Chapter 4

Genetics of Arachis Hypogaea

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INTRODUCTION

The peanut is a complex genetic organism, frustrating to the scientist employing textbook procedures of intercrossing marker stocks, making backcrosses, recording segregating classes, fitting the data to standard ratios, and announcing his results. A basic difficulty lies in the absences of precise taxonomic definition of material employed in research.

Many peanut cultivars have been described and a number of attempts made to organize these into taxonomic classifications. In this chapter the nomenclature of Krapovickas (87) is adopted. Under his classification the cultivated species, *Arachis hypogaea* L., consists of two subspecies, each containing two botanical varieties:

subspecies *hypogaea*
- variety *hypogaea* (the Virginia group)
- variety *hirsuta* Kohler

subspecies *fastigiata* Waldron
- variety *fastigiata* (the Valencia group)
- variety *vulgaris* Harz (the Spanish group).

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In the context of this review each infraspecific taxon contains a morphologically distinct group of cultivated varieties.

Plants of botanical var. *hypogaea* are spreading (runner) to upright (erect bunch) in growth habit, have alternate branching, lack inflorescences in main stem leaf axils, possess appreciable fresh seed dormancy, flower longer and mature later than those of subspecies *fastigiata.* In the U.S. both the Virginia and the Runner market types are components of the var. *hypogaea,* or Virginia, botanical group. The distinction between these two market types is an arbitrary one based on pod size and seed count. Variety *hirsuta* has been little used in genetic investigations and is omitted from further discussion in this chapter.

Plants of subspecies *fastigiata* are upright in growth, have sequential branching, have inflorescences in main stem leaf axils, possess little fresh seed dormancy, and are of shorter duration than ss. *hypogaea.* Subspecies *fastigiata* includes both the Spanish and Valencia U. S. market types. In much of the world culture, Spanish peanuts are termed "bunch", "erect", or "upright" but this habit also occurs for both large and small-seeded cultivars in the Virginia (var. *hypogaea* group.)

Growing evidence (63, 29, 30) indicates that intervarietal crosses within the same subspecies of *A. hypogaea* may give simpler genetic ratios for various traits than crosses between cultivars in different subspecies. For ease of reference the latter crosses are termed "infraspecific" crosses (63).

Natural variability in the cultivated peanut is substantial and has provided ample resources for the development by selection and hybridization of cultivars adapted to different environments. This has resulted in high yields for the grower together with desirable processing and end-user quality characteristics. Additional heterogeneity has been caused by irradiation and other mutagenic agents. Of the wild species. *A. monticola* Krap. et Rigoni is freely cross-compatible with *A. hypogaea* and has been successfully employed in the development of a new cultivar (62). A wealth of other wild species are available for genetic exploitation when procedures for effecting further interspecific crosses are evolved.

Inheritance of numerous characters, either dominant or recessive in behavior, has been recorded in the peanut, beginning with the work of van der Stok in 1910 (134). The finding of both simple and complex genetic ratios has been almost commonplace. This is not unexpected in an alloploid species where 20 bivalents are generally found in meiotic metaphase. The basic chromosome number of the genus is $x = 10$.

Knowledge of the inheritance of qualitative and quantitative characters in peanuts is necessary for conducting an intelligent improvement program. It is the purpose of this review to bring together widely scattered bits of information pertaining to the genetic systems of the peanut. In an attempt to make the treatment as complete as possible unpublished information has been included when available.

A complete review of previous literature on inheritance of characters is not presented here. Several earlier summaries cover portions of the genetic field, including those by Hull (76), Gregory *et al.* (54), Seshadri (127), and Gillier and Silvestre (47). Loesch and Hammons (101) reviewed their research with induced macromutants and Emery *et al.* (42) summarized research in North Carolina on genetic variability within mutated backgrounds of a macromutant locus.

The qualitative character section is limited largely to traits for which a factorial hypothesis of inheritance has been proposed. A somewhat extensive literature describes research attempting to correlate various characters in variety collections and in early generation hybrids. All of the correlations reported in such papers cannot be described

here; this review will focus primarily upon those traits of greatest value in the genetic improvement of peanuts.

INHERITANCE OF QUALITATIVE CHARACTERS

A number of inheritance studies of characters controlled by nuclear genes in peanuts has been reported with a majority of examples following expected Mendelian segregation for a "diploidized" allotetraploid. The most frequent expectations are the monogenic (3:1) or duplicate digenic (15:1) models. In the following account the genetic information fitting these two models usually will be stated without elaboration. The reader should consult the referenced investigations for statistical adherence of data with proposed models.

Habit Of Growth

Plant Growth.—Two geotropically distinct growth habits in peanuts—spreading (runner, trailing) and upright (bunch, erect)—have long been recognized and these provide a basis for several varietal classifications. Intermediate between the spreading and upright forms, one or more semi-spreading (bunch-runner, runner-bunch) kinds sometimes may be differentiated. A brief review of investigations of growth habit inheritance indicates that more research is required to fully elucidate the genetic systems governing this complex characteristic.

Badami (14) proposed a bi-factorial difference, with erect habit recessive to procumbent (79). In his Valencia X Sine cross, Hayes (70) noted the F_2 progenies consisted of "runners and bunches, and a series of intermediate grades" and other plants totally unclassifiable. By grouping the runner and intermediate classes, he explained his results as a two gene (15:1) difference with runner dominant.

Differences in growth habit of F_1 plants from reciprocal crosses involving the prostrate and the erect habit of growth led Husted (80) to suggest "a cytoplasmic difference in the two forms." In another cross between bunch and prostrate peanuts of the Virginia type, habit of the F_2 generation could not be definitely classified into discrete phenotypic classes.

From their analysis of the behavior of F_1 and F_2 progenies of seven crosses between spreading and bunch varieties, Patel *et al.* (117) stated that "the F_1 plants in all of them showed complete dominance of the spreading habit, the F_2 population segregated mainly into the bunch and spreading groups." Repeated attempts to formulate further phenotypic classes failed to give any intelligible ratios. From another cross, involving two bunch varieties, H.G. 1 (of natural cross origin in a spreading variety) and Spanish 10, where the F_1 was spreading and in F_2 spreading and bunch could be fit to a 9:7 ratio, they deduced that spreading resulted from two complementary factors.

However, following further study of the progenies of numerous crosses these workers concluded (127) that what was reported as a 9:7 ratio was actually a 9:3:3:1 segregation of spreading, semi-spreading, bunch and erect, respectively. The common bunch (= Spanish) S_1S_1 type when crossed with spreading gave the trigenic F_2 segregation of 36 spreading : 24 semi-spreading : 4 bunch. From their analyses four loci are postulated, with these symbols (modified after Seshadri, 127):

Erect	s_2s_2
Common bunch = Spanish	S_1S_1
Semi-spreading (H.G. 1)	S_2S_2
Common semi-spreading	S_3S_3
Common spreading	S_2S_2 .. S_4S_4

It can be shown from the suggested constitutions that a variety of F_2 ratios may be expected from hybridizations among such genotypes.

Hull (76) classified varieties into three groups of plant habits, assigning genotypes:

Valencia	*va*1 *va*1 *va*2 *va*2
Spanish	*Va*1 *Va*1 *va*2 *va*2
Runner	*va*1 *va*1 *Va*2 *Va*2

As early as 1938, Higgins (71) recognized that inheritance of growth habit was much more complex than had been previously thought. When he crossed a bunch variety with a runner, the first generation plants were intermediate but "with a decided leaning toward the pistillate parent." He classified the F_2 plants as bunch, intermediate, and runner, in a ratio of approximately 1:2:1. Since comparatively few of the bunch and runner plants bred true in the F_3 generation and some of the intermediates did breed true, Higgins postulated that at least two factors, with opposite rather than supplementary effect, were involved in growth habit inheritance.

Using crosses involving four spreading and two phenotypically distinct erect varieties, Dalal (34) obtained 3:1 ratios for 5 spreading X erect crosses, but the F_2 population for the cross of the two erect varieties segregated 9 spreading : 3 erect-bushy : 4 erect-open plants. The latter two classes represent the erect parents. F_3 data confirmed this behavior. He symbolized genetical constitution as *S*1-*S*2- (spreading), *S*1-*s*2*s*2 (erect-bushy), and *s*1*s*1*S*2- (erect-open).

Katayama and Nagatomo (86), from their study of growth habit in 28 cross combinations among 6 parental lines, found in F_1 dominancy of prostrate > intermediate > erect. Certain crosses gave distinctively different F_1 phenotypes in reciprocal combination from which they postulated cytoplasmic inheritance. In the F_2 generation, 2, 3 or 4 growth habit phenotypes were classified but the progeny size (maximum 32) was inadequate to differentiate alternative hypotheses.

A new interpretation of the inheritance of growth habit in peanuts was advanced by Ashri and Goldin (11) and elaborated by Ashri (2, 3, 4). Their studies with hybrids involving seven bunch varieties show that two plasmons and two nuclear genes interact to produce the runner or the bunch habit. Dominant alleles *Hb*1 and *Hb*2 lead to the development of a runner habit in both plasmons. In the "V4" (Virginia Beit Dagan No. 4) plasmon they are complementary with *Hb*1-*Hb*2-being runner and all other genotypes being bunch. The F_2 ratio is 9 runner to 7 bunch.

In the "Others" plasmon, however, the dominant alleles are additive and perhaps also complementary. At least three dominant alleles, in any combination, are required to produce a runner; with 2, 1, or 0 dominant alleles, the plants are bunch in this plasmon. *Hb*1*Hb*1*Hb*2*Hb*2, *Hb*1*Hb*1*Hb*2*hb*2 and *Hb*1*hb*1*Hb*2*Hb*2 are runner in the "Others" plasmon, while all other genotypes are bunch. The F_2 ratio, in the "Others" plasmon, is 5 runner : 11 bunch. Critical evidence supports this genetic model (3).

Further research in Israel (4) indicates that there are probably additional plasmon types and plasmon-sensitive genes interacting with them. Ashri infers that there has been divergence for more than two plasmon types in the *A. hypogaea* germplasm, and that more than two nuclear genes are involved. These genes would interact differently with each plasmon and with each other in each plasmon.

Based upon crosses in the Sudan, Tahir (140) considered runner habit dominant to spreading-bunch and upright-bunch habits, but a range of intermediate forms appeared. Upright-bunch habit was recessive to spreading-bunch, and the open habit (varieties A-15, A-30) was dominant to compact habit (Barberton) in upright-bunch crosses. The absence of frequency data prohibits critical appraisal of this paper.

In crosses of two spreading varieties each with the late-bunch variety K-17 as pollen parent, Hassan and Srivastava (68) observed a dominance of bunch habit over spreading in the F_1 and in F_2 an apparent monogenic segregation with bunch plants in greater frequency. From these results, they suggest that "the change in pattern of dominance may be due to the fact that genes determining habit of growth are different in different varieties."

It is possible to calculate a good fit of the F_2 data of Hassan and Srivastava (68) to the 5 bunch : 11 runner hypothesis for Ashri's (3) revised model. Further interpolation of their data is speculative without appropriate crosses.

In recent research in Israel, treatment of peanuts with gibberellin changed the diageotropic orientation of lateral branches of runners to that of erect ones, and two growth retardants changed the negative geotropic growth of the erect type to a plagiotropic position (55). From these studies, genetic differences in growth habit appear to be correlated with levels of endogenous gibberellin antagonists, one of which may be a compound similar to abscisic acid.

Where two nuclear genes are segregating in F_2, the familiar 9:3:3:1 ratio may be modified by genic interaction in at least six ways. These characteristic interactions, termed complementary, duplicate, recessive suppressor, dominant epistatic, recessive epistatic, and additive action, give two or three phenotypic classes. Ashri's (3) model assumes complementary interaction in the "V-4" plasmon and "additive and perhaps also complementary" in the "Others" plasmon. Since duplicate gene and epistatic interactions are commonplace in peanuts, the reviewer postulates that these types of interactions may also be confidently anticipated to appear when a sufficiently wide diversity of peanut germplasm has been evaluated.

In fact, since either of the six kinds of genic interactions could be expressed in each of the two known plasmons, as well as in the additional plasmons postulated by Ashri (4), and since two or more additional nuclear genes almost certainly exist, an almost unlimited variety of plant growth habit distributions may appear in hybrid populations.

Plant Type.—The Valencia plant type appeared in the progenies of several of Hull's (76) crosses of Spanish X Runner. It behaved as a recessive set of duplicate genes, va_1, va_2, where each parent carried alternate recessive and dominant pairs.

Branching—The relationship of the number and arrangement of the reproductive and vegetative axes of peanuts to their varietal differentiation forms the basis for an acceptable varietal classification (54). The variation in both branching order and pattern which permits classification is distinct enough to invite genetic analysis.

The production of numerous secondary (n + 2) and tertiary (n + 3) branches characterizes cultivars in the Virginia (var. *hypogaea)* group, in contrast to few secondary and rare tertiary branches in subspecies *fastigiata* (the Spanish and Valencia groups). In crosses between branched *(BB)* and non-branched *(bb),* Patel, *et al.* (117) obtained a monogenic difference. The reassortment of growth habit and type of branching was not independent in their cross between the spreading, branched (var. *hypogaea)* Philippine White and the bunch, non-branched (var. *fastigiata)* Corientes-3 varieties; about 30% crossing over occurred betweeen spreading and branched.

Dominance of the alternate pattern of vegetative and reproductive branches in ss. *hypogaea* to the sequential pattern in ss. *fastigiata* types has been observed numerous times by many investigators (e.g., 121; 140), without specific explication of the number of loci controlling this characteristic which is of a varietal order of magnitude.

Perry (121) investigated inheritance in four different branching pattern populations, including X-ray induced alterations to vegetative ("V") or reproductive ("R")

branching forms in a *hypogaea* ("H") control variety, and a natural reproductive fastigiata ("F") variety[1]. F_1 hybrid behavior for the four branching patterns indicated that: (i) the loci controlling branching pattern in "F" were different from those of "R", (ii) the branching pattern of "H" was dominant to that of "F", "V", and "R", (iii) the "F" branching pattern appears to be dominant to the "V", (iv) the locus controlling the "V" pattern appears to be the same from four independent X_2 families, and (v) at least some of the loci controlling the "R" branching appear to be the same in some of the independent X_2 families studied. A severe hurricane destroyed Perry's F_2 hybrid material, precluding the formulation of more definite conclusions.

Main Stem Inflorescence.—The presence or absence of inflorescences in leaf axils of the main stem axis is a key diagnostic characteristic separating the two subspecies into distinct entities. Results of a study by Hammons (63) indicate that the occurrence of vegetative vs. reproductive branches is controlled by two sets of duplicate loci interacting with epistasis between sets of loci, producing in F_2 a phenotypic ratio of 225 plants with vegetative branches : 31 plants with reproductive branches on the main stem. Gene symbols J_1, J_2, K_1, and K_2 designate the duplicate alleles. Either J_1 or J_2 and K_1 or K_2 interact to produce vegetative branches in main stem leaf axils.

The relationship, if any, between the genetic system determining main stem flowering and that controlling branching pattern has yet to be determined. As Hammons (63) has shown, an understanding of the genetic mechanisms modifying the frequency of reproductive events on any order of branches is essential for continued breeding improvement of the peanut.

Perennialtity and Duration.—Arachis hypogaea is an annual species in agricultural practice but many *Arachis* species are perennial. Seshadri (127) noted that perenniality was dominant.

The length of the growing period is of critical importance in areas where variety choice is influenced by rainfall and temperature patterns. Earliness *(e)* is recessive (13, 14) to late *(E)*. Patel *et al.* (117) observed incomplete dominance (1:2:1) and used different symbols *(L, l)*. Hassan (67) confirmed this behavior, using different parents.

Sterile Brachytic.— Brachytic plants have very short stem internodes, a sharply reduced leaf rachis, shorter petioles, and are male and female sterile. They have been reported under various names (abnormality, sterile plants or dwarfs, etc.) by different investigators and they are almost exclusively associated with infraspecific hybridizations (30). Hull (76) reported monogenic control. Other researchers (5, 70, 80, 117) suggested two complementary factors (15:1). Husted (80) symbolized the loci as *Xx, Yy*; Patel *et al.* (117) assigned symbols N_1n_1, N_2n_2.

More recently, Coffelt and Hammons (30) reported that brachytic was inherited in a 243:13 tetragenic ratio in an extensive F_2 population. Their results indicate that the two infraspecific parental cultivars differ at four unlinked loci, Bs_1, Bs_2, Bs_3, Bs_4, involving two sets of factors with complementary-duplicate action. Two dominant alleles, one at each of any two of the four loci, give normal plant growth. Plants homozygous recessive at any three or all four loci are brachytic. Normal is completely dominant.

Coffelt and Hammons (30) reevaluated previous results (5, 70, 80, 117) and showed that the data gave good fits to the tetragenic model.

Varisai Mohammad *et al.* (143) encountered an abnormal stunted plant in all crosses of a white-seeded bunch peanut with 5 spreading varieties. Their data will fit either the digenic or the tetragenic models.

[1]Symbols supplied by R. O. H.

These investigations in infraspecific cross populations demonstrate the genetic load of undesirable recessive alleles that can accumulate in an autogamous species such as peanut where many traits are controlled by duplicate loci.

Floral Characteristics

The flowers of *Arachis hypogaea* are aerial, papilionate and zygomorphic and are commonly yellow. The color of the standard petal ranges from white through various yellow and orange intermediates to a deep burnt orange or amber.

Corolla Color.—Hayes (70) and John *et al.* (85) distinguished five intensities of corolla color, and Hayes observed dominance of deeply-colored to light. Poona White Flower, a spontaneous mutant from Poona Local, when crossed with Poona Local (91) gave an F_1 intermediate or faint orange in color, and segregated 1:2:1 in F_2 and F_3 for orange, pale orange and white respectively, indicating that orange *(Or)* is partially dominant over white *(or)*.

Patil (120) subsequently crossed six other varieties with Poona White Flower and got 15 yellow : 1 white corolla color in F_2. He proposed Yfl_1 and Yfl_2 for the duplicate loci.

Bilquez and LeComte (22) investigated flower color inheritance in crosses of three varieties for which they assigned the genotypes shown in parenthesis: Senegal 61-13 *(AAYY)*, Senegal 28-204 *(aaYY)*, and Senegal 64-02 *(aayy)*. The latter variety originated as a mutant following irradiation of the 28-204 variety. In their model, two independent pairs of alleles govern flower color: *Yy* controlling the yellow base pigment (probably a flavone) and *Aa* controlling production of a red pigment (anthocyanin). However, the results of their analysis and the conclusion they drew are not in full agreement. A marked deficit of plants showing colors appropriate to the *yy* genotype was attributed to certation. Further research is needed to determine the genetic behavior responsible for these poor fitting results[2].

Standard Crescent.—The standard petal of the peanut flower has a purple crescent at the base from which radiate purple lines. Gradations in intensity of coloration occur in different varieties, ranging from complete absence to a prominent pattern. The common cultivars have a distinct crescent on their standards.

In crosses of the white-seeded A.H. 6742 bunch variety, which has no crescent, with five varieties having a distinct, well-defined crescent, Srinivasalu and Loganathan (131) concluded that purple crescent is a dominant character controlled by two duplicate genes. F_2 plants with no crescent had usually stems devoid of anthocyanin pigment and the seed testa was white.

From inheritance studies carried out in Madras it was concluded that the production of purple crescent on the standard is determined by a factor which is expressed in the presence of the factor(s) for stem color (127). The studies also revealed that in the Philippine White variety the factor for crescent is present while the factor for stem color is absent but the contrary condition holds in the Nambiquara variety. Varisai Mohammad *et al.* (143) confirmed the duplicate gene inheritance for standard petal crescent, also using A.H. 6742, and again noted relationship of the crescent with stem pigmentation.

At Mainpuri, U. P., India, Srivastava (132) distinguished an intermediate "loose" crescent in progenies of the cross between the extreme "compact" and "absent" forms. The F_2 segregation of 11 compact : 4 loose : 1 absent was attributed to a cumulative ef-

[2]The recessive suppressor (13:3) model is plausible for their cross 28-204 x 64-02; then, an expectation for F_2 distribution of 39:13:9:3 in cross 61-13 x 64-02 is met. — R. O. H.

fect of duplicate factors. The duplicate recessive d_1d_2 genes, responsible for colorless testa (72), appear to determine absence of standard crescent, with D_1D_2 responsible for its presence (132). The compact X loose cross segregated 15:1.

Thus, two pairs of non-allelic sets of factors appear to affect both testa color and the structure of the standard crescent. Contrary to previous reports (127, 131, 143), the relationship between anthocyanin pigmentation of stems or pegs and seed testa color is not invariable, but pigmentation of stem, crescent and peg may be attributed to the duplicate factors $R_1r_1R_2r_2$ of Patel *et al.* (117) corresponding to $F_1f_1F_2f_2$ of Higgins (72). Srivastava (132) suggests designating these "pigment factors."

Because of their function in determining crescent formation on the standard petal of the corolla, Srivastava (132) also proposed that the factors $D_1d_1D_2d_2$, defined by Higgins (72) for the expression of testa color, should be renamed as "crescent factors." Such change in terminology is untenable. Research by Hammons (58), Harvey (66), Yona (147), and Ashri (6) clearly support Higgins' model (72) that testa color is governed by the D_1D_2 duplicate loci.

Nevertheless, the conclusion by Srivastava (132), that presence of both sets of factors (F_1F_2 and D_1D_2) are necessary for expression of a purple crescent, warrants more investigation.

The intensity of standard crescent color is also under genetic control. When loose X absent crescent were crossed, the normal bright colored crescent of the F_1 hybrid segregated a tetragenic ratio of 225 bright : 15 feeble : 16 absent crescents in the F_2, indicating two sets of duplicate factors for bright crescent (132).

Other Floral Traits.—Hayes (70) claimed that early fading of flowers was dominant to late fading, but critical data are lacking. Studies in Madras, India indicated that in crosses between late fading (Spanish) and early fading (spreading) types, the F_1s were intermediate as were a majority of the F_2 generation (127).

Inheritance of the shape of the wing petal of the corolla has been investigated. Boat shape was dominant (3:1) over broad or scoop shape wing in a cross between these shapes. In another cross, between two simple broad winged parents, the F_1 was "chinned" or "projected", and the F_2 ratio of 9 chinned : 7 simple supports the assumption of two factors, *ch* and *w,* that separately produce normal broad wing, but combine in a complementary action to produce chinned (132).

Sterility.—No one has yet established the prescence in peanuts of a self sterility system suitable for study of the possible exploitation of hybrid vigor. Several pollen sterile forms have been noted in the literature (for review, see Coffelt and Hammons, 30), but these plants have usually been completely female sterile also, or unable to support embryo development.

Hammons (64) investigated the genetic behavior of a self-sterile but pollen-fertile plant which appeared spontaneously at Tifton. Although the character is recessively inherited, extensive F_2 data suggest monogenic control in certain crosses and trigenic inheritance in others. Additional research will be necessary for an understanding of sterility mechanisms in present material. An intensive search for male sterility genes in peanut is long overdue.

Plant And Foliage Traits

Chlorophyll Deficiencies.—There is a difference between the Virginia (dark green) and the Spanish-Valencia group (light green) in leaf color. Badami (13) observed dominance of dark green *(G)* over pale green *(g)* leaf; Dalal (34) confirmed this result, using G_1 and g_1 symbols.

Infraspecific crosses usually give albinos which die shortly after seedling emergence. Badami in 1928 suggested triplicate gene inheritance of chlorophyll, with dark green the triplicate dominant and albino the triplicate recessive (79). Subsequently, several workers fitted results to the digenic (15:1) ratio and assigned symbols: $G_1g_1G_2g_2$ by Patel *et al.* (117); $L_1l_1L_2l_2$ by Hull (76); *AaLl* by Katayama and Nagatomo (86); and $Clpl_1$ $clpl_1$ $Clpl_2$ $clpl_2$ by Patil (120).

Recently, Coffelt and Hammons (29) reinterpreted the results for the former three studies (117, 76, 86) and found those data to be compatible with their trigenic model. This model (29) postulated duplicate loci (C_1c_1 and C_2c_2) for chlorophyll development interacting in an epistatic manner with a third locus (*Ll*). Either dominant *C-* locus gives green, the homozygous recessive at the *C-* loci and one dominant *L* result in albino, and the triple recessive conditions a zygotic lethal. An F_2 segregation of 60 green : 3 albino : 1 zygotic lethal occurs.

In addition to the above examples, the green : albina segregation reported by Syakudo and Kawabata (139) also gives an acceptable fit for the trigenic ratio proposed by Coffelt and Hammons (29). Data for Patil's (120) digenic model were not supplied.

More recently, Coffelt and Hammons (31) observed a variable effect of seed size upon the ratio of albino seedlings in F_2 progenies of reciprocal infraspecific crosses. After seed were sized into 10 incremental classes on a nested set of grading screens, the F_2 plant family data confirmed their previously reported trigenic ratio of 60 green : 3 albino : 1 zygotic lethal. However, the seed size classes were not independently distributed: significantly more albinos appeared in the smaller and significantly fewer in the larger seed sizes. Their results show the importance of avoiding selection pressure when evaluating genetic populations for mendelian expression.

In contrast with the above investigations, and with the numerous other qualitative characters in peanuts for which diploid and /or allopolyploid inheritance is the rule, Miryuta (111) has postulated a tetrasomic ratio (1:35) for albino seedlings. His model requires a self-regulating system of selective pairing to keep homologous sister chromosomes together. Our present knowledge of cytogenetic behavior and of inheritance mechanisms in peanuts rules out such preferential pairing.

Gillier and Silvestre (47) mention an almost yellow leaf dominant mutant at Bambey, Senegal, but a genetic model to explain the type of inheritance involved has yet to be published.

Tripp (142) attributed virescent seedlings in the progeny of an introduced peanut (P. I.) to a monogenic recessive. The virescent seedlings lacked chlorophyll and usually died within a short time but could be maintained in restricted light.

Hammons (as yet unpublished) found a spontaneous mutant to a rusty-leaf phenotype which inherits as a recessive.

Inheritance studies by Tai *et al.* (141) on two chlorophyll-deficient mutants, aureus and lutescens, indicate that each mutant is determined by duplicate homozygous recessive loci, with duplicate dominant epistasis for normal green pigment. Gene symbols au_1au_2 for aureus (golden yellow) and lu_1lu_2 for lutescens (yellowish) were proposed. F_1 plants from reciprocal crosses between the mutants were normal green, attributed to complementary gene action. The F_2 gave four phenotypic classes: normal green, aureus, lutescens, and a seedling lethal, in a 225:15:15:1 ratio.

Induced chlorophyll deficiencies are discussed in the subsequent section on heritable mutagenic changes.

Leaf Shape.—Hayes (70), from a limited F_2 progeny, inferred dominance for the first mentioned of these pairs of traits: presence of red color on leaflet vein to its ab-

sence, normal leaf to a crinkled leaf, leaf shape of the Sine variety to that of Valencia variety.

The elliptical shape of leaflet on the primary axis in one variety was recessive to the elliptical-oblong shape for another variety in Hassan's (67) studies. Further, large leaflet was dominant, but the absence of clear-cut segregation in F_2 suggested that more than two genes were involved. Badami (14) noted an intermediate leaflet size in F_1 but a wide range in F_2.

Krinkle-leaf is a dominant one-gene *(Krkr)* conditioned character ideally suited for detecting natural outcrossing contamination because hybrid seedlings are unmistakably identifiable soon after emergence (59). Krinkle-leaf originated as a spontaneous mutant. We used the Krinkle-leaf marker to obtain an extensive series of pedigreed natural crosses to expedite genetic and breeding research with peanuts (60). The advantages of the method are that it is relatively inexpensive, the number of F_1 hybrids is independent of the limited time usually available for conventional crossings, and screening for hybrids can be done on marginal land areas.

Although the Krinkle-leaf line has been crossed with several hundred genotypes, linkage of the character with other traits has yet to be detected. Independent assortment of Krinkle-leaf with five testa color loci has been reported (59), and the *Krkr* locus is not associated with at least two growth habit loci (Hammons, unpublished).

Srivastava (133) recorded a Mottled-leaf mutant which reduced the size and yield and apparently behaves as a monogenic dominant.

A plant with spear-shaped small leaflets and reduced internodal and calyx tube lengths, isolated by Bhide and Desale (21) from the Kopargaon-1 cultivar, bred true itself, and when crossed to Kopargaon-1 gave normal-leaf F_1 plants with monogenic inheritance in F_2 and F_3.

Genetic studies by Matlock *et al.* (108) of a naturally-occurring narrow leaflet plant indicate control by a single gene pair with narrow leaflet *(N_1)* partially dominant to normal *(n_1)*. Heterozygotes can be easily separated under greenhouse culture, but reduced vigor and seed set under field conditions limit usefulness of the mutant as a marker.

Ashri (7) isolated a small leaflet segregant in the progeny of a cross between Mani Pintar and Pearl varieties. The trait appears to be controlled by two duplicate genes, designated *$S1_1$ and $S1_2$*. It is a good marker with complete penetrance but its expressivity changes during the season.

Stem Pigmentation.—Expression of stem color in peanuts appears to be similar to that of most plant anthocyanins in that the degree of pigmentation is influenced by environment.

Badami (14) noted a dominant violet tinge on the stems which appears to be associated with hardiness. Hayes (70) recorded simple dominance of dark red stem to light red. In crosses between cultivars with anthocyanin pigment in stems and those without or lacking such conspicuous pigment, Patel *et al.* (117) reported duplicate gene inheritance (15:1), and assumed that the factors *R_1 and R_2* not only produce purple pigment in the plant but also rose color in the seedcoat.

In 1964 Hammons (59) drew attention to the fact that a critical understanding of genetic behavior in the peanut is best accomplished by studying a character in a varied spectrum of cross combinations. This procedure, termed "multicross" testing, enhances the possibility of detecting duplicate locus interactions, epistasis, partial or incomplete dominance, modifying genes and linkage. Our recent experience with infraspecific hybrid

populations (63, 29, 30) supports the proposal that multicross testing can give a better understanding of qualitatively inherited gene interactions.

Further support for using this procedure comes from reports on the genetic behavior of plant stem pigmentation in peanuts. Since Patel *et al.* (117) attributed purple pigment and rose seedcoat to the action of the duplicate loci R_1 and R_2, and since other duplicate loci are known to inhibit testa color expression {Higgins (72), Hammons (58)}, then different genetic ratios may be expected when different parents are chosen.

Such is the case in Patil's (120) study where, in four crosses involving the Poona White Flower with other varieties, segregation was 3 purple : 1 green for stem color, but a fifth cross gave 9 light purple : 7 green. Patil symbolized the loci as *Pst and Pstl.* Culp *et al.* (32) observed incomplete dominance for a purple-petiole marker employed in natural crossing research.

Stem Pubescence.—Two types of stem hairiness are recognized. In crosses by Patel *et al.* (117) between the sparsely hairy *(hh)* Philippine White and the hairy *(HH)* Corientes-3 varieties the F_1 was hairier than the latter parent. The F_2 sorted into 1 very hairy : 2 sparsely hairy : 1 slightly hairy, suggesting a single main factor for hairy vesture Badami (14) also reported hairy stem to be dominant.

Recently, Patil (120) recorded 3 very hairy : 1 sparsely hairy stems in the F_2s of five cross combinations with the Poona White Flower variety and proposed the *Hst* symbol for this trait. Moreover, in one cross the gene for hairiness showed a linkage with that for reticulated pod *(Rp)* with a crossover value of 31.51 percent measured by the product ratio method.

Fruit And Seed Characteristics

Pod size and seed testa color were chosen by van der Stok (134) to initiate genetic work on the peanut. Research during the subsequent six decades shows that he could hardly have chosen more complexly inherited features.

Pod Size.—Van der Stok's (134) hybridization of a variety having small thin pods and another having large thick pods gave a greater difference than the 3:1 ratio, suggesting multigenic inheritance. However, Badami (14) claimed large-sized pods were dominant with three factors governing inheritance. Hassan (67) also reported dominance of large-sized pods. But genetic models to support qualitative inheritance have not been developed.

Other Pod Attributes.—Badami (14) also found that the presence of constriction in the pods is recessive to its absence, with two factors. Recently, Hassan (67) confirmed the dominance of shallow constriction, but his deep X shallow crosses give close agreement with the trigenic complementary (45:19) model. He explained these results by assuming that *A* is a basic gene with *B* and *C* complementary to *A* but not to each other. Then shallow constriction appears when *A* is present together with *B* or *C* or both. Mauboussin (unpublished), however, suggests dominance for presence of constriction (47). Thus, more study is required.

According to Seshadri (127), thin pericarp was dominant in Badami's material and governed by five factors. Thin pericarp was linked with pigmy seed but the method of determining the linkage is not stated.

Although Badami (14) reported at least four factors for deep reticulation on the pods, with deep reticulation dominant to shallow, Patil (120) found 3 prominent : 1 not distinct in F_2 and F_3 progenies from crosses of six varieties with Poona White Flow-

er. He assigned the symbol *Rp* for reticulation on pods. Mauboussin (unpublished) also found that pattern of reticulation depended on one pair of genes, with reticulated dominant (47).

Inheritance of number of seed in a pod was seen by Badami (14) as controlled by three factors with three (or many) seeded pods dominant over fewer than 3-seed. Results by Tahir (140) tend to support the dominance of the higher numbered class. But in Madras (India) a contrary report that 1- to 2-seed condition is dominant over 1- to 3-seeded is recorded by Seshadri (127).

Seed Characteristics.—Seed dormancy, as found in ss. *hypogaea* peanuts in contrast with non-dormancy in ss. *fastigiata,* in an inherent property of the seed. It does not depend upon an impervious or protective seedcoat. Stokes and Hull (135) found dormancy to be incompletely dominant to non-dormancy. Hull (76) measured the "rest" period in peanut seeds in terms of average time to emergence for seeds planted as soon as possible after harvest. He assumed a multigenic control of what he called "seed condition necessary to rest", with a normal frequency distribution. Marked transgressive segregation over the dormant parent occurred in four crosses.

The mode of inheritance of seed dormancy was also investigated by Lin and Lin (97), using reciprocal crosses involving varieties with differing intensities of dormancy. Germination tests were conducted 14 days after harvest. F_2 and F_3 behavior was monogenic with *D* symbolizing the dominant gene controlling seed dormancy.

The F_1 of a cross between long-seeded (runner) and short-seeded (Spanish) was intermediate leading Hull (76) to conclude that seed length was largely controlled by physiological maternal influence rather than by the embryo genotype. However, in a limited population, Hayes (70) observed long seed dominant to short, 15:1. Hassan (67) considered large seed dominant to small without supplying a genetic model.

A rough testa character (reticulated testa) of possible field hybrid origin was investigated by Tripp (142). He postulated duplicate recessive epistasis for the 9 rough : 7 smooth F_2 distribution.

In Senegal, Martin (107) reported that shelling outturn appeared to be governed by only one pair of genes without dominancy, whereas five pairs of genes control seed size, four of them having isodirectional effects.

Testa Color.—Investigations on the inheritance of seedcoat or testa color of peanuts have been more numerous than those for any other trait. Because of the interaction of many testa color genes and the difficulty of classifying colors of varying intensity, the genetic explanations of the inheritance of some colors have been inconsistent. Genotypic formulae of parental lines and F_2 phenotypic ratios from the literature are presented in Table 1.

It is the consensus of opinion that genetic factors affecting testa colors may be characterized by the interactions at five primary loci, although certain additional loci are involved in other specified instances.

Pigment production or testa color development is governed by duplicate genes D_1D_2 (72). One dominant allele suffices to produce pigmentation (66) or its precursor (147). The basic factors which produce the colors variously termed *flesh, rose, pink, russet, tan,* etc., by different investigators, also are duplicate loci, and following Higgins' terminology (72) are symbolized F_1F_2. These are equivalent with the R_1R_2 *(rose)* of Patel *et al.* (117), but Higgins' research was the first to show that both sets of duplicate loci interacted to give phenotypic expression, and is followed here. One dominant *F* allele is sufficient to produce the flesh-rose-pink testa color These four loci also interact with another locus, *R,* to govern the expression of the red, flesh and white

Table 1. The genetic basis of testa color inheritance in peanuts (*Arachis hypogaea* L.). Genotypic symbols and F_2 ratios reported by the authors cited.

Genotypes	Parental Phenotypes[1]	F_2 Ratio[1]	Author and reference
— —	Red X light red	3:1	Van der Stok (134)
R X *r*	Red X rosy (brown)	3:1	Badami (14)
— —	Brick red X light tan	3:1	Stokes & Hull (135)
— —	Red X tan	3:1	Hayes (70)
— —	Brick red X russet	3:1	Husted (80)
p Rd R_1R_2 X *p rd* R_1R_2	Red X rose	3:1	Patel *et al.* (117)
P rd R_1R_2 X *p rd* R_1R_2	Purple X rose	3:1	"
p rd R_1R_2 X *p rd* r_1r_2	Rose X white	15:1	"
P rd R_1R_2 X *p rd* r_1r_2	Purple X white	45P:15Rs:4W	"
p Rd R_1R_2 X *p rd* r_1r_2	Red X white	45R:15Rs:4W	"
P rd R_1R_2 X *p Rd* R_1R_2	Purple X red	12P:3R:1Rs	"
— —	Russet X tan	3:1	Hull (76)
F_1F_2 X f_1f_2	Flesh X white	15F:1W	Higgins (72)
R F_1F_2 X *r* F_1F_2	Red X flesh	3R:1F	"
R F_1F_2 d_1d_2 X *r* f_1f_2 D_1D_2	White X white	675R:225F:124W	"
R F_1F_2 d_1d_2 X *r* F_1F_2 D_1D_2	White X flesh	45R:15F:4W	"

Table 1. The genetic basis of testa color inheritance in peanuts *(Arachis hypogaea* L.)
Genotypic symbols and F_2 ratios reported by the authors cited.

Genotypes	Parental Phenotypes[1]	F_2 Ratio[1]	Author and reference
R F₁F₂ d₁d₂ X *R F₁F₂ D₁D₂*	White X red	15R:1W	Higgins (72)
R F₁F₂ d₁d₂ X *R F₁F₂ D₁d₂*	White X red	3R:1W	"
R X *r*	Flesh X creme	3:1	Ilieff (81)
V X *v*	Dark lilac X creme	1:2:1	"
r F₁F₂ D₁D₂ X *r f₁f₂ D₁D₂*	Pink X white	15pk:1W	Hammons (64)
R f₁f₂ D₁D₂ X *R F₁F₂ d₁d₂*	White X white	225R:31W	Hammons (58)
R f₁f₂ D₁D₂ X *r F₁F₂ D₁D₂*	White X flesh	45R:15F:4W	"
R f₁f₂ D₁D₂ X *r F₁F₂ d₁d₂*	White X white	all white	"
r F₁F₂ d₁d₂ X *r f₁f₂ D₁D₂*	White X white	225F:31W	"
r F₁F₂ d₁d₂ X *r F₁F₂ D₁D₂*	White X flesh	15F:1W	"
r f₁f₂ D₁D₂ X *r F₁F₂ D₁D₂*	White X flesh	15F:1W	Hammons (59)
R F₁F₂ D₁D₂ X *r F₁F₂ D₁D₂*	Red X flesh	3R:1W	"
R F₁F₂ d₁d₂ X *r F₁F₂ D₁D₂*	White X flesh	45R:15F:4W	"
Rkr X *rkr*	Red X light rose	3:1	Patil (120)
Rk₁Rk₂ X *rk₁rk₂*	Lt. rose X white	15:1	"
Rk₁Rk₂ X (?)	Lt. rose X purple	45P:19	"

Table 1. The genetic basis of testa color inheritance in peanuts *(Arachis hypogaea* L.). Genotypic symbols and F_2 ratios reported by the authors cited.

Genotypes	Parental Phenotypes[1]	F_2 Ratio[1]	Author and reference
Rd r_1r_2 X *rd* R_1R_2	White X rose	45R:15Rs:4W	Varisai Mohammad *et al.*(143)
r F_1F_2 d_1d_2 X *r* f_1f_2 D_1D_2	White X white	225F:31W	Harvey (66)
R F_1F_2 d_1d_2 X *R* f_1f_2 D_1D_2	White X white	225R:31W	"
R f_1f_2 D_1D_2 X *R* F_1F_2 D_1D_2	White X red	15R:1W	"
r F_1F_2 d_1d_2 X *R* F_1F_2 D_1D_2	" "	45R:15F:4W	"
r f_1f_2 D_1D_2 X *r* F_1F_2 D_1d_2	White X flesh	15F:1W	"
r F_1F_2 D_1d_2 X *R* f_1f_2 D_1D_2	Flesh X white	45R:15F:4W	"
r F_1F_2 D_1d_2 X *r* F_1F_2 d_1d_2	Flesh X white	3F:1W	"
R F_1F_2 D_1D_2 X *r* F_1F_2 D_1d_2	Red X flesh	3R:1F	"
P r F_1F_2 D_1D_2 X *p R* F_1F_2 D_1D_2	Purple X red	12P:3R:1F	"
P r F_1F_2 D_1d_2 X *P r* F_1F_2 D_1D_2	Purple X flesh	3P:1F	"
r F_1F_2 *w* D_1D_2 X *r* F_1F_2 *W* d_1d_2	Wine X white	45F:15Wn:4W	"
r F_1F_2 *W* D_1d_2 X *r* F_1F_2 *w* D_1D_2	Flesh X wine	3F:1Wn	"
P_1P_2 R_1R_2 X p_1p_2 R_1R_2	Purple X rose	15P:1Rs	Prasad & Srivastava (122)
p_1p_2 R_1R_2 X p_1p_2 r_1r_2	Rose X lt. rose	15Rs:1	"
P_1P_2 R_1R_2 X p_1p_2 r_1r_2	Purple X lt. rose	255:1	"

Table 1. The genetic basis of testa color inheritance in peanuts *(Arachis hypogaea* L.). Genotypic symbols and F_2 ratios reported by the authors cited.

Genotypes			Parental Phenotypes[1]	F_2 Ratio[1]	Author and reference
* —	X	—	Red X rose	13R:3Rs	Srivastava (132) *
* —	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_1d_2	X	—	White X red	9R:3Rs:4W	"
R T d_1d_2	X	*R T* D_1D_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[2]
r_1r_2 — D_1D_2	X	R_1R_2 F_1F_2 d_1d_2	R/V X white	15color:1W	Ashri (6)
r_1R_2	X	R_1r_2	Flesh X R/W	13R:3F	Ashri (9)

[1]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—non-variegated solid or self-color, R/V—red-variegated. *—see text description.
[2]Gibbons, R. W. Agric. Res. Council, Malawi, personal communication, 1969.

phenotypes. Higgins (72) postulated and Hammons (58) critically demonstrated that the presence of a flesh factor (F_1 or F_2) is necessary for the development or expression of red testa color. Harvey (66) confirmed this requirement.

Thus, with two sets of duplicate loci operating in a complementary-inhibitor manner, the phenotypic class in any cross depends not only upon their interaction, but upon the dominant-recessive condition at the loci governing red (*R*, or R_1 R_2), purple (*P*), wine (*Wn*), etc., pigment. Hammons (58) has shown the formulae of 14 true-breeding white testa genotypes expected from the interaction of the 5 basic loci. It is, thus, clear that an interesting profusion of genetic ratios could appear as additional interacting loci are introduced into the system.

The relationship of the purple locus, *P*, with the basic color factors, F_1F_2, and with red, *R*, is not entirely clear. With complete dominance of *P* (117), inheritance such as the digenic epistatic 12 purple : 3 red : 1 rose and trigenic 45 purple : 15 rose : 4 white ratios is encountered (Table 1). But Krapovickas and Rigoni (89) concluded that purple testa was incompletely dominant to flesh (palido), and that dark purple depended upon at least two pairs of genes with cumulative effect. In one cross, Harvey (66) also found purple testa incompletely dominant to flesh, and although *R* was not required for the development of purple, that gene did modify its expression.

The complexity of these interactions is shown in the data of Srivastava (132). Upon crossing purple X white, he observed a greyish red F_1, and in F_2 six phenotypes in a modified ratio of 105 greyish red : 45 deep purple : 30 light purple : 45 deep red : 15 rose : 16 white. He interpreted this result to show incomplete dominance of purple which was not expressed when the factors for red or rose were in the heterozygous condition.

There is evidence also that red testa is more complex than was previously thought. This is not entirely unexpected, for with five basic loci interacting in the complementary-inhibitor manner, nine true-breeding red testa genotypes are expected, but few of these can be visually differentiated. Recessive suppressor and epistatic action, or incomplete dominance may occur.

Thus, when Krapovickas and Rigoni (88) found some plants with red testa in the F_2 and F_3 from crosses between the pink Guaycuru variety and other lines possessing uniform pink testa, they suspected an epistatic factor in Guaycuru for red testa inhibition. Later, Yona (147) suggested that *R* was partially dominant to *r* in certain crosses.

An alternative possibility is that of a second red locus. Srivastava (132) observed red dominant to rose in two crosses, but F_2 segregation followed the recessive suppressor (13 red : 3 rose) or the modified trigenic (39 red : 9 rose : 16 white) models. In yet another cross, red was recessive to rose with monogenic inheritance. The genotypically distinct dominant red and recessive red were phenotypically indistinguishable. The similarity of his result with that of Ashri (6, 9) for the red portion of variegated testa (below) is striking.

Srivastava (132) infers a single factor, *T*, for rose testa instead of the duplicate F_1F_2 loci, and he suggests that *T* is not necessary for the expression of red or purple phenotypes. Genotypic formulae are not presently available to evaluate this assumption. Harvey (66) investigated a wine phenotype which apparently inherited independently of the F_1F_2 loci, but was dependent upon D_1D_2.

Abundant evidence (58, 66) establishes the necessity of a *D* for color development and an *F* for red testa expression. Additional research is needed to determine whether the *D* genes and *F* genes are truly duplicate.

Yona (147) extracted four pigments, flavonone, chromogene (leucoanthocyanin),

tannin and phlobaphene, from peanut seedcoats. He postulated that the precursor produced by D_1D_2 is chromogene, that by F_1F_2 converts chromogene to tannin and phlobaphene giving the rose-flesh testa. *R* produces a rose pigment that does not dissolve in ethanol. In the presence of *P,* the functions of at least some of the other controlling genes are altered, or alternatively, their products are converted to other pigments. Further research is needed for an understanding of the genetics of testa pigment biosynthesis.

There is no evidence for linkage among the seven loci studied by Hammons (58) and Harvey (66), nor between these and the Krinkle-leaf marker (59). However, Patel *et al.* (117) pointed out that the factors producing rose color in the seedcoat also produce purple pigmentation of stems.

Variegated Seedcoat.—Variegated seed due to rupture of the seedcoat as found in the Nambiquara peanut was partially dominant to the russet or tan of commercial cultivars in Stokes and Hull's (135) research. In crosses between Bolivian varieties having red-and-white-striped seedcoats and other varieties with pale, Krapovickas and Rigoni (88) observed partial dominance for both the red color and for variegation itself.

Ashri and Yona (12) interpreted seedcoat splitting as caused by a disharmony in growth rates of the seedcoat and the embryo. In their study, however, non-splitting (entire) testa was dominant to splitting.

The occurrence of a white spot on the seedcoat at the end opposite the micropylar end may appear in some crosses where one parent is white seeded. It occurs with either of the basic colored phenotypes. When Srivastava (132) crossed a white genotype, *R T* d_1d_2 with a plain red seeded one, *R T* D_1D_2, the F_1 was red and in F_2 segregation was 11 plain red : 4 white-spotted red : 1 white, indicating a digenic difference with cumulative effects.

In the cross between purple variegated Nambyquara and a non-variegated red peanut, purple was completely dominant over red with a digenic difference and variegation was completely dominant (3:1) to non-variegation. Moreover, the epistatic effect of the purple *P,* over the red *R,* and the interaction between loci, gave an F_2 ratio of 36 purple variegated : 12 purple non-variegated : 9 red variegated : 3 red non-variegated : 3 rose variegated : 1 rose non-variegated (132). In another cross, rose non-variegated X red variegated, the modified F_2 ratio of 3 rose non-variegated : 1 red much-variegated : 2 red little-variegated : 1 red non-variegated (Table 1) confirms both the incomplete dominance of variegation and the complete dominance (in this material) of rose over red (132).

A second red locus (R_2r_2) was postulated by Ashri (6, 9) from progeny behavior in crosses of the red-and-white variegated Mani Pintar (Pintado) with Pearl (R_1R_1), and of another variegated variety with three different varieties having flesh (r_1r_1 R_2R_2) testa. Ashri also noted that testa variegation is under separate genetic control. This model differs from that of Srivastava (discussed previously) in which the recessive and dominant red phenotypes occur in varieties with entire or single-color seedcoats.

Mauboussin (unpublished) also found variegated testa dominant to the normal condition and again suggested that this trait was governed by a pair of genes (47). Genetic studies at Tifton, although not complete, indicate separate genetic systems for the variegated pattern and for each component color in the pattern. Therefore, it seems evident that any combination of self (entire) color or variegation can be associated to give a more varied phenotypic diversity than when solid-color genotypes alone are crossed.

Inner Seedcoat Color.—Color variations in the inner seedcoat (with uniform color on the outer seedcoat) show heritable differences in studies by Rodriguez and Norden (125). Their results indicate that at least four loci control the color, and F_2 progenies

from different crosses segregated either monogenic, digenic, trigenic or tetragenic ratios. Gene symbols and their effects are proposed: dominant complementary factors *L* and *M* produce a dark pigment, *N* dilutes this to a lighter form, while *S* reduces the dark pigment to neutral white.

Heritable Mutagenic Changes

An unsuccessful attempt to induce chlorophyll mutations in peanuts by heating dormant seed was made by Hull and Grossman (77) in the early 1930s. They suggested that chlorophyll deficiencies in peanuts may be of the cytoplasmic type and inferred that the failure to obtain heat induced mutants might be due to polyploidy.

X-ray Induced Mutations.—The extensive research in North Carolina since 1949 on the production and breeding characteristics of the genetic variation induced by ionizing radiation was recently reported in the review edited by W. C. Gregory (53). In addition to the induction and characterization of macromutants, the scope of this research focused on the possibilities inherent in the hypothesized cryptic genetic changes of very small effect on quantitative characters. Only a limited sampling of their findings can be mentioned here; readers should refer to the review and to the other papers referenced in this section for additional results from the experiments.

The induced macromutants are listed and briefly described by Gregory (53). Genetic data for several typical examples are reported here to show the more usual patterns of inheritance observed.

Cup, a simply-inherited, single-locus mutant with pleiotropic action, was the first radioinduced heritable change described in peanuts (Hammons, 56, 57). The cup mutant is a complex of morphological features characterized by ventrally involute leaflets forming a "cup", reduced plant and fruit size, and sinuous succulent stems which snap under slight tension. Its expression is governed by a single recessive gene, *cu.* The cup phenotype was expressed in five recognizable grades of intensity. Hammons (57) investigated phenotypic variability in cup mutants and demonstrated that the gradations in mutant expressivity were genetically determined. He attributed the intensity of grade manifestation to the interaction of the changed "gene" and the modifying effects of the altered genotypic background in which it was expressed.

This feature was further analyzed by Gregory who advanced the general hypothesis (ref. 49, p. 188) that "along with the macromutants produced by radiation a very large number of small variations of both incremental and decremental character" are produced. In the extensive investigations of these "small variations" occurring in progenies from crosses among macromutants (98-101, 61, 40-42) the hereditary constitution of non-macromutant loci is termed the "background genotype".

Gregory's hypothesis was subsequently tested by Loesch (99) and Emery *et al.* (40, 41) and reviewed by Loesch and Emery (100). Loesch (98) found that the macromutant characters flop, ilex, and ilex$_{50}$ were inherited monofactorially, while hedera and corduroy were determined by duplicate factors, and all of these are recessive. Genetic information for diallel crosses among five macromutants, cup *(cu),* flop *(f),* ilex *(i),* hedera *(h_1h_2)* and corduroy *(co_1co_2),* and the control NC 4 is reported by Loesch and Hammons (101).

Gregory (51) showed that as the magnitude of phenotypic effect of mutation decreased the frequency of mutant plants increased exponentially. He further showed that the more completely these large phenotypic deviations are expunged from the population the more symmetrical become the exposure of changes of very small effect in the genome.

He then related this phenomenon to Fisher's adaption sphere and discussed its implications for plant improvement (Gregory 51, 53).

When visible deviations of large effect were screened out from the irradiated populations, fruit yield became more symmetrically distributed suggesting that contributory changes to its variance were each individually of small effect (51, 52). A further example of the effect of removing the visible mutants from a population and then comparing a genetically independent variable in the mutant, mutant free, and control populations was furnished by measurement of seed size in the X_3 generation. The smaller seed size frequency distribution for the mutant population (figure 11 of Gregory, 53) appears to be similar to the recent research by Coffelt and Hammons (31) associating albino seedling with smaller seed sizes in infraspecific cross progenies.

Stucker *et al.* (136) derived the quantitative genetic expectations for estimating induced polygenic variance in mutant populations following roguing of macromutants, and demonstrated that the distribution of plus and minus mutations supported the hypothesis that these mutations occurred with approximately equal frequency (51).

In their fundamental research Emery *et al.* (40-42) have carefully assessed the quantitative effects of hybridizing induced macromutants, both in the presence and absence of the mutant phenotype. In the latter study, for example, the mutated backgrounds of nine 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 three specific cup backgrounds, together with the differential response to environment of specific cup hybrids were indicative of the diverse nature of the mutated backgrounds.

Radiosensitivity.—A differential primary response to irradiation among varieties of peanuts was recognized early (50). From further research it appeared that differences in radiosensitivity to X-rays do not appear in the same manner when fast neutrons are used. However, differences in sensitivity to neutrons appearing among the lines and their hybrids suggested a qualitatively different behavior of lines and their hybrids with respect to X-rays and neutrons. Therefore, genetical control of response would make possible selection among otherwise similar stocks for greater or lesser radiosensitivity (50).

This hypothesis has been investigated by Emery (38) in North Carolina. In 1956 specific radiosensitive and radioresistant parents and their F_2 progenies were irradiated and subsequently re-irradiated three times for a total of five equal dosages of gamma rays over a period of eight generations. Selection radiosensitivity was effected. The unique hybrid-irradiation populations also were evaluated for fruit yield and for any changes in frequency of mutations (38).

Elsewhere, Bilquez and Martin (24) noted distinct differences in sensitivity when a Spanish- and a Virginia-type variety were exposed as dormant (resting) seeds at 5% relative humidity to a series of 9 dosages of X-rays (range 8,000 to 40,000 R). Similar results were found by Ashri (8) with respect to the chemical mutagen diethyl sulfate. The dependence of radiation response on differences in moisture content in peanut embryos was shown recently by Emery *et al.* (39).

Other Radiation Genetics Research.—Following X-irradiation, Bilquez *et al.* (23) have reported from Sénégal clear varietal differences in radiosensitivity and recovered numerous hereditary variants, chromosomal as well as genetic. The most interesting variants for practical application include: (i) Spanish lines with greater 100-seed weight than the control 28-204 cultivar while other characteristics remained unchanged, and (ii) irradiated lines from the 29-103 Virginia type cultivar with an average weight of 78 to 96 g/100 seed as compared with 59 g/100 for the control.

These workers also achieved increases in oil percentage of a magnitude similar to the range attainable with natural variants. Irradiation of the early-maturing 28-204 gave six lines with higher oil contents (54.2-55.6%) than that of the unirradiated parent (50.6%). One of these, with an oil content of 54.4%, was more productive and had larger seed than 28-204. Irradiation of the late-maturing 28-206 variety did not yield any promising mutations (106).

Among the macromutants arising from the irradiation research in Senegal, two are of special utility for genetic purposes. Apetiolated leaves (having sessile leaflets inserted directly on the petiole), a one-gene recessive, is useful as an outbreeding marker (23). The white-flowered mutant genotype *(aayy),* induced by irradiation of 28-204 (22), was mentioned earlier in discussing genetics of corolla color.

Mutation research with peanuts has been prominent in the investigations at the Trombay (India) Atomic Energy Establishment. Patil (118, 119) and his co-workers obtained 28 mutations affecting almost every feature of the plant. Over 60% of the mutants appeared in X_2 or X_3. More than 40% of these belonged to one aberrant X_1 cytological variant, and included trisomics ($2n = 41$) and tetrasomics ($2n = 42$). Based upon experience with other crop plants, these variants could have important bearing on the progress of cytogenetic research in the peanut.

Consistent selection for increased kernel weight resulted in the isolation of a Large-pod dominant mutant in X_5. This and a tertiary-branching mutant having increased pod-setting are the only economically useful variants thus far reported in the Indian material. The rest were inferior (118).

Genetic data, reported from segregating progenies in the irradiated material (118) or from crosses among mutants (119) show dominant mutant alleles for both Large-pod *(Lp)* and Long-pod, and recessive inheritance for the xantha and albina lethals and for virescent, imparipinnate *(imp),* and darker-green *(dr).*

Patil (119) used the x-radioinduced virescent mutant to evaluate our prosposal (59) that a critical understanding of genetic behavior in peanuts is better accomplished by studying progenies from a spectrum of cross-combinations rather than from a single cross. His results indicate a monogenic difference between virescent and the Spanish Improved control cultivar, or the darker-green *(dr)* and imparipinnate *(imp)* mutants. In the Large-pod *(Lp)* cross, however, segregation of virescent followed a trigenic (45:3:16) model. Genotypic formulae may be assigned: virescent *($v_1v_2Dr_1Dr_2Imp_1W_1W_2$)* darker green *($V_1dr_1dr_2$---),* imparipinnate *($V_1imp$---),* large-pod *($V_1V_2W_1w_2$---).*

Imparipinnate and virescent are considered to be on nonhomologous chromosomes. A recombinant with *imp* leaf character and *v* chlorophyll, recovered as a double recessive (119), could be a useful marker. The expression of virescent was found to be sunlight dependent (118).

The virescent mutant induced in the North Carolina experiment has given either monogenic or digenic inheritance in different cross combinations in our research at Tifton.

Chemical mutagenesis.—Mutation induction in peanuts with diethyl sulfate *(DES)* was undertaken in Israel in 1961. Two beneficial, thin shell mutants were found (8). DES induced single-trait and pleiotropic mutations, with induction at a higher rate in the variety least sensitive physiologically to the chemical. Crosses of mutants with the original parent variety showed that DES induced polygenic mutations simultaneously with the macromutants (129); just as Gregory (49, 52, 53) and his associates (99, 100) have demonstrated with x-ray-induced macromutants in peanuts.

Five mutants, virescent *(vr)*, xanthamaculata *(xm)*, dwarf-1 *(dw_1)*, dwarf-2 *(dw_2)* and open-habit-2 *(oh_2)*, were inherited monogenically, with the mutant allele being fully recessive. Three other mutants, open-habit-1 *(oh_1)*, spherical *(sp)* and dwarf-3 *(dw_3)*, gave somewhat irregular segregations, but apparently they also were recessive and monogenic (129). Normal dihybrid segregation occurred for a *xm* X *dw_1* cross.

A most interesting dominant mutant with variable penetrance and expressivity appeared in Israel in the M_1 of the Dixie Anak variety (10). Heterozygous plants were either extremely diminutive, dwarfed and leafletless or intermediate or mixed, i.e., they grew initially as diminutive and then produced some perfectly normal branches. This change was not accompanied by a genotypic change and, thus, was not a paramutation. The mutation also affects the gibberellin levels in the peanut plant and was used to study the environmental factors affecting hormone balance and output. Diminutive plants produce normal growth when sprayed with gibberellic acid. Ashri (10) has shown that "the mutant allele is a dominant factor with a recessive lethal effect."

Differences in physiological sensitivity between varieties to several other chemical mutagenic agents also are under investigation in Israel (8).

The interaction of nuclear genes with each other and with the plasmons to control growth habit in peanuts was discussed in an earlier section. This mechanism operates through modification of gibberellin inhibitors (55) which require light for induction. The peanut system is well suited for testing for plasmon mutations. A scheme for identifying such mutants following prolonged chronic chemical mutagenesis has been outlined by Ashri (8).

Host Plant Resistance To Diseases, Insects And Other Pests

Cultivated peanuts are devoid of qualitative genetic resistance to most of the diseases and insect pests described in other chapters of this book.

Disease Resistance.—For most diseases of fungal origin ,including the economically-important leafspots, various fruit (pod) and stem rots, and seedling pathogens, no significent resistance has been uncovered among extant collections of *A. hypogaea* germplasm. Qualitative genetic data do not appear in support for the occasional claims of resistance in an extensive literature.

The *leafspots* are the most common disease of peanuts wherever this crop is extensively grown. No cultivated peanut variety is immune to leafspot although numerous workers have reported large differences in the relative susceptibility of different cultivars to the fungi, but most of these comparisions rated both early- and late--maturing varieties on definite dates rather than at comparable stages of maturity. Studies in Georgia led to a reversal by Higgins (74) of his postulation in 1938 (71) that resistance to the leafspots was inherited as unit characters. In our research (64) when disease measurements were made at the same growth stage, both early-maturing (ss. *fastigiata)* and late-maturing (ss. *hypogaea)* cultivars are equally susceptible to leafspots. Our observations extend over 3-4 seasons for 200-250 diverse cultivars planted annually at Tifton, Ga., in inverse relation to their duration periods in order to achieve a uniform maturity date.

These observations have been confirmed by Mughogho (114) in Malawi, who concluded that "although late-maturing varieties appear to be more tolerant to the disease at a given date from planting than early-maturing varieties, they are not resistant as is generally thought."

His failure to obtain hybrids combining resistance to leafspot with high yielding ability led Higgins (74) to conclude that "apparently susceptibility to leafspot is positively correlated with quantity and maturity of the nut crop."

Since the ideal control would be genetic, resistance has been sought in the wild species of *Arachis,* some of which have shown resistance and immunity to *Cercospora arachidicola* Hori and *Cercosporidium personatum* (Berk. & Curt.) Deighton (syn. *Cercospora personata)* infection in innoculation tests in North Carolina. The fact that some *Arachis* species are susceptible to one leafspot pathogen but immune or highly resistant to the other led Abdou (1) to conclude that resistance to these fungi could be inherited independently. Triploid F_1 hybrids obtained by Smartt (130) between leafspot susceptible X resistant species were susceptible suggesting that resistance to these fungi may be recessive. Genetic models have yet to be presented. Interspecific hybridization programs currently are in progress in North Carolina, Malawi, Argentina, India, and elsewhere, with the aim to incorporate the resistance into highly productive adaptive cultivars.

Rosette (Groundnut Rosette Virus = GRV) is a complex of virus diseases, transmitted in a persistent manner by *Aphis craccivora* Koch. Many strains of the virus no doubt exist causing various chlorotic and stunting effects on plant and flower parts. The Mwitunde group of late-maturing, upright-bunch varieties, long grown by native peoples of East Africa, were initially thought to possess some resistance. Observations by Evans (44) indicated that the lower incidence of rosette infection was not due to inherent resistance, but rather to an apparent unpalatibility that they have for aphids.

The only known true source of resistance to rosette is some spreading-bunch varieties, with small pods and long growing season, originally selected in the frontier region between Ivory Coast and the Upper-Volta in West Africa. Berchoux (18) reported that resistance to rosette is governed by two recessive genes with duplicate action *(aabb).* He also found that resistance is apparently due to the production of an antivirus substance by the plant, a fact confirmed by Daniel and Berchoux (35). It can therefore be expected that this resistance will be maintained in agricultural production.

This genetic mechanism, and the development of suitable techniques for screening segregating field progenies to artificial infection by rosette, led to the successful transfer, via backcrossing, of rosette resistance to a commercial cultivar 28-206 R.R. (109). This is the only instance in peanut research where genetic information has been available to achieve effective control of a major disease by breeding.

Gibbons (45) in Malawi determined that the diploid ($2n = 20$) *A. repens* Handro and a tetraploid ($2n = 40$) form of *repens* induced by colchicine in Kenya, together with *A. glabrata* Benth. ($2n = 40$), failed to develop rosette symptoms when infected by aphids or by grafting. As a high level of rosette resistance is found in the I.R.H.O.[3] varieties only immunity would be useful if found in the wild *Arachis* species. Even if immunity is discovered, however, incompatability barriers will have to be overcome before this could be incorporated into the cultivated peanut.

A necrotic-etch leaf disease, investigated in our research at Tifton, inherits as a recessive characteristic (unpublished data). F_2 progenies from different matings segregate for monogenic, digenic and apparently also for trigenic distributions. This behavior adds further support to the thesis that a "wide variety of cross combinations constitutes a more critical test of locus character" in peanuts than single cross and biparental backcross procedures (59).

[3]The Institut de Recherches pour les Huiles et Oleagineux (I.R.H.O.), Paris, collected the resistant lines in Ivory Coast and Upper Volta, and determined their resistance to rosette in research at Bambey, Senegal.

Peanut rust, caused by *Puccinia arachidis* Speg., has posed a threat to the U. S. peanut crop since early in this century. Within *A. hypogaea* germplasm, Bromfield (25) found three sources of physiologic resistance to rust. None of the three genotypes meet present U. S. commercial requirements. A susceptible natural hybrid plant, spotted in an increase plot of one resistant line, gave progeny segregating in a ratio indicating that resistance is recessive and controlled by duplicate loci (K. Bromfield and W. K. Bailey, personal communication, 1971). Certain wild *Arachis* species also are resistant to rust.

The genetic system for resistance to bacterial wilt, incited by *Pseudomonas solanacearum* (E. F. Smith) E. F. Smith, appears not to have been elucidated. The Schwarz 21, Matjan and Georgia 119-20 varieties, although highly resistant to several strains of the bacterium, are not immune to all three isolates tested by Jenkins *et al.* (84).

Recently, Hammons (65) called attention to the genetic vulnerability of peanuts to disease epiphytotics as single variety culture is being increasingly substituted for the diversity of varieties previously grown. He also documented the relatively narrow germplasm base of current cultivars. In view of the high risk of crop loss from a sudden outbreak of a new mutant form of pest or disease, future varieties should be developed with enhanced variability to minimize the hazards. Meanwhile, the search for genetic resistance must be intensified.

Insect and Nematode Resistance.—Laboratory and field screening of *Arachis* germplasm for resistance to insect and nematode pests is in progress at most research locations where peanuts are grown. Examples of non-preference feedings, of antibiosis, or of tolerance to fall army-worm, thrips, lesser cornstalk borer, southern corn rootworm, parasitic nematodes, a mite, and other destructive pests could be cited. Thus, opportunities for improving insect control through breeding do exist, but information is lacking on the genetic basis for such resistance as has been described.

The absence of specific genetic information by which the breeder can effect improvement in peanuts by incorporating resistance to any insect or nematode pest into higher-yielding adapted cultivars points sharply to the need for intensified research seeking alternatives to complete dependence on pesticidal control (65).

Linkage

Little work has been done to establish the series of marked stocks which are prerequisite for critical linkage analyses.

An association between violet tinge in stem with hardiness and of thin pericarp with pigmy seed was suggested by Badami (14). The reassortment of growth habit and branching type was not independent in crosses between the spreading, branched Philippine White and the bunch, non-branched Corientes-3 varieties in investigations by Patel *et al.* (117). About 30% crossing over occurred between spreading and branched.

Independent assortment of genes governing a number of different characters was the rule in six crosses studies by Patil (120) in Poona, India. However, in two crosses he measured linkage of the gene for reticulum on pod *(Rp)* with other genes. The gene for growth habit *(Sph)* showed linkage with *Rp* with a crossover value of 40.42% in one cross, and the gene for stem hairness *(Hst)* showed linkage with *Rp* and a crossover value of 31.51% in the second cross. Crossover values were measured by the product ratio method.

No effort has been made to assign linkage groups for these few instances of qualitative character linkage.

GENETICS OF QUANTITATIVE CHARACTERS

The gene-character relationships described in the previous sections concern those genetic phenomena—mutation, segregation, recombination, allelic and nonallelic interaction, expressivity, epistasis, linkage, and so on—that have bearing upon the genotypic behavior of the germplasm in the allopolyploid cultivated peanut. They also give a background of genetic information as a useful guide in choosing appropriate breeding procedures for successful integration of desirable characteristics in the improvement of the crop.

Most peanut breeding is focused upon maximum yield of fruit (seed) or oil, enhanced shelling grade and milling properties, and increased quality of end-use products. Many of the morphological and physiological characteristics of interest to the peanut breeder are demonstrably influenced by macromutant genes, by duplicate-gene inheritance at nonallelic loci, and by the complex interactions thus occurring in this allopolyploid species. For yield—and it components—both major and minor genes, their modifiers, and their interactions obviously are involved. Since the weight of evidence for most self-pollinating species shows that future gains in yield will be made by manipulating genes for strictly quantitative characters, we will review here some of the efforts that have been made in characterizing the genetic variability in quantitative terms

The application of genetic information in peanut improvement is the subject of the chapter on Peanut Breeding. The independent review and appraisal of the literature will, inevitably, give somewhat different viewpoints. The writer can only hope that his selectivity will furnish a basis from which a more rapid accumulation of genetic information will be forthcoming.

Genetic Variability

The effectiveness of selection depends ultimately on the magnitude of variability in the germplasm pool, its heritability, linkages, and the effect of the mode of reproduction (i.e., self-pollination in peanuts) upon the choice of breeding procedures for productive utilization of the variation.

Linkage.—Even less is known about the distribution of genes conditioning quantitative characters on the chromosomes of the peanut than the meager data recorded for linkage of qualitatively-inherited traits. However, if we assume that the genes conditioning such characters are distributed randomly among the 20 pairs of chromosomes, then the effects of linkage on estimates of genetic variance is likely to be negligible. Since there appears to be little restriction on recombination in the progeny of the interspecific *A. hypogaea* X *A. monticola* cross (123), tight linkages would be less likely in *A. hypogaea* intervarietal crosses

However, in view of the complex series of interacting duplicate loci and epistatic genes conditioning qualitatively-inherited traits, a varied spectrum of polygenic interactions controlling or modifying quantitative characters may be confidently expected as procedures for analyzing such interactions are elaborated.

Heterosis and Combining Ability.—Estimates of heterosis and combining ability of peanuts are meager. Stokes and Hull (135) thought there was little vigor among F_1 hybrids in 11 different crosses, but Higgins (73) observed marked vegetative vigor and very high pod yields in certain instances when he crossed 16 varieties in all possible combinations. Individual plant yields in Spanish X Virginia crosses reached a pound of shelled seed for many F_{1S}. Hammons (64) subsequently recorded 661 pods weighing 1.96

pounds for one F_1 hybrid plant and 1156 mature seed from another F_1 in such infraspecific crosses, and an average of more than 700 seeds/plant for a number of F_1s (29). This achievement means that the production level of the F_1 generation in peanuts is not as severely limiting for genetic and breeding research as was once thought (54).

In the self-pollinated peanut hybrid vigor is largely ephemeral; the yield superiority over the better parent usually disappeared by about the fourth selfed generation in Higgins' (73) nursery.

Transgressive segregation occurred for fruit form but not for fruit size in crosses by Ilieff (81). F_1 fruit size was similar to that of the female parent, a Spanish, but F_2 distribution was binomial suggesting that size was conditioned by multiple factors.

Diallel crosses involving two Virginia, one Spanish, and two Valencia cultivars also exhibited marked heterosis for top weight in Virginia X Spanish or Virginia X Valencia combinations in Japan (138). Such hybrid vigor did not appear in F_1 plants between varieties within each type, nor in Spanish X Valencia crosses.

In Taiwan, Lin (93) noted significant hybrid vigor for length of mainstem and branches, especially in the F_2, from crossing a Spanish type with Florispan Runner (derived from Spanish X Virginia hybridizations).

Investigations on heterosis using crosses among three varieties differing in maturity and habit of growth (Hassan and Srivastava, 69) also showed superiority of the F_1s over their better parents in yield as well as in number of branches and leaflet length. Observavations on a heterotic effect are of little use in a breeding program without estimates of combining ability as an aid in identifying superior parents.

Gregory (unpublished annual report, N. C. State Univ., 1945), in diallel crosses among 10 diverse peanut lines, found estimates of general combining ability (GCA) to be significant and of greater magnitude than specific combining ability (SCA) for yield and yield components. This agrees with experience in other self-pollinated crop species (see Parker *et al.,* 116). Gregory further observed that lines selected in advanced generations came from crosses that performed well in the F_1 generation.

Parker *et al.* (116) estimated combining ability for 17 characters measured on F_1 hybrid seedlings produced by diallel crossing of six peanut lines representing three geographic areas of South America. In the controlled environment of a phytotron, estimates of GCA were found to be more important than SCA.

However, when Wynne *et al.* (146) measured heterosis and combining ability for these same 15 F_1 hybrid combinations under field performance a different result was noted. Estimates of SCA were significent for 16 of 17 characters and estimates of GCA were significant for 8. SCA was greater for yield and for most fruit characters. Crosses of Virginia X Valencia gave greater vegetative heterosis, but the Valencia X Spanish combinations gave greatest heterosis for yield and fruit characters. Either "dominance of genes or geometric gene action" was postulated to have contributed to the high estimates of SCA for the fruit characters, but high GCA estimates for fruit length implied additive gene effects for fruit size. These authors (146) concluded that the phytotron environment (116) may be of limited use in predicting field performance of peanut hybrids.

Variability In The Germplasm Pool

A number of investigators have surveyed the genetic variation within the germplasm pool for information concerning the possibilities of effecting improvement. These workers have not always recognized the fact that populations including varieties from both

subspecies of *A. hypogaea* are more variable than a collection of varieties in either of the Spanish, Valencia or Virginia types. Also a population consisting of cultivars of one type will be more variable than any single variety in the population. Furthermore, a collection including examples from diversely separated ecogeographic regions is usually more variable than select populations from a local area. Frequently, in the literature reviewed, the estimates of genetic variability and correlations have failed to consider that the major source of variation in a given collection was that existant between the botanical varieties.

Correlations Among Characters In Variety Collections.—A growing number of investigators have correlated measurements of quantitatively-inherited traits in variety collections of peanuts. This review seeks to acquaint the peanut geneticist with this body of information, but most of the discussion covers work during the recent decade.

Emery (43) in North Carolina first found that within a variety the formation of single and multiseeded pods is independent of the number of seed in a pod. His results, which constitute a pure-line theory in peanuts, have been confirmed a number of times by workers, including van der Stok (134), unfamiliar with this research.

Van der Stok's (134) cross of small-thin x larger-thick pods gave an array of F_2 types from which he established "maintainer" lines whose hull characteristics exhibited measurable differences from those of the parental varieties, thereby indicating multigenic control.

As early as 1924, Nevano (115) concluded that the best way to improve peanuts was to choose plants bearing the largest number of "seed pods" without considering their weight or size and the number of nuts. He observed very close correlations between dry pod weight and their total number ($r=0.874$) and the weight of plants with fruits attached ($r=0.794$). Hence yield could be increased in his material by choosing the heaviest plants.

Over the next quarter-century, correlation analyses between various characters associated with yield were reported by Stokes and Hull (135), Sun (137), Maralihalli (104), Hayes (70), Hull (76), Humphrey (78) and Dalal (33), among others. Some of the correlations between yield of pods and other traits offered scope for selection in their populations, but the experimental material and conditions differed greatly for these studies. Thus caution should be used in comparing their results.

During the 1950s correlation analyses were extended to larger and more diverse germplasm collections and to more variates. Lin (92) in Taiwan studied 26 variates in 60 varieties and the 4 characters, numbers and weights of pods and seed per plant, were all highly correlated. Work of Mital and Mehta (113) with 90 strains showed that different attributes are correlated in the erect (Spanish) and the spreading (Virginia) groups. The importance of this difference was affirmed by Shad (128) who showed that the combined effect of four characters (numbers of pods, pegs, flowers, and branches), accounted for about 83%, 77%, and 73% of the variation in pod yield for the spreading, semi-spreading, and erect groups, respectively. Merchant (110) also demonstrated that the associations between characters differ for growth habit groups.

From partial regression analyses, Mishra (112) also obtained different estimates of the effect of leaflet dimensions on seed size variation in spreading and erect groups of varieties. At Ludhiana, Chaudhri (27) used regression analysis over two seasons to confirm an association of yield with number of pods. Dorairaj (37) contrasted the correlations for several variates in the important Indian varieties TMV-1 (spreading) and TMV-2 (erect), and again found different associations of yield components between the two.

The associations of seven other quantitative characters with yield in the single variety TMV-2 were measured by Chandra Mahan, *et al.* (26) as a basis for forming a selection index. Based upon the highly significant multiple regression coefficient (.98) between predicted and observed values for yield, the number of mature pods had the dominant influence on ultimate yield.

In most of these studies, no distinction was made between the environmental and the genetic contribution to the correlations. The construction of selection indices and the measurement of genetic variability in terms of its genetic and environmental components was investigated in a series of studies at Ludhiana, India (82, 83, 15, 16).

In the first study (82) pod yield in 73 varieties was positively correlated with four components, but regression analyses indicated that only two characters, number of mature pods and total number of pegs, influenced yield. The selection index based on these two characters accounted for 49% of the variation in pod yield, and number of mature pods alone accounted for 47% .These workers made a similar study with 59 erect (Spanish) varieties (83). Regression analysis revealed that the number of mature pods and total branch length influenced pod weight. Selection indices show that the characters they studied accounted for 45% to 71% of the variation in pod weight.

Genetic variability of 13 quantitative characters affecting pod yield and oil content was measured by Badwal, *et al.* (15) in a collection of 60 varieties, including 20 each for spreading, semi-spreading and erect habits of growth. They estimated genetic variability (GV) in terms of the genetic variance (Vg) expressed as percentage of phenotypic variance (Vp), that is, GV = (Vg/Vp) x 100. However, an estimate of GV alone does not give the magnitude of possible improvement, i.e., the possible increase in metric terms, that can be effected through selection for a strongly manifested character of particular interest. Accordingly, these workers measured possible improvement by estimating genetic advance (GA). Then, they expressed GA as a percentage of the mean, (GA/mean) x 100, to facilitate comparison of genetic advance for different characters.

GV and expected GA were highest for 100-seed weight, indicating wide scope for improvement in seed size For several characters, high GV was offset by low GA, indicating limited opportunity for selection *(in this germplasm pool)* for those traits. The need for estimates of genetic advance to support genetic variability data is, therefore, emphasized (15).

With the same germplasm pool, Badwal and Gupta (16) found that pod yield was strongly correlated with different yield components in the three growth habit groups. Progress was predicted from the multiple regression analyses.

Heritability (H) estimation has been used to specify that portion of the genetic variability that is due to genetic causes. In six erect varieties, Mahapatra (102) used the variance-covariance relationship to estimate heritabilities for six attributes variously correlated with pod yield.

High heritability estimates were obtained for five quantitative traits in nine varieties by Kulkarni and Albuquerque (90). Genetic advance was greatest for number of developed pods. The high yielding potential of three cultivars was interpreted as partly due to favorable interaction between several genotypes comprising each variety.

Basu and Asoka Raj (17) got high heritabilities for the number of days to flowering, pods/plant, and 100-pod weight. Since the genetic coefficient of variance (GCV) was high for the number of pods per plant, they concluded that selection may be based on phenotypic performance.

The GCV not only helps to measure the range of GV, but also provides a measure for comparing the GV present in different characters. However, for estimation of the heritable portion of the variation, heritability estimates are used together with the GCV. Thus, Majumber, *et al.* (103), in Bihar, observed a wide range of phenotypic variation for 11 of 17 quantitative characters measured in a collection of 45 peanut varieties. Six of the 17 had comparatively high GCV's. All the characters except number of pods and pod yield—both economically important—had high H. Despite low heritabilities for pod yield in the study, heritability estimates together with genetic gain would be more useful than the heritability value alone in predicting the effect of selecting for best individuals. The high heritabilities and the high genetic advances for numbers of branches, nodes, and leaves were ascribed to additive gene effects.

Significant differences were recorded by Sangha and Sandhu (126) in each of 11 yield components studied in 54 varieties, 27 each from spreading and erect groups. Genotypic coefficient of variation and genetic advance, expressed as percent of the mean, were very high for four components in each group, but only for pod number in both groups. Genotypic correlation coefficients were generally higher than phenotypic ones. Although the material offers considerable scope for improvement, the partial and multiple correlations signify that different selection criteria would be required within the Virginia and the Spanish groups.

A large amount of genetic variability was found for such characters as number and weight of mature pods/plant in 108 varieties investigated by Dixit, *et al.* (36). Most of the characters had high heritabilities, especially 100-pod and 100-seed weight.

The interrelationship of yield components to yield was evaluated in Taiwan in a series of experiments using the path coefficient analysis to assess the relative importance of various components. In one study (94) of 173 varieties, including 38 Virginia Runner, 35 Virginia Bunch and 100 Spanish, intertype differences among the plant characters were significant. Significant positive correlations were obtained for six pairs of varibles, but correlations frequently varied in significance depending upon the type. For example, in the Spanish type, pod yield was directly affected by number of pods per plant rather than the average weight per pod.

Data from the second experiment (95) for 7 agronomic characters of 30 Spanish type varieties, grown in different seasons (fall vs. spring), gave significant seasonal differences for different components when analyzed by the path coefficient method.

Evidence from two year field trials in Taiwan (28) showed that neither variety x year nor variety x location interactions attained significance, indicating that varieties were highly adapted. The second order interactions (variety x year x location), however, were highly significant.

Estimates of heritability are affected by plant spacing. Lin, *et al.* (96) obtained higher heritabilities for pod yield and for number of pods in wide than in narrow drill spacings, and the heritability value for average weight of pod was generally higher than 68%, being highest at the denser spacing. Estimates of selection differential and genetic advance, however, were higher in wide spacings for yield of pods, number of pods and average weight per pod.

Variability In Segregating Generations Of Crosses

Intervarietal Crosses.—Information concerning genetic variability in segregating generations of intervarietal crosses is less extensive than the quantitative investigations with pools of varietal germplasm. The peanut plant develops its pods (fruits) under-

ground which makes visual selection in the field of little value except for foliar or stem diseases. Growth is indeterminate so there is no definitive yield for a given strain.

Bernard (19) measured the magnitude of the genetic and environmental variability for 10 traits in the F_1-F_4 generations of 19 crosses. Each trait was evaluated as to its importance in an optimum selection criterion on the basis of its direct economic value, its heritability, and its genetic correlation with yield and other economic traits (20). All traits appeared to have sufficient genetic variability for appreciable changes to be effected through selection. Bernard found that weight of seed was more heritable than seed yield. Most significantly in his study, selection for an index including yield and any or all of the other nine characters was not superior to selection for yield alone.

Genotypic correlations higher than phenotypic correlations were obtained by Syakudo and Kawabata (139) for 15 characters in the F_2 generation for diallel crosses among one variety each for the Spanish, Valencia and Virginia types, but the values themselves, with few exceptions, were very low. Broad sense heritabilities were calculated for all characters. The values for plant-type index and height of the main stem axis were high (0.89 and 0.82, respectively). Flowering date and oil content did not correlate with the other 13 characters studied in the 3 intertype crosses.

The inheritance of six characters was analyzed by Lin (93) in F_2-F_3 progenies of a Spanish x Virginia cross. Genetic variance was principally dominance variance for number of pods and weight of pods, while additive effect was more important for length of main stem and the length of branches. Seven different formulae were compared for estimating the heritability of the six quantitative characters. Heritability values for the agronomically important traits, number of pods and weight of pods per plant, were relatively small. Genotypic, environmental and phenotypic correlations also were calculated for all possible combinations of characters. Of major interest is the significant correlation between number of pods and weight of pods.

Estimates of heritability of F_2 plant traits are influenced by a number of factors involved in the evaluating of nursery populations. As noted previously, Lin, *et al.* (96) found heritabilities affected by plant spacing. For estimates of heritability to have utility in estimating expected genetic advance from selection, all extraneous environmental variables must be considered.

Recent studies in France (105), in hybrid and backcross progenies between two varieties with contrasting oil contents, shelling outturns, and seed weights, have shown heritability of these characters was about 70%; varietal differences are estimated to be due to 2, 1 and 5 pairs of alleles, respectively. Gains from retaining the best 30% of the F_2s were respectively 1.5, 2.2 and 7.0% of the F_3 means. Oil content and kernel size were unrelated.

Interspecific crosses.—There is little information available on the phenotypic and genotypic correlations between several traits in the segregating populations of interspecific hybrids of *Arachis*. Raman and Sree Rangasamy (123) found genetic variability to be high in each of three growth habit groups, bunch, semi-spreading and spreading, distinguishable in F_3 of the interspecific cross *A. hypogaea* x *A. monticola,* thereby offering scope for selection gain. Significant and positive associations based on correlation coefficients were recorded between yield and four other attributes. Variability in such characters as length of primary branches, number of secondary branches, pod yield and shelling percentage appeared to be controlled by additive genes. Thus, selection based on these traits can be exepected to lead to the isolation of stable, superior progenies.

In practice, selection for pod yield and shelling percentage was effective in developing the Spancross variety (Hammons, 62) in progenies from an early-maturing, bunch (Spanish) plant appearing in the F_5 generation of an interspecific cross, *A. hypogaea* X *A. monticola.*

Correlation and regression coefficients also have been estimated for four characters in the F_3 and BC_1 F_3 populations of the hybrid *A. hypogaea* X *A. glabrata* var. *hagenbeckii* (Harms.), and the BC_1 F_4 population of *A. hypogaea* X Allotriploid {F_1 *A. hypogaea* X *A. villosa*} (Ramanathan and Raman, 124). High correlations between shelling percent and weight of 100 pods were obtained in all these populations.

Induced Quantitative Variability

Gregory (48) induced a remarkable increase in the genotypic variance of the polygenic "fitness" character, yield of pods, by x-ray treatment of seeds of a pure-line variety of peanuts. Since that time, the influence of ionizing radiations upon the genotypic variances which govern quantitatively inherited characters has been evaluated by Gregory and his coworkers and reported in a number of publications (49, 51-53, 40-42, 136). It is not our purpose here to review this important research. The reader interested in the quantitative genetic variation induced by irradiation and its implications in the improvement of peanuts is referred to the original literature.

In the self-pollinated peanut epistatic variance may be of more importance to breeders than dominance variation, because the latter is necessarily ephemeral in such breeding systems. Many of the morphological and physiological characters in which the peanut breeder is interested are probably based upon epistatic gene interactions. Therefore, much more research is needed to obtain estimates of variance components and heritabilities for use as guidelines in efficient peanut breeding programs.

Correlations Among Quality Attributes

A knowledge of the magnitude of the variation in chemical constituents of the peanut seed is essential for improving the end-use quality characteristics of various peanut products. Genetic diversity in the fatty acid composition and stability of peanut oil and in protein content has been investigated for a number of genotypes in studies in Georgia.

Linoleic acid was most closely associated with oxidative rancidity of the oil in studies (75) of 26 genotypes. Oils obtained from different botanical varieties differed considerably in their tendency to develop oxidative rancidity and this tendency was correlated with the content of linoleic acid. Holley and Hammons (75) reported a correlation of -0.92 between linoleic acid content and oil stability. This correlation was based on 66 genotypes grown in a single season. These authors also reported large yearly variations in protein content and in stability of oils from the 26 peanut genotypes grown for 8 years but did not account for this variation.

Available data show considerable variation among peanut genotypes for both major and minor fatty acids. The most extensive data are those of Worthington and Hammons (144) and Worthington *et al.* (145), and these authors review pertinent literature

Year to year differences in oil stability, for 110 genotypes grown at a single location, were large and could not be accounted for by relatively small yearly variations in fatty acid composition (144). Correlation coefficients among fatty acids showed signi-

ficant positive correlations between linoleic acid and palmitic, behenic, and lignoceric acid, and correlations of linoleic acid with stearic and oleic acid were significant but negative. These variations clearly show that ample variation exists in the germplasm pool to effect improvement in quality of peanut oil.

In a related study (145) the range in oil stability (autoxidation induction period), for 82 genotypes of diverse ecogeographic origin, over a 3-year period, was 11.6 to 18.5 days. The range in fatty acid values was: 7.4-12.9% palmitic, 1.6-5.3% stearic, 35.7-68.5% oleic, 14.1-40.3% linoleic, 0.9-2-2% arachidic, 0.6-2.0% eicosenoic, 1.3-5.1% behenic, and 0.6-2.0% lignoceric acid. These are the most extensive data on the genetic variability available in seed lipid composition for breeding manipulation in the peanut.

Recent studies in France (105, 107) estimating the number of major quantitative genes governing oil content and shelling outturn were described in an earlier section.

OUTCROSSING AND CYTOGENETICS

Natural Outcrossing Variability

The peanut has generally been classed as an obligate self-pollinating species, but varying rates of natural outcrossing occur, with seasonal and varietal fluctuations in frequency, in different parts of the world (59, 60, 32, 46).

Natural cross contamination in the breeding nursery was noticed by van der Stok (134), and has been recognized as a problem in maintaining varietal purity, particularly in the more humid areas, wherever suitable markers have been employed to measure its occurrence (59).

Extensive investigations of natural crossing in the vicinity of Tifton, Ga., have been reported elsewhere[4] and will not be described here. The problem of maintaining varietal integrity in seed increase plantings is considered in the following chapter on Peanut Breeding. Our concern here is with the fact that natural hybridization provides a source of genetic variability which can be utilized.

Hammons (60) has developed a new peanut research procedure involving directed natural crossing to obtain pedigreed hybrids for genetics and breeding investigations. He suggested the term "Pedigreed Natural Crossing" when a genetic marker such as Krinkle-leaf is employed as the pollinator. Since the time-consuming manual procedures of artificial cross-pollination are laborious and limit the number of crosses that can be made, pedigreed natural crossing should be considered wherever the rate of natural crossing warrants its use.

Already Hammons (60) and Emery (unpublished personal communication) have demonstrated the utility of the procedure in genetics and breeding investigations.

In addition to constituting a source of genetic variability which can be recognized with suitable markers and exploited by the geneticist, natural crossing can constitute a serious source of error in genetics and breeding research when sib mating occurs. Thus, natural outcrossing at all generations can effectively perpetuate sufficient genetic variability to give varietal instability in commercial fields or aberrant genetic ratios in the nursery.

[4]Publications by R. O. Hammons and D. B. Leuck, 1963 to 1969. For a recent review of much of this work and research elsewhere, *see* Gibbons and Tattersfield (46).

Cytogenetics

Cytogenetic research in the cultivated peanut and its wild *Arachis* relatives is beyond the scope of the present review[5].

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