 4 characters—number of pods, pod weight, number of seeds, or seed weight—should result in a corresponding increase in the 3 remaining traits. Pod breadth was also significantly correlated with g per 100 seeds. Other significant correlations were obtained; however, they were small in magnitude. Broad-sense estimates of heritability for g per 100 seeds, pod length, pod breadth, and the pod length per pod breadth ratio were high (0.71-0.90). Low heritability estimates were observed for number of pods, pod weight, number of seeds, seed weight, and seeds per pod.

Tai and Young (1975) studied the inheritance of protein and oil content using 6 cultivars and their F_2 populations. They concluded that both protein and oil content were quantitatively inherited. Correlations between protein and oil content were negative and varied from nonsignificant to highly significant in the various populations. Holley and Hammons (1968) had previously reported a tendency for a reciprocal relationship between oil and protein content. However, enough exceptions were found for the 26 cultivars tested to invalidate an absolute reciprocal relationship between oil and protein.

The inheritance of amino acid and fatty acid composition in the parents and the F_2 generation of 3 crosses was studied by Tai and Young (1975). These traits were also found to be controlled by genes acting in a quantitative manner. Some transgressive segregants were found for some of the amino and fatty acids. Correlations among the 18 amino acids and 8 fatty acids were inconsistent across parental and F_2 populations.

Nine F_2 families from crosses among 6 peanut cultivars and breeding lines were used by Tai and Young (1977) to investigate the inheritance of dry matter accumulation and free arginine as a measure of maturity. Dry matter accumulation was inherited as a quantitative trait, whereas the free arginine level was found to be controlled by 2 major genes with partial dominance for low arginine. Broad-sense heritabilities were often lower for dry matter (0.38 to 0.78) than for the arginine level (0.60 - 0.93).

Mohammed et al. (1978) estimated heritabilities, phenotypic correlations, and genotypic correlations for yield, fruit size, and maturity using the F_2 and F_3 generations of 2 crosses between a virginia and 2 spanish lines. Broad-sense heritability estimates based on within-plot variance for yield were high, ranging from 0.42 to 0.82 for 4 year location environments. Broad-sense heritability estimates were also high for fruit length, ranging from 0.79 to 0.92. Estimates of heritability for several maturity traits were lower and less consistent over environments. Estimates of heritability computed by offspring-parent regression were much lower than variance estimates of heritability for all traits. Heritability for the 2 crosses for yield of pods was only 0.21 and 0.16 and for weight of seeds 0.10 and 0.06. Heritability estimates for fruit size were higher, 0.42 and 0.50, for fruit length, 0.18 and 0.27, and 0.41 and 0.51 for weight of seeds from 20 fruits. Estimates of heritability for a fruit maturity index were 0.20 and 0.35 for the 2 crosses. The discrepancy between the variance and regression estimates of heritability for the F_2 populations suggests that the use of broad-sense heritabilities computed from within-plot variances for early generations of crosses involving diverse peanut lines are inflated for predicting genetic advance from selection. The variance estimates of heritability are biased upwardly with the most important source of bias being inflated

genotypic variance estimates, probably resulting from competition among plants within a plot. The regression estimates of heritability are probably more useful in predicting response to selection. These estimates are biased less by nonadditive genetic variance and genotype x environment interaction.

Gibori et al. (1978), using a 9 x 9 diallel cross involving widely divergent cultivars as parents, estimated heritabilities and correlations for pod size and yield, days to first flower, and weight of plant from the F_2 generation. Their estimates of heritability were calculated from the diallel data using the methodology of Hayman (1954, 1958) and Jinks (1954, 1956). These authors suggest that the high heritability estimate obtained for pod yield per plant (0.79) indicates that phenotypic selection of best plants in large F_2 populations followed by careful progeny testing would increase productivity. Pod yield per plant was not highly correlated with the other 3 traits, suggesting that selection for yield cannot be accomplished by indirect selection. Gibori et al. (1978) found a positive but low genetic correlation between fruit size and yield, indicating that selection for both large pods and high yields is possible.

Layrisse et al. (1980) estimated correlation coefficients for cross means and Spearman rank correlations for general combining ability effects of 9 traits measured on the F_2 generation diallel cross of 10 diverse parents. Correlation coefficients based on cross means are phenotypic; those based on general combining ability effects are phenotypic correlations that approach genetic correlations. Fruit yield and seed yield were significantly correlated with oil and protein content. Oil and protein contents were positively correlated but only the phenotypic correlation was significant.

Wynne and Rawlings (1978) estimated heritability for yield and several fruit traits for the F_5 and F_6 generations of a cross between 2 virginia cultivars. Narrow-sense estimates of heritability over reciprocal crosses and environments ranged from 0.54 for yield per plot to 0.89 for fruit length. Progress from selection in late generations should be expected from these heritability estimates.

Sandhu and Khehra (1977) determined heritability and genetic advance for the F_3 progenies of 2 peanut crosses for resistance to leafspot, pod yield, 100-kernel weight, oil content, and protein content. Broad-sense estimates of heritability were high for all traits except yield in both crosses. However, the estimated advance from selection was only high for resistance to leafspot. Hadley et al. (1979) estimated heritability for resistance to Cylindrocladium black rot disease to range from 0.48 to 0.65, depending upon the method of calculation. Their estimates were obtained in the greenhouse for the F_1 and F_2 generations of a 4-parent diallel.

Type of Gene Action

The development of more efficient breeding procedures requires an understanding of the type of gene action governing the inheritance of quantitative traits (Brim, 1973). Although methods for characterizing genetic variability in self-fertilizing species are available (Hanson and Weber, 1961; Cockerham, 1963; Stuber, 1970), little information has been obtained on the various types of gene action and their relative importance in the inheritance of important traits in peanuts.

Heterosis. Heterosis or inbreeding depression usually indicates that nonadditive gene action is important. Several investigators have reported estimates of heterosis for peanuts. Marked heterosis for vegetative traits and pod yield were obtained for seveal crosses by Higgins (1940) when he crossed 16 cultivars in diallel. Individual plant yields were highest for spanish x virginia crosses. Gregory et al. (1980) analyzed data from a diallel of 10 diverse peanut lines made in 1944. He found hybrid vigor for F_1 hybrids between subspecies. Most F_2 hybrid means were equal to midparental values although some F_2 means were exceptionally high or low. Syakudo and Kawabata (1963) found appreciable heterosis for top weight in virginia x spanish and valencia x virginia F_1 hybrids. Hybrid vigor was not found in crosses between cultivars within each botanical variety, nor in spanish x valencia crosses. Pod length of F_1 plants was intermediate between that of the parents. Lin (1966) found significant hybrid vigor for length of main stem and branches for F_2 plants grown in Taiwan from the cross of a spanish type by Florispan Runner (a virginia cultivar). The superiority of the F_1 hybrids over their better parents for yield as well as for the number of branches and leaflet length was shown by Hassan and Srivastava (1966) using crosses among 3 cultivars differing in maturity and growth habit. Parker et al. (1970) noted that F_1 crosses of valencia x virginia gave greater heterosis than did crosses of virginia x spanish or valencia x spanish for several seedling characters measured in a controlled environment for a diallel cross of 6 peanut lines collected from 3 centers of diversity in South America. Wynne et al. (1970), using the same parents as Parker et al. (1970), reported that F_1 hybrids from virginia x valencia parents gave greater heterosis than other crosses for vegetative plant characters. Crosses of valencia x spanish gave greatest heterosis for yield and fruit characters. The highest yielding cross, however, resulted from a cross of virginia x spanish parents. Hammons (1973a) reported heterotic responses for fruit yield for F_1 hybrids resulting from crosses made between the subspecific peanut groups. Five cultivars representing virginia and spanish types in all possible hybrid combinations were evaluated in Senegal by Garet (1976). Heterosis was found in certain crosses for pod and seed size, pod and seed number per plant, and shelling outturn. In all cases where heterosis was observed, the cross was made between virginia and spanish parents. Layrisse et al. (1980) found that hybrid vigor for fruit yield, seed yield, and 100-seed weight persisted in F_2 progenies of a diallel cross of 10 lines. The entries of the diallel were 2 lines from each of 5 centers of genetic diversity in South America. The parents of the crosses with significant heterosis generally came from different centers of diversity. Isleib and Wynne (1980) crossed 28 diverse peanut lines with an elite virginia breeding line and grew the F_1 and F_2 generations at 2 North Carolina locations. Included in the parental sample were cultivated peanuts from 5 South American centers of diversity, Africa and China; *A. monticola*, a tetraploid species of *Arachis*, was also included. Positive heterosis was observed for pod yield, number and size. Parents from ssp. *fastigiata* generally had greater heterotic responses than parents from ssp. *hypogaea*. Maximum responses were achieved with fastigiate parents from the Peruvian center of diversity.

The evidence that heterosis in peanuts, like heterosis in other crop species such as wheat (Fonesca and Patterson, 1968; Sun et al., 1972; Widner and Lebsock, 1973), alfalfa (Sriwatanapongse and Wilsie, 1968), cotton (Marani, 1963, 1968), corn (Moll et al., 1962), and tobacco (Matzinger and Wernsman, 1968), is related to genetic diversity. Heterosis in peanuts is generally observed in crosses between the subspecific groups. These results imply that gene action differs in crosses made within and crosses made between botanical varieties. Additive genetic variance is of primary importance in crosses made between parents chosen from a single botanical variety but both additive and nonadditive genetic variance may be significant in crosses made between parents from different botanical varieties.

Combining Ability. Mating designs such as a diallel have been used to partition genetic variability into portions due to general combining ability (GCA) and specific combining ability (SCA). GCA is usually considered to indicate additive genetic effects while SCA is usually considered to indicate nonadditive genetic effects.

A few diallel analyses have been conducted in peanuts. Gregory et al. (1980) crossed 10 of the most diverse peanut lines in his collection in 1944 and studied combining ability in the F_1 generation by using vegetative cuttings. He found GCA to be highly significant and several times greater in magnitude than SCA for yield and several yield components.

In a series of papers the results from several combining ability experiments involving 6 diverse parents were reported (Parker et al., 1970; Wynne et al., 1970, 1975). Parker et al. (1970) estimated combining ability for 17 characters measured on F_1 hybrid seedlings generated from a diallel cross of 6 lines, 2 each from 3 centers of diversity in South America. In a controlled phytotron environment, estimates of GCA were found to be more important than SCA. When Wynne et al. (1970) measured combining ability for the same F_1 hybrid combinations in a single field environment, estimates of SCA were reported to be more important tha GCA for yield and several yield components. However, if a more appropriate analysis of the data for the case when the parental lines are homozygous cultivars is made (Wynne, 1974; Baker, 1978), estimates of GCA are found to be significant for all 17 characters. Furthermore, GCA estimates are larger than estimates of SCA for all except 1 character. Estimates of combining ability were also obtained for the F_2 generation of these 15 crosses in both spaced and drill-planted tests (Wynne et al., 1975). Estimates of GCA and SCA were highly significant for yield, fruit length, seeds per kg, % extra large kernels, and % sound mature kernels in the drilled tests. GCA estimates were larger than SCA estimates for all traits except percent sound mature kernels. In the space-planted test, GCA was significant for all traits and SCA was significant for all traits except weight of sound mature kernels. GCA estimates were of greater magnitude than SCA for all traits. The GCA x location interaction was significant for yield and fruit length and the SCA x location interaction was significant for yield.

Garet (1976) evaluated the F_1 hybrid progeny of a complete diallel cross of 5 cultivars chosen to represent a wide range of variation in Senegal. Estimates of GCA were significant for pod and seed yield per plant, the number of pods and seeds per plant, 100-pod weight, 100-seed weight, oil content, and shelling outturn. SCA and reciprocal effects were also significant for all traits except oil content. Since GCA effects were larger than SCA estimates for all traits except shelling outturn, Garet (1976) concluded that the major part of the total genetic variability was additive for all characters except shelling outturn. A graphic

analysis of the data for pod yield per plant, 100-pod weight, and shelling outturn using the methods of Hayman (1954) confirmed the conclusions reached through the analysis of combining ability variance.

Pod yield per plant, days to first flower, pod size, and plant weights were studied by Gibori et al. (1978) by analyzing F_2 data from a 9 x 9 diallel cross utilizing cultivars of virginia, valencia, and spanish types. They reported bidirectional dominance for pod yield per plant and days to first flower while the alleles giving small pods were dominant and the alleles for large plants showed dominance and overdominance. Estimates of genetic components of variance indicated that additive genetic effects were significant for all traits and more important than nonadditive effects for all traits except plant weight.

Ten peanut lines, 2 from each of 5 centers of diversity in South America, and the F_2 generation of all possible crosses among them were used by Layrisse et al. (1980) to estimate combining ability for yield, fruit and seed traits, and protein and oil content. Both GCA and SCA were significant for all traits except for the SCA for protein percentage. The component of variation of GCA was larger than the SCA component for all traits.

A few combining ability studies have also been conducted on physiological traits and disease resistance. Hadley et al. (1979) determined combining ability for resistance to Cylindrocladium black rot, caused by *Cylindrocladium crotalariae* (Loos) Bell and Sobers, using the F_1 and F_2 generations from a 4-parent diallel. Resistance was rated in the greenhouse. GCA was significant for reaction to the disease for both generations, suggesting that resistance was primarily due to additive genetic effects. Kornegay et al. (1980) determined the inheritance of resistance to 2 Cercospora leafspots, *C. arachidicola* (early leafspot), and *C. personatum* (late leafspot), in virginia-type peanuts using field-grown F_1 and F_2 generations from a 6 parent diallel. GCA was significant for both F_1 and F_2 generations, indicating that resistance to both fungi and tolerance to infection were primarily due to additive genetic effects. Crompton et al. (1979) used a complete diallel among 4 virginia and 2 spanish lines to estimate combining ability for seed calcium concentration and total adenosine phosphates. GCA, SCA, maternal effects, and reciprocal effects were all significant for calcium concentration, while only SCA was significant for total adenylates. Reciprocal and SCA components of variation were more important for calcium concentration than the GCA component of variation, although GCA was sufficiently large to also be important. In a greenhouse study, Isleib et al. (1980) measured nitrogen fixation for the parents and F_1 generation of a diallel cross of 10 South American cultivars. SCA was significant and accounted for more variability than GCA for nodule number per plant, nodule mass, specific nitrogenase activity, shoot weight and total nitrogen, suggesting that nonadditive gene action is important for these traits.

Variance Studies. Mohammed et al. (1978) estimated additive and nonadditive genetic effects for crosses between a virginia line and 2 spanish lines using a generation means analysis. Estimates of additive effects were significant for yield, maturity and fruit size traits. Nonadditive genetic effects were also significant for yield and fruit size.

Genetic variances for yield and several fruit traits for the F_5 and F_6 generations of an intercultivar cross were estimated by maximum likelihood procedures from a nested mating design by Wynne and Rawlings (1978). Estimates

of additive and additive by environmental variances were significant for yield and the fruit traits measured. Estimates of additive x additive epistatic variance were essentially zero for all traits; however, estimates of additive x additive x environmental variances were larger than their associated standard deviations for all traits except yield.

Additional genetic variance estimates using appropriate mating designs are needed for peanuts. Not only are additional estimates of genetic variance needed for intercultivar crosses, but also the type and magnitude of genetic variance for important traits of both adapted and exotic intersubspecific crosses need to be characterized. Without this information, efficient breeding procedures utilizing the range of diversity found in peanuts cannot be implemented.

Epistasis. The available evidence suggests that additive genetic variance is the principle component of genotypic variance for traits of economic importance in peanuts. The question remaining to be answered is how important are nonadditive effects. The significant heterosis observed in some peanut crosses suggests that dominance deviations occur but these heterozygous combinations cannot presently be utilized in peanut improvement. Epistatic variance, especially of the additive x additive type, may be important to peanut breeders since it can be fixed in homozygous genotypes. Hammons (1973a) suggests that many important traits may be affected by epistatic variance. Significant estimates of epistatic variance for quantitative traits would not be surprising since the peanut is an allotetraploid and several qualitative traits have been found to be controlled by duplicate genes (Hammons, 1971, 1973a).

A few investigators have detected the presence of epistatic variance in peanuts. A generation means analysis was used by Sandhu and Khehra (1976) to determine the importance of epistatic variance for 2 crosses at 2 locations in India. Nonadditive genetic effects were more important than additive effects for pod yield, number of mature pods and 100-kernel weight in 1 cross and for pod yield in the second cross both at a single location. These authors concluded that epistasis cannot be ignored in peanut crosses. Isleib et al. (1978) tested for the presence of epistatic effects using progeny from a 6 parent half-diallel of diverse peanut cultivars. Significant variability attributable to specific combining ability persisted over generations for yield and other seed characters. Epistasis was indicated since dominance deviations could not account for the variance due to SCA in the F_5 generation. Estimates of dominance and epistatic variance were obtained using an iterative weighted least squares procedure. Although their estimates were obviously biased by linkage disequilibrium, the authors reported that epistatic variance was more important than dominance for all traits. This study suggests that considerable epistatic variance may exist in crosses derived from diverse parents. Cahaner et al. (1979) used a diallel in an attempt to detect genic interactions. Six traits, measured in the F_2 generation of crosses made among 4 parents, were analyzed. A duplicate genic type of interaction was detected using the ratio of the mean within F_2 family variance and the variance among parents. Complementary genic types of interaction were also detected using the methods suggested by Mather (1967). They concluded that duplicate gene interactions were involved in the inheritance of pod yield and mean pod weight. Complementary genes were involved in the inheritance of number of flowers per plant. The number of pods per plant, dry weight of plant and the ratio of reproductive to vegetative branches were found

to be controlled by additive dominant genes.

These few studies clearly indicate that additional studies are needed to critically define the importance of epistatic genetic variance in peanut populations.

Genotype x Environment Interactions

Valid interpretations of quantitative inheritance, as well as predictions of future performance in a peanut breeding program, depend on an accurate assessment of genotypic values (Moll and Stuber, 1974). Unfortunately, genetic effects are not independent of nongenetic environmental effects. The interaction of genotype and environment reduces the correlation between genotype and phenotype which reduces confidence in the data relative to plant improvement and inheritance of quantitative traits. Genotype x environment interactions will often produce an upward bias in genetic variance estimates, causing expected response to selection to be greater than realized response.

Significant genotype x environment interactions may also influence the progress that a breeder can make in his breeding program. Small genotype x environment interactions or well-buffered cultivars are desired if the breeder wishes to develop cultivars that perform well over a wide range of environments. Conversely, if cultivars are to be adapted to specific environments, cultivar development may proceed more rapidly by exploiting any genotype x environment interactions.

Several researchers have recently reported the presence and magnitude of genotype x environment interactions for peanuts. Chen and Wan (1968) measured the genotype x environment interaction in Taiwan using 13 peanut cultivars grown at 10 locations for 2 years. Both cultivar x year and cultivar x location interactions were small for yield; however, the cultivar x year x location interaction was highly significant.

When Ojomo and Adelana (1970) determined cultivar x environment interactions for 16 cultivars grown at 3 locations for 3 years in western Nigeria, they found both the cultivar x location and the cultivar x year x location interactions to be significant.

In Punjab, India, Sangha and Jaswal (1975) found the cultivar x location and the cultivar x year x location interactions to be significant for pod yield using 12 virginia peanut cultivars.

Tai and Hammons (1978) estimated the magnitude of cultivar x environment interaction for pod yield, % sound mature kernels, % extra large kernels, % fancy sized pods, g/100 seed and some other fruit traits for tests conducted under irrigated and nonirrigated management in Georgia at 2 locations for 2 years. The 19 cultivars used represented both early and late maturity groups. Significant cultivar x location x year interaction for most traits suggested that the cultivar x year interaction varied with location. The cultivar component of variance was larger than the first-and second-order interactions.

Wynne and Isleib (1978) found results similar to those of Tai and Hammons (1978). Cultivar x environment interactions for yield and several fruit traits were estimated for 2 groups of virginia cultivars. A large cultivar x location x year interaction was observed for yield in both North Carolina studies. Both cultivar x location and cultivar x year interactions were small when compared to variation among cultivars.

Wynne and Sullivan (1978) determined the influence of the environment on seedling emergence for 8 virginia peanut cultivars in North Carolina in replicated tests conducted at 5 locations over a 3-year period. Both the cultivar x year and cultivar x location x year interactions were significant.

Yield, % sound mature kernels and % extra large kernels were determined for 2 years at 2 locations for 9 crosses with 8 lines per cross in F_4 and F_5 generations by Wynne and Coffelt (1980) in North Carolina and Virginia. Cross populations and lines within crosses were significantly different for all traits. Cross populations interacted with the year-location environments for all traits, while lines within crosses interacted with the environment for all traits except yield.

The effect of the weather on the yield response of cultivars and the genotype x environment interaction was investigated by Williams et al. (1978) in Rhodesia. They found that the cultivars were more sensitive to changes in the environment before fruit filling than during the actual fruit-filling phase.

Although genotype x environment interactions vary with the material and sites chosen for testing, genotype x environment interactions in peanuts appear to be similar to those in several other autogamous species. Matzinger (1963) concluded that second-order interactions were important for cotton, soybeans, and tobacco. In general, the second-order interaction also tends to be most important for peanuts. Thus the yield of a peanut cultivar in each individual experiment is unique and the environmental conditions differentiating the tests cannot be grouped according to years or locations.

Evaluation of Stability

Because of limited resources, peanut breeders have generally been interested in developing cultivars that are stable; that is, show a minimum of interaction with the environment. Several researchers have used regression techniques to characterize responses of genotypes under varying environmental conditions. Although many of the regression analyses used to measure phenotypic stability do not meet rigorous statistical requirements (Moll and Stuber, 1974), they have proven to be useful indicators of stability.

Joshi et al. (1972) measured the stability of 5 bunch genotypes and a local standard at 7 environments in the Gujarat state, India, using the analysis suggested by Eberhart and Russell (1966). Cultivars showed stability in all environments for yield. The local standard was low yielding in both good and poor environments, while 1 genotype, released for cultivation as 'Junagadh', performed consistently well in both poor and good environments.

Singh et al. (1975) evaluated 8 cultivars for yield and stability at 4 locations in India during a single growing season. Their data were also analyzed using Eberhart and Russell's (1966) methodology. A significant genotype x environment interaction was found. The cultivars differed in stability, with the cultivar M 13 having both high yields and average stability.

Wynne and Sullivan (1978) found that 8 virginia cultivars differed in stability over environments for the percentage of seedlings that emerged when the data were analyzed by regression. They tested at 5 locations in North Carolina during a 3-year period. Two cultivars, Florigiant and NC-Fla 14, produced high percentages of emerged seedlings and gave greater stability over environ-

ments than the remaining 6 cultivars. The authors concluded that selection for cultivar stability for seedling emergence over environments should be effective.

The genotype x environment interactions for pod yield and days to maturity were found to be significant by Yadava and Kumar (1978) for 15 bunch genotypes grown in 4 environments at Hissar, India. The linear component of the genotype x environments interaction was significant for both traits, while the deviations from regression were also significant for days to maturity. One cultivar was consistently early and high yielding in all environments. Yadava and Kumar (1978) also used 17 genotypes grown in 4 environments to estimate genotype x environment interactions and stability parameters for 100-kernel weight, oil content and shelling percentage. The linear and nonlinear portions of the genotype x environment interactions were significant for all 3 traits. One cultivar had consistently high 100-kernel weight and oil content in all environments. Another cultivar had high shelling percentage and was stable over all environments. The data convinced the authors that stability parameters for the different traits were governed by independent genetic systems.

In order to achieve stability of yield over a wide geographical area and over seasons, Norden (1980) has released cultivars that are early generation composites of 4 to 10 sister lines selected in the F_4-F_8 generations. Two such cultivars, Florigiant and Florunner, have been grown in the southeastern United States with outstanding yield results.

The relative yield advantage and stability of this type of multiline was compared to its pure line components in North Carolina and Virginia using 2 multilines composed of 4 sibling homozygous lines grown in 16 environments (Schilling et al., 1980). An analysis was conducted to obtain the relative stability among lines and the adaptation of each line to a range of environments. The 2 multilines did not yield more than the better pure lines or the pure line means. The stability for seed yield of the multilines and the pure lines was not different. The regressions indicated that the mixtures were adapted to all environments, whereas variability existed among the pure lines for this parameter. These results suggest that pure line cultivars can be selected that are well adapted and stable across environments.

These studies, although limited in number and scope, suggest that the adaptation and stability of a peanut line, both traits being under genetic control but acknowledged to be difficult to determine (Simmonds, 1979), should be evaluated and considered before a line is released for production.

Implications on Breeding Procedures

An understanding of quantitative genetics facilitates the decisions a breeder must make concerning his breeding objectives, the development of genetic material with breeding potential and the testing and evaluation of the generated material (Moll and Stuber, 1974).

The available data suggest that additive genetic variance is the principal component of genotypic variance in traits of economic importance in peanuts. The pollination system of the peanut makes it highly unlikely that breeders will use breeding procedures that do not lead to pure lines. Furthermore, evidence from other self-fertilizing species indicates that in most cases homozygous lines can be found which surpass the F_1 hybrid (Brim, 1973).

Homozygous genotypes will still be the goal of breeders even if future studies show that additive x additive epistatic variance constitutes a large proportion of the genotypic variance for some traits in specific crosses. Since breeders will likely continue to produce homozygous genotypes, presently used breeding procedures such as the pedigree, modified pedigree, bulk and backcrossing methods will be the predominant methods used for cultivar development during the next decade.

These conservative breeding procedures have generally limited germplasm diversity in cultivars available for commercial production (Hammons, 1972). With preponderance of additive genetic variance, the limited recombination allowed by traditional breeding procedures and the broad range of genetic diversity available in peanuts (Banks, 1976; Hammons, 1976), emphasis should be directed toward the use of broad-based genetic populations in which recurrent selection can be practiced. Such procedures are presently being evaluated for utility in peanuts (Wynne, 1974; Wynne and Isleib, 1980).

Although numerous studies have reported the phenotypic correlation of traits, few genetic correlations have been reported in peanuts. With inadequate data it is impossible to speculate if correlated responses can be used to select for increased yield. Since several traits must be considered simultaneously in a peanut selection program, index selection should be practiced. However, the meager evidence available suggests that selection for yield *per se* is most important.

Early generation testing to eliminate undesirable crosses should be effective in crosses where additive genetic variance is predominant. Perhaps the low heritability for yield and significant genotype x environment interactions have limited the use of this procedure in peanuts.

The adoption of the multiline method used by Norden (1980) may be helpful in obtaining cultivar stability and adaptation to a wider production area. The presence of large genotype x environment interactions for yield suggests that breeders should adopt a multiline procedure or evaluate pure line cultivars for their stability and adaptation over a range of environments.

The quantitative genetic data in peanuts are so meager that speculation about their implications on breeding procedures is hazardous. Until additional information is obtained, the peanut breeder cannot be confident that he is using the most efficient techniques in developing and utilizing peanut cultivars.

CYTOPLASMIC INHERITANCE

A character may be controlled by both nuclear and cytoplasmic factors or by the interaction of nuclear and cytoplasmic components. Most traits are thought to be under nuclear genic control although a few traits have been demonstrated to be under cytoplasmic control. In most crop plants chlorophyll deficiencies and male sterility have been shown to be cytoplasmically inherited (Harvey et al., 1972). Comparatively few agronomic traits in the peanut have been reported to be controlled by the cytoplasm. Husted (1934) suggested that cytoplasmic effects influenced growth habit of F_1 plants from reciprocal crosses

involving parents with prostrate and erect growth habit.

Ashri (1964, 1968a,b) reported that reciprocal cross differences in growth habit were found when the Israeli line Virginia Beit Dagan (V4) was crossed to any of several other peanut lines. Ashri (1964) designated the 2 cytoplasms as V4 and Others. When V4 was used as the female parent, all F_1 progenies had a runner growth habit. In Others cytoplasm F_1 plants had a bunch growth habit. The F_2 segregation within V4 cytoplasms produced a good fit to a 9 runner:7 bunch ratio, while segregation in the Others cytoplasm gave a 5 runner:11 bunch ratio. Ashri (1964) assigned the genotype Hb_1 Hb_1 hb_2 hb_2 to the V4 parent and hb_1 hb_1 Hb_2 Hb_2 to the Others parent. Ashri (1968a) revised his model, indicating that Hb_1 -Hb_2- genotypes produced runners in V4 cytoplasm while all other genotypes produced bunch plants. Conversely, in the Others cytoplasm, genotypes Hb_1 -Hb_2 Hb_2 or Hb_1 Hb_1 Hb_2- produced runners but all other genotypes have bunch growth habits. A third cytoplasm G and a third locus Hb_5- were reported by Ashri (1976). In the G cytoplasm the Hb_1 and Hb_5- show complementary gene action. Hb_1 and Hb_5 are complementary in V4 cytoplasm while Hb_2 and Hb_5 are additive in the Others cytoplasm.

The plasmon constitution of 68 different peanut lines was studied in crosses with 1 of 3 testers having the V4, O, or G plasmons (Ashri, 1976). It was concluded that the G and V4 plasmons are rare; the O plasmon is widespread, being present in at least 3 of the 4 botanical varieties of cultivated peanuts. Ashri and Levy (1976) have used gamma-rays and chemical mutagens to induce at least 14 cytoplasmic mutants that influence growth habit in peanuts. However, Resslar and Emery (1978) suggested that the differences in growth habit observed by Ashri are due to dissipating maternal effects of the V4 parent rather than cytoplasmic inheritance *per se*.

A few additional studies have reported that factors other than nuclear genes influence the inheritance of characters in the peanut. Significant maternal effects were observed by Parker et al. (1970). Characters showing maternal effects were number of leaves, cotyledonary branches and leaf width.

Pod constriction was found to be influenced by the cytoplasm by Coffelt and Hammons (1974b). They reported that Argentine and Early Runner cytoplasms affected the F_2 segregation ratios in the reciprocal crosses made between the 2 cultivars.

Wynne and Emery (1974) found significant reciprocal cross differences for intersubspecific crosses grown in the phytotron. Reciprocal crosses of virginia x spanish lines were different for days to first flower, plant height, number of fruit per plant and fruit weight. Reciprocals of a valencia x spanish cross were different for plant height, number of fruit, number of pegs and fruit weight. In both crosses means were superior when the spanish line was used as the female parent.

Crompton et al. (1979) found reciprocal cross differences for seed calcium concentration for a 6-parent diallel. They concluded that reciprocal cross differences could not be explained on the basis of maternal effects alone but must have resulted from cytoplasmic differences. Crosses involving NC 4, a virginia cultivar from North Carolina, and a spanish line (PI 123643) accounted for the significant variation. Garet (1976) found reciprocal cross effects to be significant for yield, fruit and seed size and shelling percentage in a 5-parent diallel of diverse genotypes. Reciprocal cross differences were due to differences observed for the cross of KH 3278, an early maturing line, with GH119-20, a cultivar from the USA, and PR64B, a line developed in Malawi.

Layrisse et al. (1980) also found differences among reciprocal crosses for fruit length, fruit weight and oil + protein percentage in a 10-parent diallel of diverse cultivars. They concluded that these differences were produced by the interaction of nuclear and cytoplasmic factors. These examples of agronomic traits which are, or may be controlled by, extrachromosomal factors, and the studies cited earlier in this chapter demonstrate how few traits have been shown to be outside nuclear genic control. The paucity of our present knowledge is partly due to the difficulty of demonstrating differences in cytoplasmic factors and the lack of concentrated research efforts in this area. A peanut geneticist can alter more characteristics by manipulation of nuclear genes than by manipulating plasmogenes. Nevertheless, in the cases where cytoplasmic factors exert control over a trait, they may be useful. A systematic search for extrachromosomally inherited traits such as cytoplasmic male sterility would be valuable in exploiting useful genetic variability in the peanut.

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Chapter 4

BREEDING OF THE CULTIVATED PEANUT

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Peanuts (*Arachis hypogaea* L.) are the most widespread and potentially the most important food legume in the world. The object of peanut breeding is to develop this potential by creating cultivars which meet the demands of the peanut grower, processor, and consumer.

Branch (1979), with the aid of several U. S. peanut breeders, recently compiled a list of peanut breeding goals. These, classified according to needs of differing industry segments, included: for growers - higher yields, pest resistance, and environmental stress-tolerance; for processors - more uniform maturity and more favorable shelling and blanching characteristics; and for the consumer - improved nutritional seed properties with fruit and seed of preferred shape, size, texture, color, flavor, and aroma.

An extensive explanation of the peanut breeding process and the progress which has been made towards achieving these goals has been written in the book "Peanuts:Culture and Uses" (Norden, 1973). This chapter reports current progress in peanut breeding programs and examines the problems facing these programs in the future.

GENETIC VARIABILITY

As Gregory (1962) pointed out, the basic resources upon which a plant breeder must draw for genetic material are finite and exhaustible. These basic sources are: 1) the hereditary differences among cultivars of cultivated peanuts; 2) the differences that may be created artificially by the use of mutagens; and 3) differences which occur among the wild relatives of the cultivated species. The genus *Arachis* originated in South America (Krapovickas, 1973; Smartt et al., 1978) and extends over more than 2.6 million km² of the continent (Banks, 1976). This genus includes 50 or more species from 7 clearly differentiated taxonomic sections. The cultivated peanut is thought to have originated as a wild allotetraploid between the quasi-annual *A. batizocoi* and the perennial *A. cardenasii* nom. nud. (Gregory et al., 1980).

Plant Introduction

Collections of peanut germplasm in the USA are fairly extensive. The bulk of the present collection was obtained through collection expeditions sponsored by the USDA with the cooperation of state experiment stations and foreign countries. Further explorations in South America are needed before this valuable germplasm is lost.

The most complete catalogued collection in the USA which is accessible to plant breeders is the one maintained by the Southern Regional Plant Introduction Station at Experiment, Georgia. Approximately 4,000 accessions are