Genetics and Breeding of Groundnut

Compiled by

Faujdar Singh and D.L. Oswalt

Skill Development Series no. 4

ICRISAT

Human Resource Development Program

International Crops Research Institute for the Semi-Arid Tropics
Patancheru, Andhra Pradesh 502 324, India

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CONTENTS

Introduction

The objective of a crop breeding program is to create variability and select the desirable genotype(s) for cultivation or for breeding purposes. Groundnut, being a highly self-pollinated crop, requires special attention in emasculation, crossing, and selection as these processes require special skills and may be time consuming. Genetic studies assist the breeder in understanding the inheritance mechanism and enhance the efficiency of a breeding program. Considerable progress has been made in genetics and plant breeding of groundnut during the last three decades (see reviews Wynne and Gregory 1981; Wynne and Coffelt 1982; Norden et al. 1982; Reddy 1988; and Wynne and Halward 1989). An attempt has been made to compile the recorded experiences of groundnut breeders and geneticists. Questions are provided to assist in self evaluation of selected skills by the, readers.

Genetic Studies in Groundnut

Detailed literature reviews of the inheritance of characters in groundnut have been reported by Hammons (1973), Wynne and Coffelt (1982), Reddy (1988), and Wynne and Halward (1991).

Qualitative inheritance

Inheritance studies of plant and flower characters (Table 1), pod and seed characters (Table 2), and disease resistance (Table 3) are summarized while linkage studies are discussed separately.

Table 1. Inheritance studies of plant and flower characters in groundnut.

Character(s)	Genetics	Reference(s)
Growth habit		
Spreading (S) vs bunch(B)type	Spreading dominant S x B = 3S:1B (monogenic)	Patel et al.1936; Dalai 1962; Jadhav and Shinde 1979
	Spreading digenic B x S = 15S:1B (duplicate) B x B = 9S:7B (complementary)	Hayes 1933 Patel et al. 1936; Dalai 1962
	Bunch type dominant S x B = 3B:1S (monogenic)	Hassan and Srivastava 1966a;Balaiah et al.1977
	Semispreading (SS) dominant B x SS = 3SS:1S (monogenic)	Balaiah et al. 1977
	Growth habit determined by four genes	Essomba et al. 1987

Table 1. Continued

Character(s)	Genetics	Reference(s)
Plant type		
Spanish	Controlled by duplicate genes (Va_1 Va_1, va_2 va_2)	Hull 1937
Valencia	Controlled by double recessive genes (va_1 va_1, va_2 va_2)	Hull 1937
Runner	Controlled by duplicate genes (va_1 va_1, Va_2 Va_1)	Hull 1937
Dwarfism	Recessive to tall (monogenic) Duplicate (15 tall:1 dwarf)	Hull 1937; Bhuiyan 1984 Hayes 1933; Husted 1934; Mohammad et al. 1966; Balaiah et al. 1977
Stem pigmentation	Dark or purple dominant to light color (monogenic) 3 dark:l light	Hayes 1933; Patil 1966; Balaiah et al. 1977; Jadhav and Shinde 1979
	Purple and green pigmentation controlled by one and two duplicate genes	Essomba et al. 1987
Leaf color	Dark green foliage dominant to light green (monogenic)	Badami 1923; Dalai 1962
Leaf shape	Elliptical-recessive to elliptical-oblong	Hassan 1964
	Marrow leaf dominant to normal (monogenic)	Balaiah et al. 1977
	Red color of leaf veins dominant to its absence	Hayes 1933
Inflorescence	On main stem controlled by two sets of duplicate loci with epistatic action Sequential flowering - controlled by duplicate pairs of recessive genes - monogenic recessive to alternate	Hammons 1971; Wynne 1975 Mouli and Kale 1982 Mouli et al.1986
Corolla color	Dark dominant to light	Hayes 1933; Patil 1965; Bilquez and Lecomte 1969; Jadhav and Shinde 1979
	Orange incomplete dominant to white	Kumar and Joshi 1943
	Yellow dominant to white controlled by duplicate genes (15 yellow:1 white) Yellow incomplete dominant to white or controlled by additive genes (9 yellow:6 pale yellow:1 white)	Patil 1966; Jadhav and Shinde 1979 Habib et al. 1980
King petal shape	Boat shape dominant to broad or scoop shape (monogenic)	Srivastava 1968
Nodulation	Determined by three genes Nonadditive genes	Essomba et al. 1987; Dutta and Reddy 1988 Phillips et al. 1989

Table 2. Inheritance studies of pod and seed characters in groundnut.

Character(s)	Genetics	Reference(s)
Pad size	Large pod dominant to small Small pod dominant to large (duplicate gene)	Balaiah et al. 1977 Cahaner 1978
Pod constriction	Absence is dominant to its presence (digenic)	Badami 1928
	Trigenically inherited	Hassan 1964
	Controlled by three nuclear and one cytoplasmic factor, complementary duplicate	Coffelt and Hammons 1974a
Seed size	Large seed is dominant to small seed size	Hassan 1964; Balaiah et al. 1977
	Controlled by five pairs of genes, four having isodirectional effect	Martin 1967
Seed shape	Long seed shape dominant to short (digenic); duplicate 15 longs 1 short	Hayes 1933
	Flat end of seed dominant to smooth	Sibale 1985
Seed number	Fewer than three seeds pod^{-1} dominant to three or more seeds/pod (monogenic)	Balaiah et al. 1977
Testa color	Monogenic Red x brown = Red Brick red x light tan = Red Red x light rose = Red White x pink or red = 3 whites: 1 red or pink (monogenic)	Badami 1928 Stokes and Hull 1930 Patil 1966 Norden et al. 1988; Branch 1989
	Digenic 15:1 ratio Flesh x white = 15F:1W White x red = 15R:1W Pink x white = 15Pk:lW Purple x rose = 15P:lr	 Higgins 1940 Higgins 1940 Hammons 1957; 1972 Prasad and Srivastava 1967
	Rose x light rose = 15R:llr White x red = 9R:3Rs:4W	Prasad and Srivastava 1967 Srivastava 1968
	Purple color inherited by three pairs of genes	Patel et al. 1936; Mohammed et al. 1966; Srivastava 1968
	White and purple color inherited by four or five pairs of genes	Hammons 1963; Prasad and Srivastava 1967; Srivastava 1968
	White seed coat color dominant to pink or red (monogenic)	Norden et al. 1988
Seed dormancy	Incomplete dominance to non dormancy (monogenic)	Stokes and Hull 1930; Lin and Lin 1971
Protein content	High protein content dominant to low protein	Shany 1977
Oil content	Low oil content dominant to high oil	Shany 1977
	Two recessive genes (Ol_1 and Ol_2) controls high oleic acid character	Moore and Knauft 1989

Note: Seed size and testa color are reported as governed by more than three genes.

Table 3. Inheritance studies on disease resistance in groundnut.

Character (s)	Genetics	Reference (s)
Groundnut rosette virus (GRV)	A pair of independent complementary genes 1 resistant : 15 susceptible	de Berchoux 1960; Nigam and Bock 1990
Early and late leafspot	Resistance is recessive	Smartt 1964; Sharief 1972
	Controlled by two or more nuclear genes	Sharief et al. 1978
	Quantitatively inherited	Sharief et al. 1978; Kornegay et al. 1980; Norden 1980
	Additive gene	Anderson et al. 1986; Green 1985
	Multiple recessive genes nonadditive gene action	Nevill 1982
	Influenced by cytoplasmic factors, and additive genes	Coffelt and Porter 1982; 1986
	Resistance to early and late leafspots independently inherited	Anderson et al. 1985
Rust	Resistance recessive to susceptibility and controlled by two or three genes	Bromfield and Bailey 1972
	Controlled by duplicate recessive genes	Nigam et al. 1980; Knauft and Norden 1983; Knauft 1987
	Resistance recessive to susceptibility and controlled in additive fashion F_2 ratio 1 resistant: 6 intermediates 9 susceptible	Tiwari et al. 1984
	Controlled by additive, additive x additive, and additive x dominant gene effects	Reddy et al. 1987
Necrotic etch	Resistance dominant to normal condition with digenic ratio 15 nondiseased : 1 diseased	Hammons 1980
Sclerotinia blight	Controlled by cytoplasmic factors	Coffelt and Porter 1982
Seed coat splitting	Monogenic, duplicate additive and complementary	Bovi et al. 1983
Verticillium wilt	Duplicate recessive	de Berchoux 1960

Linkage Studies

Badami (1923) observed linkage between violet color and hardiness in stems and thin pericarp with small seed. Patel et al. (1936) reported a nonrandom assortment of growth habit and branching type in a cross between 'Philippine white' (spreading branched type) and 'Corientes 3' (bunched, and nonbranched type) with a crossover value of 30%. Patil (1965) reported linkage between growth habit and pod reticulation with a crossover value of 40%; and stem hairiness with pod reticulation with a crossover value of 31%. Coffelt and Hammons (1973) reported linkage between small seed size and albino seedlings.

Stalker et al. (1979) reported linkages of late maturity, small seed size, separate pod cell, and low yield with leafspot resistance in crosses involving cultivated groundnut and wild species (A. cardenasii).

Balaiah et al. (1984) suggested linkage involving the genes controlling the growth habit, branching number of primaries, number of secondaries, pigmentation on the shoot, and leaflet shape. The crossover between the loci controlling these characters ranges from 6 to 39%. Mouli et al. (1984) reported linkage between the bifurcate nature of leaf and small size of leaflet. A locus for testa variegation (V) and one of the two genes controlling nodulation (N) were reported to be linked (Dashiell 1983).

Quantitative Inheritance

Estimates of heritability, genetic advance, gene effects, and heterosis, have been reported in groundnut.

Heritability and Genetic Advance

High heritability combined with high genetic advance was considered an indication of additive genetic variance (Johanson et al. 1955). However, it was reported that heritability values were highly influenced by the environment in groundnut (Lin et al. 1971).The heritability and genetic advance estimates are listed in Table 4.

Table 4. Heritability (H - broad sense and h - narrow sense) and genetic advance (G) studies in groundnut.

Character(s)	Component(s)	Reference(s)
Pod yield plant^{-1}	High (H)	Lin et al. 1971; Reddy 1968; Majumdar et al. 1969; Dixit et al. 1970; Sangha 1973b; Patra 1975; Sandhu and Khera 1976; Lakshmaiah 1978; Gibori et al. 1978
	High (h) Moderate (h) Low (H)	Wynne and Rawling 1978; Cahaner 1978 Basu et al. 1986a Bernard 1960; Lin 1966
Mature pods plant^{-1}	High (H)	Kulkarni and Albuquerque 1967; Majumdar et al. 1969; Lin et al.1971; Basu and Ashokraj 1969; Alam et al. 1985; Sandhu and Khera 1976; Sivasubramaniam et al. 1977
	High (H and G)	Dholaria and Joshi 1972; Sangha 1973a; Kushwaha and Tawar 1973; Alam et al. 1985
	Low (H)	Lin et al. 1971
100 pod mass	High (H)	Cahaner 1978; Basu and Ashokraj 1969; Dixit et al. 1970
	Low (H)	Hammons 1974; Lakshmaiah 1978; Xiang et al. 1984
100 seed mass	High (H)	Basu and Ashokraj 1969; Dixit et al. 1970; Sangha 1973b
	High (H and G)	Dholaria and Joshi 1972; Sangha 1973a; Kushwaha and Tawar 1973; Badwal et al. 1967; Badwal and Gupta 1968
	Moderate (H) and high (G)	Alam et al. 1985
Pod length	High (H)	Kushwaha and Tawar 1973
	High (h) Low (H)	Wynne and Rawling 1978 Sibale 1985
Pod breadth	High (H)	Kushwaha and Tawar 1973
Seeds pod^{-1}	Low (H)	Hammons 1974
Days to 50% flowering	High (H)	Basu and Ashokraj 1969
Primary branches	High (H)	Kulkarni and Albuquerque 1967; Majumdar et al. 1969; Dixit et al. 1970; Raman and Sreerangaswamy 1970
Plant height	High (H)	Kulkarni and Albuquerque 1967; Dixit et al. 1970; Alam et al. 1985; Basu et al. 1986a
Secondary branches plant"'	High (H and G)	Alam et al. 1985; Reddy 1968; Dixit et al. 1970; Raman and Sreerangaswamy 1970
Maturity	Low (H)	Mohammed et al. 1978

Note: High and low values of heritability are in relation to the characters studied in the experiment.

Gene Effects

Fisher (1918) partitioned genetic variance into additive effect, dominance, and epistasis, i.e., interactions, additive x additive, additive x dominance, and dominance x dominance. Interactions and gene effects other than additive are also referred to as nonadditive. The implication of gene effects in plant breeding has been dealt with as follows:

- When the additive gene effect for a trait is high, the character under consideration could be improved using simple selection procedures. Therefore, plants with desirable traits could be selected even in the early generations. Thus procedures like pure line selection, pedigree selection, and their modification are useful.

- When dominance or over dominance gene effects are predominant, the best way is to utilize F_1S as commercial hybrids. This option is not available to groundnut breeders, because it is a cleistogamous crop. However, recurrent selection procedures could be used to bring the desirable additive genes into broad based populations.

- When epistasis is involved, all selections should be deferred until the F_5 generation. However, on the basis of early-generation testing one can discard the low-yielding and undesirable crosses for economic traits (poor seed quality) or those susceptible to biotic and abiotic factors. Therefore, use of bulk population selection and/or its modifications like bulk-pedigree and single seed descent selection procedures are recommended. However, additive x additive epistasis, being an interaction of fixable gene effects, could be fixed and thus provide an opportunity to select desirable plants.

The most common designs used by the geneticist to study the genetic parameters and their interpretations are line x tester, diallel, triallel, and quadriallel. These designs give estimates of gene effects and general and specific combining ability effects for the parents and crosses involving the parents. The general combining ability (GCA) effect is attributed to additive gene effect and additive x additive gene interactions that are fixable and could be easily exploited through selection. On the other hand, a specific combining ability (SCA) effect is due to dominance and epistasis (additive x dominance and dominance x dominance) that is not fixable. The other methods useful for genetic analyses are the generation mean analysis, North Carolina designs (NCI, NCII, NCIII), and their modifications. The genetic studies on quantitative traits are summarized in Table 5.

Table 5. Genetic variances and gana effect studies in groundnut.

character(s)	Genetic component(s)	Reference(s)
Pod yield	GCA variance' > SCA	Wynne et al. 1970, 1975; Wynne 1976; Garet 1976; Gibori et al. 1978; Habib et al. 1985
	Nonadditive	Schilling 1986; Sandhu and Khera 1976
	Additive and non additive	Mohammed et al. 1978
	Additive gene effect	Sridharan and Marappan 1980; Basu et al. 1987
Pod number plant^{-1}	GCA variance > SCA	Habib et al. 1985
	Nonadditive	Sandhu and Khera 1976; Dwivedi et al. 1989
	SCA variance > GCA	Khanorkar et al. 1984
100 pod mass (mean pod mass)	Additive and nonadditive	Schilling 1986
	Nonadditive	
	Duplicate gene	Cahaner et al. 1979
100 seed mass	Additive and nonadditive	Reddy et al. 1986
	Nonadditive	Sandhu and Khera 1976
	Additive	Sridharan and Marappan 1980
Seeds pod^{-1}	Nonadditive	Schilling 1986
Pod length	Nonadditive	Schilling 1986
	Additive	Dwivedi et al. 1989
Pod size	Nonadditive	Schilling 1986
	Additive and nonadditive	Mohammed et al. 1978
Plant height	GCA variance > SCA	Habib et al. 1985
	Additive	Sridharan and Marappan 1980
	SCA > GCA	Khanorkar et al. 1984
Primary branches plant^{-1}	GCA variance > SCA	Habib et al. 1985
	SCA variance > GCA	Khanorkar et al. 1984
	Additive and nonadditive	Reddy et al. 1986
	Additive dominant genes	Cahaner et al. 1979
Secondary branches plant^{-1}	Additive and nonadditive	Reddy et al. 1986
Days to 50% flowering	Additive and nonadditive	Reddy et al. 1986
	Additive	Basu et al. 1987
Days to maturity	GCA variance > SCA	Habib et al. 1985
	Additive	Basu et al. 1987
Shelling percentage	GCA variance > SCA	Labana et al. 1981
	Additive	Basu et al. 1987
	SCA variance > GCA	Dwivedi et al. 1989
Oil content	SCA variance > GCA	Basu et al. 1988
Protein content	SCA variance > GCA	Basu et al. 1988
Iodine value	SCA variance > GCA	Basu et al. 1988
Nitrogen fixation	Epistasis (nonadditive)	Phillips et al. 1989; Nigam et al. 1980

(Note: GCA variance indicates additive genetic variance; SCA variance indicates nonadditive genetic variance.)

Table 5 suggests that both additive and nonadditive genetic variances are important in the inheritance of economic traits of groundnut. However, their estimations will depend on the parents involved in crosses. The conclusions derived for one set of crosses may or may not hold true for another.

Heterosis

A considerable amount of heterosis (Table 6) has been reported in groundnut. In general crosses involving Valencia x Spanish parents had high heterosis for pod yield and its component characters.

Table 6. Estimates of heterosis over aid-parent (MP) and better parent (BP) in groundnut.

Character(s)	Cross	Heterosis	Reference(s)
Pod yield	Spanish x Virginia	Positive	Higgins 1940
	Valencia x Spanish	High	Wynne et al. 1970
	Subspecific group	High	Coffelt and Hammons 1974
		F_1 37.02% more over BP	Raju 1978
	Virginia x Spanish	High heterosis	Raju et al. 1981
	Virginia x Virginia	Moderate heterosis 37.44 to 95.33% over MP; and 4.20 to 70.3% over BP	Sridharan and Marappan 1980
	Spanish x Spanish	High positive; Heterosis 5.2 to 30.5% over MP	Basu et al. 1986c Isleib and Wynne 1983
Top mass	Virginia x Spanish Virginia x Valencia	Positive	Syakudo and Kwabata 1963
Pod length	Virginia x Spanish	F_1 equal to MP value	Syakudo and Kwabata 1963
	Virginia x Valencia	Upto 11.2% over MP	Isleib and Wynne 1983
Branch number		F_1 superior to BP	Hassan and Srivastava 1966a
Leaflet length		F_1 superior to BP	Hassan and Srivastava 1966a
Days to 50% flowering	Valencia x Virginia	F_1 superior to MP	Parker et al. 1970
Vegetative characters	Virginia x Valencia	High heterosis	Wynne et al. 1970
100-pod mass plant^{-1}	Virginia x Spanish	F_1 higher than BP Heterosis ranges 6.38 to 30.2% over MP; and 35.8 to 165.2 % over BP	Garet 1976 Sridharan and Marappan 1980 Dwivedi et al. 1989
100 seed mass	Virginia x Spanish	F_1 higher than BP	Garet 1976
	Virginia x Spanish	F_1 high heterosis	Raju et al. 1979
	Virginia x Virginia	Moderate heterosis Heterosis ranges 6.38 to 30.2% over MP	Raju et al. 1979 Sridharan and Marappan 1980
Pods plant^{-1}	Virginia x Spanish	F_1 higher than BP; 20.5% more over BP; 23.33 to 87.5% over MP; and to 38.4 over BP	Garet 1976 Raju 1978 Sridharan and Marappan 1980
Mature pods	Spanish x Spanish	Up to 17.5% over MP	Isleib and Wynne 1983
Shelling percentage	Virginia x Spanish	F_1 higher than BP; Ranges from -23.3% to +10.3% over BP	Garet 1976 Dwivedi et al. 1989

Character Association

The knowledge of the nature and magnitude of the association among characters are important for indirect selection when the desirable character has low heritability. The efficiency of indirect selection is measured as a correlated response (CRY).

CRY = ix x hx x hy x rg x Py.

Where

ix = selection intensity;

hx and hy = heritability of characters x and y;

rg = genetic correlation between x and y characters; and

Py = phenotypic standard deviation of y in that the correlated change is sought through selection on x.

When a selection is to be made on several characters using the simultaneous selection model (Singh 1972) the use of a correlation study is helpful in avoiding undesirable changes in other correlated characters while selecting for some characters (Table 7).

Table 7. Summary of character association studies in groundnut.

Character	Correlated with	Reference(s)
I. Positive correlations with:		
Pod yield	Number of mature pods plant^{-1}	Alam et al. 1985; Deshmukh et al. 1986; Dholaria et al. 1973; Chandola et al. 1973; Nevano 1924; Dorairaj 1962; Jaswal and Gupta 1966; Lin et al. 1969; Bhargava et al. 1970; Dholaria and Joshi 1972; Phadnis et al. 1973; Kushwaha and Tawar 1973; Patra 1980; Yadava et al. 1981, 1984; Sandhu and Khera 1977; Coffelt and Hammons 1974b; Liao et al. 1989
	Number and mass of seeds plant^{-1}	Phadnis et al. 1973; Dholaria et al. 1973; Redona and Lantican 1986
	Secondary branches plant^{-1}	Lakshmaiah et al. 1983; Alam et al. 1985; Sandhu and Khera 1977
	Primary branches plant^{-1}	Chandola et al. 1973; Prasad 1981; Balkishan 1979; Bhargava et al. 1970; Khangura and Sandhu 1972; Sandhu and Khera 1977
	Shelling (%)	Kataria et al. 1984; Raju et al. 1981; Khangura and Sandhu 1972; Patra 1980; Yadava et al. 1984
	100 seed mass	Deshmukh et al. 1986
	Number of pods plant^{-1}	Phaokantarakorn and Waranyuwat 1987; Liao et al. 1989
	Days to maturity	Alam et al. 1985

continued

Table 7. *Continued*

II. Path-coefficient studies:		
A. Direct effects		
Yield	Primary branches	Khangura and Sandhu 1972; Yadava et al. 1984
	Secondary branches	Lakshmaiah et al. 1983
	Mature pods plant^{-1}	Deshmukh et al. 1986; Badwal and Singh 1973; Chandola et al. 1973; Sandhu and Khera 1977; Raju 1978; Balkishan 1979; Lakshmaiah et al. 1983; Yadava et al. 1984; Nigam et al. 984
	100 seed mass	Badwal and Singh 1973; Yadava et al. 1984; Deshmukh et al. 1986
	Number of seeds pod^{-1}	Balkishan 1979
	Days to maturity	Yadava et al. 1984
B. Indirect affect via:		
Yield	Secondary branches Shelling (%)	Badwal and Singh 1973
III. Negative correlation with protein content:		
Oil content		Tai and Young 1975

Genotype X Environment (GxE) Interactions

GxE interaction has considerable influence on the progress of crop improvement. High yielding cultivars with the least genotype x environment interactions are normally desirable. However, when a cultivar is to be selected for a specific environment, the GxE interactions are desirable. Chen and Wan (1968) observed cultivar x year and cultivar x location interactions were low for yield and the cultivar x year x location interaction was highly significant. Several studies indicated that cultivar x year x location interactions were significant for yield and yield components in groundnut (Chen and Wan 1968; Tai and Hammons 1978; Ojomo and Adelana 1970; Sangha and Jaswal 1975; Wynne and Isleib 1978). Thus no advantage could be gained by subdividing the production areas into subareas for breeding or testing purposes (Wynne and Isleib 1978).

Further significant linear and nonlinear components of genotype x environment interactions were reported for 100 seed mass, oil content, and shelling percentage. The magnitude of the linear component of GxE was high for pod yield, 100 seed mass and oil content. The nonlinear component was important for days to maturity and pod yield (Kumar et al. 1984). The stability parameters for the different traits were governed by an independent genetic system (Yadava and Kumar 1978a, 1978b, and 1979). Shorter and Norman (1983) made an environmental classification based on cultivar x environment interactions. This indicated that there were no temporal or closely

related regional environment groups with similar cultivar x environment interactions, and concluded that lower critical percentage differences between new and established cultivars in prerelease trials can be obtained by adding environments rather than replications.

Pod yield, percentage of sound mature seeds, and percentage of extra large seeds studied in F_4 and in F_5 generations showed that populations of individual cross and lines within the cross were significantly different for all the characters. Populations of different crosses interacted with the year, location, and environments for all traits, whereas lines within a cross interacted with the environment for all the traits except pod yield (Wynne and Coffelt 1980). Reddy et al. (1984) observed that seasonal differences in groundnut yields were more pronounced than varietal differences. The magnitude of variety x season interaction was high in the Virginia type, being less interactive than the Spanish type. An individual variety with stability across the locations was identified.

Schilling et al. (1983) developed multilines using sibling lines composited between the F_4 and F_5 generations. The relationships among sibling components of two groundnut multilines across the environment were calculated. For one multiline three component lines did not differ significantly from the multiline nor did deviations from regression and stability variances differ among components. Conversely, components of the second multiline displayed significant variability for yield, regression coefficient (b), and deviation from regression (S^2d) . The data indicated that the compositional scheme for groundnut multilines is a feasible method to circumvent GxE interaction.

Norden et al. (1986) studied the stability of four groundnut multilines and their component lines. They found highly significant interactions of genotypes (population) with environments for pod yield, percentage of fancy pods, 100 seeds mass, percentage of extra large seeds, and sound mature seed yield. Large differences in yield and market quality traits were not found between sib-lines. However, differences were found in stability estimated from regression coefficients and deviation from regression of multilines compared to their component lines. This was possibly due to a buffering action resulting from greater genetic variability. Multilines did not have greater stability in all cases, but the difference between the multiline and its least stable component line was generally greater than the difference between the multiline and its most stable component line. Thus, the chances of improving the yield stability and market acceptability of a groundnut cultivar were increased when the multiline approach was followed.

Groundnut Breeding

The main breeding goals should meet the requirements of a grower, a processor, and a consumer. A grower requires high yield, pest resistance and tolerance of environmental stresses, and yield stability. A processor requires uniform maturity favorable to mechanization and processing characteristics. The consumer requires good quality oil and groundnut seeds with acceptable shape, size, color, and taste for confectionery purposes (Wynne and Gregory 1981; Branch 1979).

Efforts have been made to accomplish these requirements at ICRISAT under five projects.

- Breeding for resistance to foliar diseases (leafspots and rust).
- Breeding for resistance to soilborne diseases (pod rot, Aspergillus flavus, and collar rot, A. niger).
- Breeding for resistance to pests. This includes thrips, jassids, leafminer, spodoptera etc.
- Breeding for drought resistance or tolerance.
- Breeding for adaptation to specific environments and requirements. This includes cultivars for oil production with varying duration (early, medium, and late type) and for direct consumption.

Germplasm Collection and Evaluation

A large number of groundnut accessions are available in the national programs of many countries. ICRISAT maintains a world collection of over 12 000 accessions of groundnut from 92 countries of which 60% were obtained from the USA, South America (Peru, Bolivia, Brazil, Argentina); western Africa (Senegal, Burkina Faso, Mali, Nigeria), southern Africa (Zambia, Zimbabwe, Mozambique, Tanzania), and Asia (India and Indonesia) (V. Ramanatha Rao, ICRISAT, personal communication 1988).

A germplasm line could be used directly as a variety, if it is found suitable. When some collections have genetic variability, they are subjected to selection (pure line or mass selection) to isolate desirable genotypes. The third way to use the germplasm accession is as a parent to transfer the desirable characteristics into established genotypes or to obtain the transgressive segregants.

Bailey (1968) estimated that 75-80% of the groundnut cultivars grown in the USA were derived wholly or in part from selections introduced from foreign countries. Higgins and Bailey (1955) by exercising selections in the different lots of farmers' groundnuts of USA identified six groundnut varieties; GFA Spanish, Dixie Spanish, Southeastern runner 56-15, Virginia bunch 67, Virginia bunch G2, and Virginia runner G26.

Spanish varieties released through pure line selections in USA were Argentina (1951), Comet (1977), and Spantex (1950). Virginia varieties released were Virginia 56R (1957) and Virginia 61R (1962).

Hybridization

The objective of hybridization is to recombine characters from different lines into a desirable genotype for commercial utilization. The results of crossing will be known after several years, therefore, it is necessary to consider the following points before starting a hybridization program:

Wall defined objectives. The breeding objectives should be well defined before taking up hybridization, such as resistance to diseases, insect pests or improvement in oil content.

Choice of parents. Select the parents based on the breeding objective. One parent can be a desirable variety of the area and the other parent or parents may have a desirable trait(s) not present in the first parent. It is safe to select the parents for a particular trait from various sources (Tables 8a, 8b, and 8c).

Hating design. Depending on the breeding objectives and the traits available in different sources single, double or three way crosses are attempted. The other way is to attempt crosses using mating designs suitable for biometrical studies. This will help in understanding the genetics of characters as well as to identify the material for a breeding program.

When the number of parents involved in a cross exceeds two, it creates a problem in crossing. As the number of parents increases the number of buds to be crossed must be increased to realize the maximum recombinations. Groundnut, being a highly self-pollinated crop (cleistogamous) makes it difficult to use population improvement procedures. However, diallel selective matings (Jensen 1970) and modified recurrent selection schemes (Compton 1968) were applied in groundnut improvement (Wynne 1976). At ICRISAT Center, single crosses, three-way crosses, and double crosses are made.

Table 8a. Groundnut genotypes reported resistant to tolerant of diseases.

character	Genotypes with desirable traits
1. Early leaf spots (*cercospera arachidicola*)	FESR-5-l-B-b4, FESR-5-2-B-64, NC3033, and PI 109839, ICG 7878, ICG 6284
Late leaf spots *Phaeoisariopsis personata*	UP 81206-1, UF 81206-2, 72 x 32B 3-2-2-2-l-b3-B NC3033, AC3139, PI Nos. 203395, 203397, 261893-2-1-1-13, 261893-1-3-B, 261893-2-1-4-1-2B, 261906-1-1-1-2-3B and NC 3033, Southern Runner', ICG 7756, ICG 1710, ICGV 86699
2. Rust (*Puccinia arachidis*)	PI Nos. 259747, 341879, 350680, 380622, 315608, 314817, 405132, Tarapota, DHT 200, Israel line 136, PI 314817, NC Ac 17133, PI 25947, NC Ac 17090, and EC 76446
Lines resistant to late leaf spot and rusts (Interspecific hybrid crosses)	CS9, CS30, CS22, CS62, CS31, CS26, CS36, CS2403, CS820/1, CS13-1-B1-B3-B1, CS16-B2-B2-B1, CS29/1-B2-B1-B1, and NC Ac 17090
3. Web blotch (*Phoma arachidicola*)	Florunner, Florigiant, and GK3
4.	Florispan, and F334A-B-14
5. Sclerotinia blight (*Sclerotinia sclerotiorum*)	NC 11165, Chico, PI 535817
6. CBR-Black rot	NC 3033, Argentine, NC2, VAGP1, NC Ac 18016
7. Pythium pod rot (*Pythium myriotylum*)	PI Nos. 341885, 365553, 535816 and Toalson
8. Southern stem rot (*Sclerotium rolfsii*)	NC2
9. Aflatoxin (*Aspergillus flavus* and *A. parasiticus*)	Tolerant: Florunner, Daron IV, Shulamit, PI 337394F, PI 337409, J 11, U4-7-5, VRR 245, GFA-1, GFA-2, Ah 7223, UF 71513, 55-437
10. Rosette virus (Vector Aphis craccivora)	RG 1, RMP 40, RMP 12, RMP 91, KH 14-9A, and M-25-68
11. Bud necrosis	ICGV No. 86029, 86030, 86031, 86032, 86033, and 86038
12. Necrotic etch leaf disease	Jenkins Jumbo

Table 8b. Groundnut genotypes reported resistant to or tolerant of insect pests.

Character	Genotypes with desirable traits
1. Lesser cornstalk borer (*Elasmopalpus lignosellus*)	Florunner and Comet
2. Southern corn root. worm (*Diabrotica undecimpunctate*	NC 6
3. Thrips (*Frankliniella fusca*)	PI 280688, NC Ac 343, low damaged lines, NC Ac 2242, NC Ac 2214, NC Ac 2240, NC Ac 2232, and NC Ac 2230
ICRISAT pest resistant lines (low incidence)	ICG(PRS) 13, ICG(PRS) 4, ICG(PRS) 68, ICG(PRS) 77, and ICGPRS 36
4. Termites	NC Ac 224 0, and NC 343
5. Jassid (*Empoasca kerri*)	NC Ac 2214, NC Ac 2240, and NC Ac 2230, ICGV 87157, and ICG(FDRS) 10

Table 8c. Groundnut genotypes desirable for drought resistance, earliness, quality, and confectionery type.

Character	Genotypes with desirable traits
Drought resistant/ tolerant lines	GNP 35, ICG 1660, ICG 3386, ICG 3736, ICG 296, ICG 405, ICG 1697, ICG 4790, ICG 4747, ICG 6997, ICG 2960, ICG 3301, ICG 4544,ICG 4728, ICG 3657, UP 67, Arbrook (PI 262817)
Earliness	Chico, 91176, 91776, ICGS(E) 71, ICGS (E) 61, and ICGS (E) 11
Quality	Oil: Tainan 10 (57.1%)
	Protein: NC-F1a 14 (32%)
Confectionary type	ICRISAT genotypes HYQ (CG) 514, HYQ (CG) 53, HYQ (CG) S5, ICGV 86564, ICGV 86577
Nitrogen fixation	NC 7, NC Ac 2821

Sources for Tables 8a,8b, and 8c: Norden et al. 1982, Subrahmanyam et al. 1980, ICRISAT 1985, 1986, 1987, 1990, and Reddy et al. 1991.

Choice of Selection Procedures for Groundnut

Both additive and nonadditive gene effects are evidently important for economic traits in groundnut. However, the former appears more important than the latter. Therefore, the breeding method that exploits both additive and nonadditive gene effects may be suitable for the improvement of groundnut. Due to limitations in attempting large scale crossing, use of recurrent selection procedures are restricted. Therefore, a basic goal in most groundnut breeding programs is to develop pureline cultivars or multilines by using siblings to obtain wide adaptability and resistances to biotic and abiotic factors. Thus it is desirable to make single, three-way, or double crosses to pool the characters from different genotypes in the local cultivar that has wide adaptation. These crosses are grown with large F_2 progenies so that further selection can be made using pedigree, modified pedigree, bulk, single seed (SSD), or single pod descent methods. An accelerated pedigree selection method (Valentine 1984) or stratified mass selection (Holly and Wynne 1986) and a sequential selection method (Branch et al. 1991) were found useful in groundnut.

The accelerated pedigree selection (APS) involves an initial selection based on the assessment of the lines rather than the plants. These lines are derived by the accelerarted generations procedure. Unlike the SSD method the line selection can begin in an early generation, that will minimize the risk of differential mortality. The length of the APS breeding cycle is shorter than that of either the pedigree or SSD selection methods. In addition to enhancing the efficiency of selection, the APS is expected to result in more genotypes being retained and a closer selection for the desirable combination of characters (Valentine 1984).

Stratified mass selection for higher seed yield was effective in interspecific crosses, but was only effective in one of the three intrasubspecific crosses (Holly and Wynne, 1986). The confounding effect of shelling percentage with seed yield and the small number of F_2 plants evaluated may be partially responsible for the lack of effective selection in two of the intrasubspecific crosses for high seed yield having higher shelling percentage. However, the high and low selections when evaluated in the F_4 generation did not differ for shelling percentage except for one intrasubspecific cross.

A sequential selection method was proposed (Branch et al. 1991) to minimize genotype by environment interactions. In this procedure early generation selections at more than one location identified pure-line genotypes with wider adaptability. This method involves cyclic early generation selections through different environments. Plants were selected in each generation at each location and were grown at different locations for evaluation. This method was found significantly better than the pedigree method and at par with the single seed descent method of selection for pod yield in groundnut (Branch et al. 1991).

An alternate approach to overcome breeding limitations of the pedigree method is the use of recurrent selection. Modifications of the recurrent selection techniques to include closely related species should further broaden the base. Guok et al. (1986) carried out phenotypic recurrent selections for yield in a tetraploid population derived from a cross of Arachis hypogaea x Arachis cardenasii Krap. Resistance to late leaf spot was recorded for selected families. Ten families selected for high pod yield and large pod size from the

segregates of the original cross were randomly intermated to the initial population. After two cycles of recurrent selection using S_1 testing, the response to selection was compared with individual parents of the three cycles (C_1, C_2, and C_3) in four environments. Two cycles of selection resulted in an increase in pod yield of 210 ± 70 kg ha^{-1} $cycle^{-1}$, however, seed mass, shelling percentage and extra large seeds decreased significantly. Little variability was observed among lines after the second cycle. Genetic variability for resistance to late leaf spot existed among the parents over the 3 years.

It is evident from the foregoing discussions that the pure line selection, mass selection, recurrent selection, and bulk selection with its modifications are useful for handling segregating materials of groundnut. The details of these procedures are available in standard plant breeding books.

Procedures for establishing groundnut breeding nurseries in the greenhouse, and a nursery in the field (MP 1), emasculation and crossing (MP 2), and a simple procedure for handling of segregating generations (MP 3) are separately discussed.

Utilization of Wild Species

Diseases and pests cause serious yield losses to groundnut production. The range of genetic variation, particularly resistance to pests, and diseases is limited in cultivated groundnut (Arachis hypogaea). The collections of wild species from South America have contributed a wide range of genes that confer resistance to important pests and diseases. This germplasm provides opportunity for genetic improvement of cultivated groundnut.

Several Arachis species are identified (Table 9) with resistance to pests and pathogens. Particularly important are those which either have resistance to many (multiple) pests and diseases or are resistant to diseases for which variability is not available in the cultivated species.

The tetraploid A. hypogaea is classified into section Arachis along with the compatible diploid species that are resistant to several diseases and pests. Appropriate genome and ploidy manipulations make it possible to incorporate desirable genes from the wild diploid into Arachis hypogaea as discussed in MP 4.

Table 9. Wild Arachis species with multiple resistance to diseases and pests.

Section/Species	Disease/Pest[1]								
	RUS	LLS	ELS	PS	PM	TSW	THR	APH	JAS
Arachis									
A. duranensis	I[2]		R			R			R
A. villosa	I						R	R	R
A. correntina	I				R	R	R	R	R
A. cardenasii	I	I			R	R	R		R
A. chacoense	I	R	R/I		R	R	R	R	
A. stenosperma	R	R	R						
Arachis spp.		R(2)[3]		R(l)	R(3)				
Erectoides									
A. appressipila	I	R							
Arachis spp	R(3)	R(2)	R(l)			I(3)	R(3)		
Rhizomatosae									
A. glabrata	R	I	R	R	R		R	R	R

1. RUS = Rust, LLS = Late leaf spot, ELS = Early leaf spot, PS = Peanut stunt virus, PM = Peanut mottle virus, TSW = Tomato spotted wilt virus THR = Thrips, APH = Aphids, JAS = Jassids.
2. I = Immune, R = Resistant.
3. Figures in parentheses are number of species.
(Source: ICRISAT 1987)

Mutation Breeding

Induced mutation has produced desirable results in several self-pollinated crops like wheat and rice as well as groundnut. There are examples where mutants were identified directly for cultivation. Useful mutants have been identified for yield and quality traits in groundnut (Patil 1975).

Success of mutation breeding depends on:

- The identification of clear objectives.
- Incorporation of the desired characters.

Efforts to produce mutations in groundnut have been successful for both qualitative and quantitative characters using chemical as well as physical mutagens. Ashri and Levy (1976) used ethylmethane sulphonate (EMS) and diethyl sulphate in groundnut for producing mutations. Levy and Ashri (1978) found ethidium bromide to be a very effective mutagen in groundnut.

A variety TG 1 was developed by using X-rays (75 kr) and repeated selection for improved seed mass. TG 1 had 0.7 to 0.9 g seed^{-1} compared to 0.4 to 0.5 g seed^{-1} of its parent in the All India Coordinated Research Project on Oilseeds (AICORPO) during 1969-72 (Patil 1975).

Further high yielding lines such as TG 16, TG 17, and TG 19 were derived by hybridization of different mutants with cultivars (Patil 1977). Hybridization of mutants and improved cultivars

followed by radiation treatment have produced alterations of characters in subspecies fastigiata and subspecies hypogaea. and also modifications in plant type (Mouli et al. 1982). Genotypes developed by mutation breeding are given in Table 10 and mutagenesis in MP 5 and MP 6.

Table 10. Groundnut varieties developed through mutation breeding.

Name of mutant (variety selected)	Genotype irradiated/ pedigree	Inducing mutagen	Improved characters over parent
A. Direct mutants			
TG 1 (Trombay Groundnut 1) released as Vikram	Bold 1	X-rays 75 kr	High seed mass 0.7-0.9 g seed as compared to 0.4-0.5 g seed"[1] of parent, and yield
LV 3A	LV 3	20 kr-Gamma rays	Improved shelling %
TG 18A	TG 18	-do-	Large pod, dormancy, early maturity, and 76% seed out turn
Co 2	PoL 1	EMS	Early maturity, 77% seed out turn
B. Mutants utilised in crossing program			
TG 7, TG 13, TG 8, TG 9, TG 10, TG 11, TG 12	TG 1 x Virescent F_5	Mutant crossed with other genotype	Medium to large pods, and dormancy
TG 16	Virescent/ TG 1	Selected in F_6	Large pod
TG 17	Darker green/ TG 1	Selected in F_4	Medium pods and dormancy
TG 19A	TG 17 x TG 1		Dark green foliage, large pods dormancy

Source: Patil 1975; Mouli et al. 1982; and Sivaram et al. 1989.

MP 1. Establishing Groundnut Crossing Nurseries

A. A crossing nursery in the greenhouse

Hybridization of groundnut is commonly done in a greenhouse to ensure maximum seed setting under controlled conditions. The plants are grown in 15 L pots (30 cm diameter) on greenhouse benches in sterilized fertile soil. In each pot, 2-4 groundnut plants are maintained for hybridization.

Material and facilities required.

- Pots and gravel.
- Sterilized soil, sterilized sand, and composted farm manure.
- Chemicals - Bavistin and carbofuran.
- Fertilizer - Diammonium phosphate
- Seed
- Greenhouse

Preparing pot for sowing. Prepare a soil mixture containing sterilized soil, sterilized sand, and compost in the ratio of 4:2:1. Put 2-3 cm of gravel in the base of each pot. Then fill the pot with the soil mixture leaving 2-3 cm at the top. Now make holes for sowing seed 5 cm deep and put 50 g diammonium phosphate pot^{-1} in the holes and some granules of carbofuran. Sow two Bavistin treated seeds $hole^{-1}$.

After sowing, place the pots on stones or bricks and irrigate well. Leave only 2-4 seedlings pot^{-1} and place the pots on iron benches fitted with thick wire net.

Intensive care is required to keep plants healthy and free of diseases and pests.

The temperature of the greenhouse should be maintained between 22-30^{o}C at flowering with the humidity ranging from 60-70%. The soil moisture is maintained at 80-85% of field capacity.

Label each pot with plastic pegs to identify the genotype and cross to be made.

B. A crossing nursery in the field

The crossing nurseries (blocks) are established in a well prepared field. A balanced supply of plant nutrients is essential in the nursery with adequate N, P, K and calcium in the fruiting zone.

It is convenient to sow a crossing nursery on a 75 cm ridge-and-furrow system. Groundnuts are planted in 5-9 m rows of female or male parents alternate to each other. This facilitates collection of flowers for pollination. The number of rows for each parent (female and male) should be decided as per the objective of the crossing, and amount of seed required. When a broadbed-and-furrow system is followed the emasculation can be attempted on plants from the furrow side or from top of the bed.

The female and male parents are labeled with tags of different color. For example, the male parent with a red and the female parent with a blue tag. The name of the parent and number of rows sowed should be mentioned on each tag.

Optimum soil moisture should be 40% of the total soil volume in the podding zone regardless of soil moisture content in the rooting zone (Ono et al. 1974). Therefore, PURFO or sprinkler irrigation is necessary after emasculation to create the required humidity and to supplement the water loss during bright sunny days. Half an hour irrigation every evening is recommended when the rains fail and the temperature is high.

Temperatures from 22 to 33°C are ideal for flowering and fruiting of groundnut. The optimum soil temperature is between 28-30°C.

MP 2. Emasculation and Crossing in Groundnut

Anthesis. Flowering starts about 25-30 days after seedling emergence. The dehiscence of the anthers takes place (at ICRISAT Center, Hyderabad) from 0400 to 0500 and flowers open from 0530 to 0730.

Anthesis is affected by the temperature and humidity (Norden 1980).Therefore, it is necessary to control these two factors in the greenhouse. During flowering time, the humidity should be above 70% and the temperature between 28 and 30°C.

Emasculation. Emasculation of groundnut can be accomplished on warm bright days from 1330 to 1630. On cloudy or rainy days, emasculation could be delayed until 2100-2200 (Norden 1980). Nigam et al.(1.990) discussed the detailed technique of artificial hybridization in groundnut.

Steps for emasculation.

1. Select the well developed bud for emasculation, and remove all other buds at the node to ensure that only one flower develops at that node. Pull the leaf down gently to expose the bud.

2. With one hand hold the bud between your thumb and index finger.

3. Remove the sepal on the side of the keel and push down the sepal on the side of the standard.

4. Open the standard petal with the forceps and pull down the wing petals.

5. Hold back the standard petal with the thumb and index finger. Break open the keel with the point of the forceps. Move the keel up and pull it free of the stigma and anthers. The keel is pulled down and held out of the way with the thumb and index finger, while all anthers along with their filaments are removed.

6. Now return the standard petal to its original position over the stigma. Usually no attempt is made to cover the emasculated flowers for protection from outside pollen.

7. A small thread is put on the hypanthium of the emasculated flowers for identification (Norden 1980) or on the stem above the bud axis. Use different colored threads on different days to identify emasculated buds for pollination. A record of the number of buds emasculated should be maintained for each parent.

Pollination. On the morning after emasculation, the standard petal is usually expanded and the stigma is exposed between 0600 and 0730. A healthy flower from the male parent (pollen source) is selected. Its corolla is removed exposing the anthers and pollen. Now directly squeeze the pollen on to the emasculated flower stigma or on to the forceps, and transfer the pollen from the forceps to the stigma of an emasculated flower. After pollination, remove all other flowers that were not hand pollinated by breaking their hypanthium near the base.

The maximum physiological development of pollen is from 0500 to 0700. It was found that pollen remained viable up to 8 days when stored in a sealed desiccator over calcium chloride in a refrigerator at 6 C.When flowers were stored at 28 C and at a relative humidity of

56% the pollen remained viable for only 8.5 h (Hassan and Srivastava 1966b).

Pollination success. Hybridizing groundnuts in the greenhouse may result in over 70% success. A success rate of 44% was reported in India from field hybridization, starting at 0630 during the monsoon season (Jul to Aug), compared to 27% when pollination was started at 0830 (Norden 1980).

$$\frac{\text{Number of pegs or pods developed} \times 100}{\text{Number of flowers pollinated}} = \text{Successful crosses \%}$$

Pod davelopment and harvaat. When fertilization is successful, the tissue below the ovary, called the gynophore, elongates into a peg carrying the ovary at its tip geotropically into the soil. In the soil the ovary takes a horizontal position and a pod develops. Mature pods can be harvested usually 55-65 days after the pegs developed.

MP 3. Handling Crosses of Groundnut

The crossed seeds are grown along with their parents to identify hybrids. Plants in the F_1 generation resembling the female parent (selfed) should be removed. Undesirable F_1S that are highly susceptible to diseases, or insects, or that are poor in quality can be rejected at harvest.

The harvested seeds on F_1 plants are grown in bulk in unreplicated plots with a large population (1000-2000 plants). The selection procedures such as bulk selection, pedigree selection, bulk-pedigree selection, or single seed (pod) descent selection can be followed for handling the segregating generations. The detail of these selection procedures can be found in plant breeding text books. A simple modified bulk selection method as practiced at ICRISAT is outlined in Figure 1. Some criteria for selections are listed (Table 11). The end product or groundnut variety can be developed as a pure line, multiline, or mixture of pure lines.

Some of the ICRISAT varieties that are released are listed in Table 12.

Table 11. Characteristics for selection of plants from groundnut populations.

Character	Criteria for selection
Earliness	Maximum early flowering in a few days
Drought resistance	Total biomass production (under stress conditions)
	Least difference in yield under drought and irrigated conditions
	High pod yield under stress conditions
Insect resistance	Leaf hairs (trichomes) repel some insects
High adaptation	Perform well under a poor environment and are responsive to rich environments
Confectionery type	Large seeded, smooth, and uniform sized seeds
Nutritional and food quality	High oleic acid/linoleic acid ratio

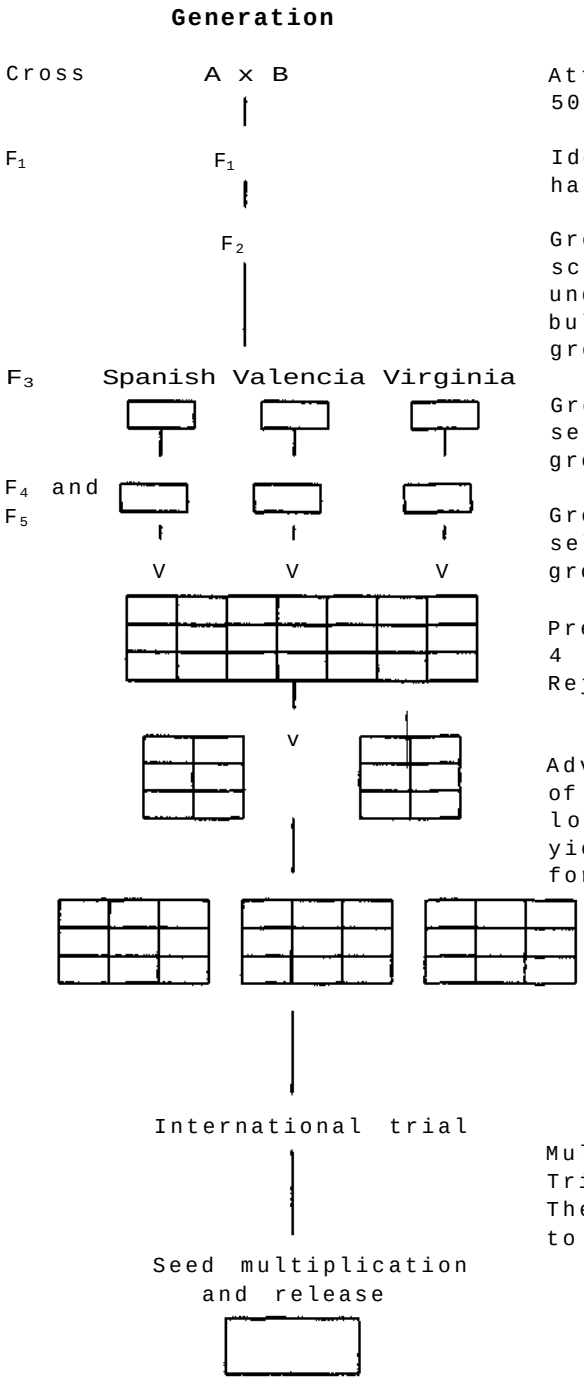


Figure 1. Modified bulk selection as practiced at ICRISAT. (Source: S.L. Dwivedi, ICRISAT, personal communication 1987)

Table 12. ICRISAT groundnut varieties released for cultivation

Variety	Season and area of cultivation	Year of release	Remarks
ICGS 11 (ICGV 87123)	Post-rainy season Andhra Pradesh, Karnataka, Madhya Pradesh, and Maharashtra States of India	1986	Spanish selection, dark green foliage, small-to medium-sized, two-seeded pods with tan-colored seeds. Yield potential 4.5 t ha^{-1}. Tolerant to bud necrosis disease
ICGS 44 (ICGV 87128)	Post-rainy season/ and rainy season Gujarat State of India In Pakistan as component line of BARD-699	1988	Spanish type, two-seeded small-to medium-sized pods, tan-colored seeds. Tolerant to bud necrosis
ICGS 5 (ICGV 87121)	Rainy season. India - Uttar Pradesh	1989	Virginia bunch, small-to medium-sized, two seeded pods with tan colored seeds. Pod yield 2.7 t ha^{-1}
ICGS 76 (ICGV 87141)	Rainy season. India - Andhra Pradesh, Karnataka, Kerala, southern Maharashtra and Tamil Nadu. Under consideration for release in Sudan	1989	Virginia selection, medium-to-small elliptic, dark green leaves. Two-seeded medium-sized pods. Seeds tan-colored. Field tolerance to bud necrosis. Good recovery for pod yield from midseason drought
ICGS 1 (ICGV 87119)	Rainy season. Bihar, Haryana, Punjab, Rajasthan and Uttar Pradesh States of India	1990	Spanish type, medium-to-small dark green, elliptic leaves; two-seeded, medium-sized pods
ICG(FDRS) 10 (ICGV 87160)	Rainy season. India - Andhra Pradesh, Karnataka, and Maharashtra	1990	Sequential flowering, bunched, two-seeded, tan-colored, medium-sized seeds. Highly resistant to rust, moderate resistance to late leaf spot. Less susceptible to bud necrosis, peanut mottle virus, stem rot, and leaf miner
ICGS 37 (ICGV 87187)	Post-rainy season. India - Madhya Pradesh and Maharashtra. In Pakistan as component line of BARD-699	1990	Spanish selection with small-medium dark green, elliptic leaves. Two seeded medium sized pods. Moderately resistant to rust and late leaf spot, tolerant to bud necrosis, and peanut mottle, photoperiod insensitive

Source: Anonymous 1990. Crop improvement in India: ICRISAT cultivars. ICRISAT Public Awareness Series. ICRISAT Plant Description Material no. 21, 24, and 27. Patancheru, A.P. 502324, India: International Crops Research Institute for the Semi-Arid Tropics.

MP 4. Incorporation of Genes from Wild Diploids into Cultivated Groundnut

This involves three steps.

A. Gene transfer from compatible species.

Genome analysis at ICRISAT, in section Arachis, revealed that a majority of diploid wild species has a common 'A' genome, but that A. batizocoi has a different 'B' genome. Both genomes have the base number 10, they are homeologous and together constitute the cultivated species A. hypogaea (Singh and Moss 1982, 1984). This has helped in identification of suitable methods (Fig. 2) for gene transfer from diploid Arachis species with 'A' and 'B' genomes (Singh 1986).

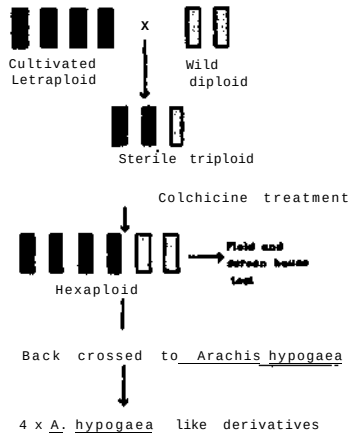
Method 1. Compatibility between cultivated tetraploid A. hypogaea and the diploid species permits direct hybridization (Fig. 2a). This crossing results in triploid hybrids that are sterile. In the triploid hybrids, chromosome numbers are doubled by colchicine treatment to produce a fertile hexaploid amphidiploid. Hexaploids are screened against various diseases and pests, and resistant segregants are back crossed with A. hypogaea till cytogenetically stable tetraploid A. hypogaea-like derivatives are obtained.

Method 2. Triploid hybrids occasionally can produce pods with viable seeds. About 82% of these seeds produce hexaploids. These progenies or progenies with less than 60 chromosomes are back crossed with A. hypogaea until stable tetraploids are produced (Fig. 2b).

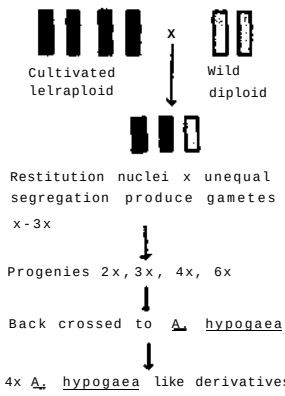
Method 3. Production of amphidiploids by doubling the chromosome number in F_1 hybrids of diploid wild species (AxA or AxB) followed by crossing them with Arachis hypogaea (4x) is another option for genetic introgression Fig. 2c). In this hybrid coherence to genomes of A. hypogaea because of homology between 'A' and 'B' genomes overcomes fertility problems when crossing to Arachis hypogaea to combine desirable traits.

Method 4. Production of an autotetraploid by doubling the chromosome number in a wild Arachis species followed by crossing them to A. hypogaea (4x) at the tetraploid level is another option (Fig. 2d) which may overcome the barriers developed as a result of ploidy differences. The partially fertile hybrids with greater allelic recombinations are produced for backcrossing to A. hypogaea.

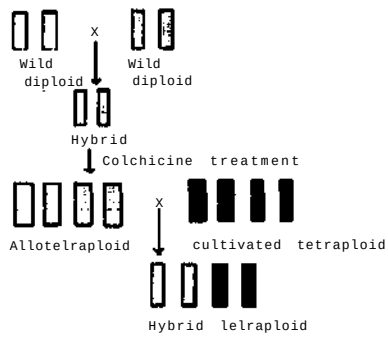
Another method is to reduce the chromosome number in A. hypogaea to a diploid level and then perform hybridization with diploid wild species at the diploid level. However, the feasibility of this option can not be assessed till production of haploids from A. hypogaea is achieved (A.K. Singh, ICRISAT, personal communication 1989).



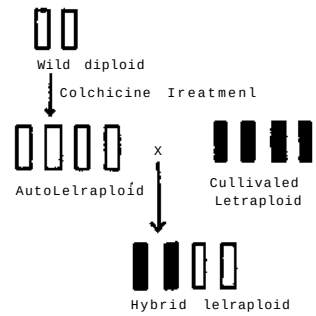
a. Production and testing of hexaploids.



b. Production of hybrid tetraploids from diploids.



c. Production of hybrid tetraploids from two wild diploids.



d. Production of tetraploids from diploids.

Figure 2. Methods of producing hexaploids and hybrid tetraploids for backcrossing to Arachis hypogaea to transfer genes from wild species into cultivated groundnut.

(Source: ICRISAT 1980, and A.K.Singh, ICRISAT, personal communication 1989).

B. Ploidy manipulations

The hybrids produced by crossing cultivated groundnut with the diploid wild species are triploid and sterile. Their fertility could be restored by induction of polyploidy using the colchicine technique developed by Spielman and Moss (1976). In this technique, actively growing branches of sterile triploid hybrids are cut 20-30 mm above the node of young laterals. Leaves, buds and petioles are removed from the next 2 or 3 nodes; a glass tube that fits tightly with the stem is filled with the colchicine solution and the second cut is made below the first cut (Singh et al. 1983). Place the glass tube immediately over the cut end to maintain the flow of colchicine (Fig. 3). Leave the tube on the plant for 24-48 h. It is important to prevent air bubbles in the tube. After removing the tube, a hexaploid branch may develop which can flower and produce a peg. Another way of ploidy manipulation is successive back crossing of a triploid hybrid with A. hypogaea that results in fertile hexaploid hybrids (Singh 1986).

C. Use of incompatible species

Incompatible species from sections Rhizomatosae and Erectoides have been crossed with A. hypogaea or diploid species of section Arachis' with the help of hormone treatments (GA3, IAA, and Kinetin) and/or in vitro embryo rescue techniques. Hybrid plants have been established in two combinations (Sastri and Moss 1982).

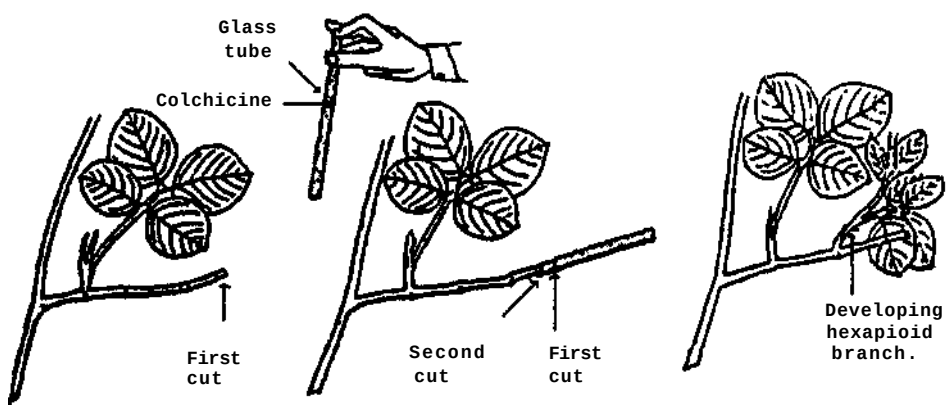


Figure 3. Method of colchicine treatment of young laterals. (Source: Singh et al. 1983)

MP 5. Induced Mutagenesis

Mutagenesis

Treating a biological material with a mutagenic agent to induce mutants is mutagenesis.

Physical mutagens. The most frequently used physical mutagens are x-rays, gamma rays, and neutrons. All these forms of radiations ionize atoms in a tissue by detaching electrons from the atoms.

X-rays are produced in special machines by bombarding tungsten or molybdenum with electrons. For gamma-irradiations seeds are normally exposed using the radioactive isotopes cobalt-60 or cesium-137. in a gamma chamber. Neutrons are obtained from a nuclear reactor where uranium-235 fuel undergoes nuclear fission.

Physical mutagenesis. The seed is dried to a low moisture content and put in sealed packets for irradiation. The seed is placed in the chamber for a fixed time depending on the dose of irradiation. In groundnut 5 kr, 10 kr, 15 kr, 20 kr, 30 kr, and 45 kr gamma irradiations are reported (Pathirana and Wijewickrama 1982). However, the most desirable groundnut mutants were recovered between 5-20 kr X-ray irradiation when .irradiated up to 75 kr (Patil 1975).

Chemical mutagens. These are agents that react with DNA by alkylating the phosphate groups as well as purine and pyrimidine bases. Among the 30-40 chemical mutagens, some of the most powerful and useful are ethyl methane sulphonate (EMS), diethylsulfate (DES), ethylene-imine (EI), N-nitroso- N-methyl Urethane (NMUT), N-nitro-N-methyl urea (NMU), and ethyl bromide (EB).

Chemical mutagenesis. The effect of a chemical mutagen depends on its concentration, duration of treatment, temperature and pH of the mutagenic solution, and water content in seeds.

For chemical mutagenesis, soak the seed in water for 2-4 h, thereafter put the seed into the chemical at the desired concentration for 5-6 h. Then put the seed in a cloth bag under running tap water for 8-10 h to wash the excess chemical off the seed surface.Remove the excess water on the seed surface by drying for a few hours in the shade.

Selecting dose level

The highest number of induced mutations result when the number of fertile M_1 plants is maximized to produce a large M_2 generation. When using sparsely ionizing radiations (x-rays and gamma rays) in greenhouse tests, an optimum dose should cause 30-50% reduction in seedling height. When densely ionizing radiations (neutrons) are used, the height reduction should be 15-30%. With chemical mutagens, the reduction should be 10-30%. In practice, an optimum dose is often achieved by using three separate doses (with an untreated control). One dose should be chosen based on reduction in seedling height in laboratory and field tests. The other two doses should be about 10% higher and 10% lower (Sigurbjornsson 1983). A dose close to LD 50 (Lethal Dose 50) should be optimum, since it provides a maximum percentage of useful mutants. LD 50 is that dose of mutagen that would kill 50% of the treated individuals (Singh 1983).

Amount of seed to be treated

A number of seeds should be treated with a mutagen to ensure identification of sufficient mutants in the M_2 and later generations. The size of the M_1 population i.e., the number of seeds to be treated is partly governed by the effectiveness and the efficiency of the mutagen.

Brock (1976) calculated M_2 progeny size and M_1 population requirements according to the various mutant segregation ratios and the probability of the occurrence of homozygous mutants. Assuming a 50% lethality in the M_1 generation of 5000 plants, 2500 fertile survivors would be tested in the M_2 generation. The M_2 generation with 20 individuals per progeny would then be 20 x 2 500 = 50 000 plants. Thus a minimum of 5 000-10 000 seeds should be treated with a mutagen.

MP 6. Handling the Mutation Breeding Population.

The M_1 generation starts with the germination of mutagen-treated seeds. The M_1 is heterozygous due to newly induced mutant genes and will segregate into mutants and nonmutants in the M_2 generation. Only dominant mutations will be expressed in the M_1 generation while recessives will be expressed in the M_2. Homozygous mutants are expressed in the M_3 generation. The M_1 generation should receive the best possible care to control weeds, insects, and diseases. This will help to transfer as many mutations as possible to the M_2 generation where selection for the desired genotypes will be done (Table 13).

The M_2 could be generated from all the surviving plants (seeds of the M_1 generation), or one can sample the better plants in the. M_1. Redei (1974) recommended a large M_1 population and small M_2 families. The single seed descent or plant to row method, should be used in the mutation breeding program to identify low frequency of mutant phenotypes.

Table 13. Handling generations of mutants.

Year or crop season	Generation	Operations
First	M_1	Sow the treated seed at wide spacing. Harvest seeds of individual plants separately.
Second	M_2	Grow individual plant progenies. Harvest vigorous, normal looking plants separately.
Third	M_3	Grow individual M_2-plant progenies (M_2) . Select superior plants among the progenies showing segregation and harvest separately.
Fourth	M_4	Grow individual M_3-plant progenies (M_3). Harvest superior and homogeneous lines in bulk. Reject segregating arid undesirable lines.
Fifth	M_5	Conduct a preliminary yield trial with suitable checks. Identify superior lines.
Sixth to eighth	M_6-M_9	Conduct replicated multilocation yield trials to identify outstanding lines for release as varieties.
Tenth	M_{10}-M_{11}	Seed multiplication and on-farm testing.

(Source: Sigurbjornsson 1983; and Singh 1983).

Success of identifying mutants in the M_2 and M_3 population may depend on ease of detection. By the M_5 or M_6 generation most of the mutants become homozygous and their seed can be multiplied for preliminary evaluation. Patil (1980) reported that over 60% of the groundnut mutants appeared in the M_2 and M_3 generations. However, economically important mutants viz., the tertiary-branching and the large pod size were isolated only after M_3. Further, consistent selection for increased seed mass resulted in the isolation of the large pod mutant in M_5. Therefore, individual plant selection plays an important role in mutation breeding.

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Evaluation

Select the most appropriate answer and check the correct answer at the end of the booklet.

1. In groundnut the spreading growth habit is dominant over
   a) bunch. b) open habit.
   c) semispreading. d) all the above.

2. Dwarfism is a_____character.
   a) dominant b) complementary
   c) additive d) recessive

3. The erect growth habit in groundnut is a_____character.
   a) dominant b) epistatic
   c) recessive d) complementary

4. Dark or purple pigmentation of groundnut stems is
   a) dominant. b) recessive.
   c) additive. d) polygenic.

5. Albinism in groundnut ranges from yellow to white. Albinism is inherited due to
   a) a single recessive gene. b) triplicate recessive genes.
   c) triplicate dominant genes. d) duplicate genes.

6. The character light green foliage on groundnut is
   a) dominant. b) recessive.
   c) epistatic. d) polygenic.

7. The dark green foliage character of groundnut is
   a) monogenic. b) digenic.
   c) trigenic dominant. d) trigenic recessive.

8. The elliptical-oblong and narrow leaf shape is governed by
   a) recessive genes. b) dominant genes.
   c) complementary genes. d) duplicate genes.

9. Inflorescence on the main axis of groundnut is governed by
   a) a single gene.
   b) two duplicate genes with epistatic action.
   c) complementary genes.
   d) three genes.

10. The dark corolla color character is due to a_____gene.
    a) recessive b) dominant
    c) epistatic d) complementary

11. The boat shaped wing petal is a_____character.
    a) digenic b) monogenic dominant
    c) trigenic d) polygenic

12. The large pod is a_____character.
    a) recessive b) dominant
    c) epistatic d) complementary

13. Yellow and white corolla colors in groundnut are inherited due to
    a) dominance. b) duplicate epistasis.
    c) incomplete dominance. d) cytoplasmic factors.

14. The number of flowers plant^{-1} is inherited due to
    a) epistatic genes. b) complementary genes.
    c) additive dominant genes. d) duplicate genes.

15. The chlorophyll deficiency in groundnut is governed by
    a) a single gene. b) two genes.
    c) three genes. d) cytoplasmic factors.

16. The presence of pod constrictions in groundnut is a_____character.
    a) dominant b) recessive
    c) epistatic d) complementary

17. The large seed size in groundnut is a_____character.
    a) recessive b) dominant
    c) additive d) polymorphic

18. Long seed shape and flat ends of seed are
    a) recessive characters. b) dominant characters.
    c) quantitative characters. d) complementary characters.

19. The red testa color in groundnut is governed by a
    a) dominant gene. b) recessive gene.
    c) epistatic gene. d) complementary gene.

20. The characters of flesh, white, pink, and purple testa colors are
    a) monogenic. b) digenic.
    c) trigenic. d) tetra genic.

21. The presence of seed dormancy is
    a) recessive to nondormancy.
    b) dominant to nondormancy.
    c) partially dorminant to nondormancy.
    d) none of the above.

22. The high protein content in groundnut is a_____character.
    a) recessive b) dominant
    c) epistatic d) duplicate

23. High oil percentage in groundnut is a
    a) recessive character. b) dominant character.
    c) digenic character. d) epistatic character.

24. Violet color and stem hardiness in groundnut are linked with a
    a) thick pericarp and bold seed size.
    b) thick seed coat and pod constriction.
    c) white seed color.
    d) thin pericarp and small seed size.

25. The characters late maturity, small seed size, separate pod cells and low yield in groundnut showed linkages with resistance to
    a) rust. b) bud necrosis.
    c) collar rot. d) late leaf spot.

26. The Spanish plant type in groundnut is controlled by duplicate genes
    a) Va_1 Va_1, va_2 va_2. b) va_1 va_1, Va_2 Va_2.
    c) va_1 va_1, va_2 va_2. d) Va_1 Va_1, Va_3 Va_3.

27. The Virginia (runners)-plant type of groundnut is controlled by duplicate genes
    a) Va_1 Va_1, Va_2 Va_2. b) Va_1 Va_1, va_2 va_2.
    c) va_1 va_1, Va_2 Va_2. d) Va_1 Va_1, Va_3 Va_3.

28. The heritability of pod yield plant^{-1} in groundnut is
    a) low. b) high.
    c) moderate to high. d) varies from high to low.

29. The heritability estimated in groundnut for mature pods plant^{-1} is
    a) high. b) low.
    c) moderate. d) varies from high to low.

30. Characters that have high heritability in groundnut are
   a) pod yield, pod mass, pod length, and seeds pod^{-1}.
   b) 100 seed mass, pod breadth, days to flowering, plant height, and primary branches.
   c) days to maturity and seeds pod^{-1}.
   d) none of the above.

31. Pod characters in groundnut include size and constriction The one that is dominant is
   a) small pod size. b) large pod size.
   c) absence of pod constriction. d) none of the above.

32. Seeds pod^{-1} in groundnut may be one or more than three and they are small to large in size. Which one is dominant?
   a) A few seeds pod^{-1}. b) Small seed size.
   c) Three or more seeds pod^{-1}. d) None of the above.

33. The characters dwarfism, yellow corolla, and spanish-plant type of groundnut are controlled by
   a) dominant genes. b) recessive genes.
   c) epistasis. d) complementary genes.

34. Resistance to groundnut rosette virus is controlled by
   a) complementary genes. b) dominant genes.
   c) recessive genes. d) duplicate genes.

35. Resistance to cercospora leafspot in groundnut is reported to be controlled by
   a) recessive genes. b) two or more nuclear genes.
   c) additive genes. d) all the above.

36. Rust resistance in groundnut is
   a) dominant to susceptibility.
   b) recessive and controlled by duplicate genes.
   c) controlled by cytoplasmic genes.
   d) none of the above.

37. Resistance to Necrotic-etch in groundnut is
   a) recessive to normal.
   b) dominant to normal with digenic ratio; 15 nondisease:l disease.
   c) complementary.
   d) cytoplasmic in nature.

38. Sclerotinia blight resistance in groundnut is controlled by
   a) dominant genes. b) recessive genes.
   c) epistatic genes. d) cytoplasmic factors.

39. The primary branches, pods plant^{-1}, 100 seed mass, and oil contents are important components of groundnut yield. The character negatively correlated with yield is
   a) number of pods plant^{-1}. b) 100 seed mass.
   c) primary branches plant^{-1}. d) oil content.

40. In groundnut, the correlation of protein to oil content is
   a) negative. b) positive.
   c) positive low. d) not known.

41. High heterosis for vegetative characters and pod yield have been reported in groundnut involving_____crosses.
   a) Virginia x Spanish b) Spanish x Virginia
   c) Spanish x Valencia d) none of the above

42. High heterosis for pod yield and fruit characters in groundnut have been reported involving _____ crosses.
   a) Spanish x Virginia
   b) Virginia x Spanish
   c) Spanish x Valencia
   d) Valencia x Spanish and Virginia x Spanish

43. High general combining ability (GCA) is indicative of additive genes where as specific combining ability (SCA) indicates nonadditive genes. Studies on groundnut indicate most quantitative characters are governed
   a) by additive genes.
   b) by nonadditive genes.
   c) by additive and nonadditive genes.
   d) monogenically.

44. When additive genetic variance is high and breeders want to develop homozygous lines, the appropriate breeding method is
   a) multiline breeding.
   b) backcross breeding.
   c) mass selection.
   d) pedigree and modified pedigree selection.

45. The important characters directly influencing groundnut yield are
   a) oil content and shelling percentage.
   b) plant height and days to flowering.
   c) 100 seed mass and mature pods plant^{-1}.
   d) secondary branches and early maturity.

46. Two characters having a negative effect on pod yield in groundnut are
   a) 100 seed mass and mature pods plant^{-1}.
   b) plant height and days to 50% flowering.
   c) oil content and protein content.
   d) primary and secondary branches.

47. Protein and oil contents are inherited
   a) quantitatively.
   b) cytoplasmically.
   c) qualitatively.
   d) due to interaction of nuclear and cytoplasmic genes.

48. The main objectives of groundnut breeding at ICRISAT are for high
   a) yield and oil content.
   b) resistance to insect pests and diseases.
   c) resistance to drought and adaptation to specific environment with early, medium, and late maturity.
   d) all the three above.

49. ICRISAT maintains a world collection of groundnut germplasm of over _____ accessions.
   a) 5 000 b) 10 000
   c) 12 000 d) 15 000

50. In groundnut, negative correlations were reported between
   a) pod numbers and mass of pods plant^{-1}.
   b) number of pods and 100 seed mass.
   c) size of pod and size of seed.
   d) number of seeds and seed mass plant^{-1}.

51. The correlation of large pod size with yield was reported to be
   a) negative. b) positive and low.
   c) positive and high. d) no correlation,

52. Multiline varieties of groundnut are useful in obtaining
   a) homozygosity. b) heterosis.
   c) stability and adaptation. d) none of the above.

53. Early generation testing in groundnut is useful to
a) incorporate one or two genes. b) obtain homozygous lines.
c) develop multilines. d) eliminate undesirable crosses.

54. Days to maturity and fruit size in groundnut are controlled by
a) duplicate genes. b) additive genes.
c) complementary genes. d) none of the above.

55. Two most important wild species of Arachis with pest resistant characters used at ICRISAT in interspecific hybridization are
a) Arachis glabrata and A. appressipila.
b) Arachis duranensis and A. villosa.
C) Arachis correntina and A. stenosperma.
d) Arachis chacoense and A. cardenasii.

56. Groundnut varieties developed by mutation breeding are
a) ICGS 11 and ICGS 44. b) TMV 2 and J 11.
c) TG 1 and TG 18A. d) CS9 and CS 30.

57. After germination, flowering in groundnut starts in
a) 10-15 days. b) 15-25 days.
c) 25-35 days. d) 35-45 days.

58. In groundnut after emasculation, pollination is carried out
a) immediately.
b) the next morning at 0600-0800.
c) the next morning at 1000-1200.
d) after 2 days.

59. The maximum physiological development of pollen in groundnut takes place between
a) 0300-0500. b) 0500-0700.
c) 0700-0900. d) 0900-1100.

60. A criteria for selecting groundnut for earliness is
a) minimum flowering in short span of time.
b) maximum flowering in short span of time.
c) continuous flowering till maturity.
d) none of the above.

61. Selection for drought resistance under stress conditions should be based on
a) total biomass production unit^{-1} area.
b) least difference in yield under stress and irrigated conditions.
c) high pod yield under stress condition.
d) all the three above.

62. For higher adaptation it is better to select a genotype that performs well under a
a) rich environment.
b) poor environment.
c) poor environment and well responsive to rich environment.
d) poor environment and nonresponsive to rich environment.

63. Large seeded, well shaped, uniform seed size groundnut are selected for
a) oil purpose. b) confectionery purpose.
c) oil and confectionery purpose. d) none of the above.

64. For nutritional and food quality purposes selection of groundnut should be based on
a) high protein content. b) high oil content.
c) high oleic by linoleic acid ratio. d) none of the above.

65. The most common selection procedure used at ICRISAT for handling segregating generations is
a) pedigree selection. b) bulk selection.
c) modified-bulk selection. d) single pod descent.

66. Preliminary yield trials start in the
a) F_4 generation. b) F_5 generation.
c) F_6 generation. d) F_8 generation.

67. Before giving material for national programs and release, it is necessary to test in multi-location international trials for
a) 1 year. b) 2 years.
c) 3 years. d) 4 years.

68. The chemical useful to induce fertility in triploids of interspecific hybrids is
a) indole acetic acid. b) EMS.
c) colchicine. d) alcohol.

69. To restore fertility in triploid hybrids of interspecific crosses, besides colchicine treatment another way is to cross with
a) a wild diploid.
b) a haploid.
c) a back cross with tetraploid cultivated.
d) none of the above.

70. Treating a biological material (seed, bud, or vegetative part) with a mutagenic agent to induce mutation is
a) breeding. b) hybridization.
c) mutagenesis. d) polyploidization.

71. The most common physical mutagens are
a) EMS, DES and EI. b) gamma rays, x-rays and UV rays.
c) acetocarmin, indole acetic acid. d) sun rays, hot water.

72. The highest numbers of induced mutation results when the number of
a) sterile M,s are maximum. b) fertile M,s are maximum.
c) sterile M_2s are maximum. d) fertile M2s are maximum.

73. An optimum dose of mutagenic agent reduces seedling height by
a) 5-10%. b) 10-20%.
c) 15-30%. d) more than 50%.

74. To ensure maximum mutations, the minimum number of seeds of groundnut should be about
a) 100-200. b) 1000-2000.
c) 3000-4000. d) 5000-6000.

75. To identify low frequency mutations in advanced generations it is better to use
a) the pedigree method. b) the bulk method.
c) single seed descent. d) recurrent selection.

76. In mutation breeding material, the preliminary trial is conducted in the
a) M_2 generation. b) M_5 generation.
c) M_7 generation. d) M_8 generation.

Correct responses to the questions.

1. d); 2. d); 3. c), 4. a); 5. b); 6. b); 7. c); 8. b); 9. b);

10. b); 11. b); 12. b); 13. b); 14. b); 15. d); 16. b); 17. b);

18. b); 19. a); 20. b); 21. c); 22. b); 23. a); 24. d); 25. d);

26. a); 27. c); 28. d); 29. d); 30. b); 31. b); 32. c); 33. c);

34. d); 35. a); 36. b); 37. b); 38. d); 39. d); 40. a); 41. b);

42. d); 43. c); 44. d); 45. c); 46. c); 47. c); 48. d); 49. c);

50. b); 51. b); 52. c); 53. d); 54. b); 55. d); 56. c); 57. c);

58. b); 59. b); 60. d); 61. c); 62. c); 63. c); 64. c); 65. c);

66. b); 67. c); 68. c); 69. c); 70. b); 71. b); 72. c); 73. d);

74. c); 75. b); 76. b).