THE INHERITANCE OF CHARACTERS IN THE GROUNDNUT *ARACHIS HYPOGAEA*.*

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Introduction.

THE groundnut is the most important oil-seed crop of the Madras Presidency with an annual acreage of about three million acres. The genetics of the crop has not received the attention that the importance of the crop would warrant. Stock (1910), Badami (1928), Stokes and Hull (1930), and Hayes (1933) have determined the inheritance of some of the characters. At the Agricultural Research Station, Palakuppam, South Arcot District, the breeding of improved types has been in progress during the last five years. Some of the characters, the inheritance of which has been studied, are of considerable economic importance. The inheritance of the following characters is reported in this paper :—

1. Chlorophyll deficiency.
2. Abnormality.
3. Growth habit.
4. Branching.
5. Duration.
6. Pubescence.
7. Testa colours.
8. Anthocyanin pigment.

Material.

A collection of about a hundred "varieties" of groundnut has afforded the authors a wide range of material for breeding work and also for the study of inheritance of characters. The characters studied have been described separately under each head. Of the varieties used in the various crosses, mention must be made of H. G. 1 (Hebbal groundnut) which is a bunch extract isolated by Dr. Badami from the progenies of a cross between a spreading

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and a bunch variety. Other varieties used in the work are pure lines isolated from the different varieties growing in the station.

There are two main seasons for growing the groundnut, *viz.*, rainfed and irrigated. Irrigated groundnuts are grown during February to June period, but this summer crop is very limited in area. The material for the crosses was grown mostly in the rainfed season—July-August to December-January. Advantage could not be taken of the irrigated season since the crop in that season was subject on the farm to the attack of diseases and pests. The material presented in the paper records the observations made from 1931 onwards.

Crossing Technique.

Flowering in the groundnut starts from the third week after sowing. The short duration bunch varieties begin to flower about two or three days earlier than the long duration spreading varieties. Flower buds appear in leaf axils singly or in clusters of two to five. The maximum number of flowers appearing in any one leaf axil never exceeded five. The flowers when in clusters develop and open in acropetal succession. The deep-seated and congested cluster of the flower buds are protected by closely packed bracts. This makes the removal of flowers not wanted, difficult, and thus a fairly large percentage of selfed seeds may be left in crossed plants. The flowers bloom between six to eight in the morning and the blooming of flowers occurs mostly at random. The flowering period lasts for about 45-60 days in the bunch varieties and 60-70 days in the spreading varieties. The flowering is very much affected by the distribution of rainfall.

Stokes and Hull (1930) have described the crossing technique in the groundnut plant. At the Agricultural Research Station, Palakuppam, the procedure described below was found adequate for purposes of crossing. Emasculation is done by opening the flower buds between 5 P.M. and 6 P.M., about twelve hours before the time of blooming. The flower bud is gently held by the left hand and with the right, the standard, wing and keel petals are gently opened by a pair of fine forceps. Then the flower is emasculated, the tips of filaments are examined with a magnifying lens so as to ensure the complete removal of the anthers. After the anthers are removed, the petals are gradually manipulated to their original position for protecting and covering the stigma. Care has to be taken to see that the calyx tube or any of the parts of the flower are not twisted or disjointed in the operation. Artificial pollination of the emasculated flower is carried out the following day between 7 A.M. and 8 A.M., when the anthesis of flowers normally occurs. The success in crossing depends on the carefulness of the workers. From 10 to 30 per cent. of the artificially pollinated flowers produce pods. Natural crossing must be extremely rare since the authors have not come across a single instance during the course of work extending over five years. Bagging with muslin bags is not considered necessary to prevent natural crossing. Bagging, however, may be a valuable adjunct where protection of flowers from beetles and of pods from birds is necessary. It has been found convenient to grow the plants for crossing in flower pots about 2 feet in diameter and 18 inches high. The plants are then at a convenient height for working and there is no difficulty felt during the rains. The crossed flower is marked by means of a particular coloured thread. When the flower fades and as soon as the gynophore is first seen, in four or five days, the thread has to be transferred to the gynophore.

TABLE I.

Inheritance of chlorophyll deficiency.

Cross number	Parents	F_1 phenotype	F_2 phenotype	
	$G_1G_1g_2g_2$ × $g_1g_1G_2G_2$		Green	Albino
25	Philippine white (spreading) × Corientes-3 (bunch) ..	Green	1468	60
25 (*a*)	Reciprocal	Green	228	15
26 (*a*)	Philippine white (spreading) × Small Japan (bunch) ..	Green	487	40
28	Philippine white × Gudiyattam (bunch) ..	Green	1097	57
34	Saloum (spreading) × Gudiyattam (bunch)	Green	543	26
35	Madagascar × Gudiyattam (bunch)	Green	352	18
35 (*a*)	Reciprocal	Green	380	22
36 (*a*)	H. G. 1 (bunch) × Spanish 10 (bunch)	Green	333	19
	Observed		4888	257
	Expected on 15 : 1 ratio ..		4823	322
	$\frac{\text{Dev.}}{\text{S. E.}} = 3 \cdot 76$			

1. *Chlorophyll deficiency*.—The occurrence of the chlorophyll deficiency has been recorded in many crops, but the outstanding work has been in *Zea mays*, where over seventy genes affecting the chlorophyll have been recorded. Since albino seedlings cannot carry on photosynthesis, they do not survive to produce seeds, and therefore the study of albinism is made through the crosses between the two green types. The albino seedlings usually appear in the second generation of crosses between the bunch and the spreading types. In no instance did the authors come across albino plants in the F_2s of crosses between spreading varieties. In the crosses among the bunch varieties also, no albinos were obtained except when H.G.1 was introduced as one of the parents. In the above table the segregation of the F_2 population is shown.

The deviation of the observed numbers from the expected numbers on the basis of 15 : 1 ratio is significant. Further evidence for the bifactorial difference hypothesis is furnished from the behaviour of F_2 in the succeeding F_3 generation. If the hypothesis is correct 15 : 1 and 3 : 1 ratios must be obtained in F_3. From Table II it may be concluded that albinism in the groundnut is digenic :—

TABLE II.

F_3 segregation for albinism.

F_2 genotypes	F_3 phenotypes	
	Green	Albino
$G_1g_1G_2g_2$—total of 56 families		
Observed	1754	110
Calculated 15 : 1 ..	1748	116
$\frac{\text{Dev.}}{\text{S.E.}} = 0{\cdot}58$		
$G_1g_1g_2g_2$ and $g_1g_1G_2g_2$-total of 86 families		
Observed	1764	536
Calculated 3 : 1 ..	1725	575
$\frac{\text{Dev.}}{\text{S.E.}} = 1{\cdot}87$		

Badami (1928) as reported by Hunter and Leake (1933) has concluded that the triple recessive is the albino. The authors are, however, able to locate only two factors for albinism. It is possible that Badami was working with different material.

The ratio of 15 : 1 is obtained through the interaction of two duplicate factors each one of which produces identical effect. It has been previously mentioned that it was not ordinarily possible to obtain albino plants from among the crosses in which only bunch parents were used, and that generally crosses between the bunch and the spreading varieties yielded albino plants in F_2. The genetic constitution of the bunch and the spreading varieties must therefore be different. Let G_1 and G_2 represent duplicate genes which produce chlorophyll. The constitution of the spreading varieties is therefore $G_1G_1g_2g_2$ and that of the bunch varieties $g_1g_1G_2G_2$. The only instance where a cross 36(*a*) between two bunch parents yielded albinos in F_2 was when H. G. 1 was crossed with Spanish 10. This peculiar behaviour of H.G.1 is understood when it is pointed out that H.G.1 was extracted from a cross between a bunch and a spreading type. The genetic constitution of H.G.1 for chlorophyll should be similar ($G_1G_1g_2g_2$) to that of the other spreading varieties.

2. *Abnormality.*—The abnormal plants referred here were dwarf and stunted in growth having congested nodes and crumpled leaves. The plants showed normal branching but some of the secondary and tertiary branches developed fully and showed a highly congested condition of the nodes. The leaves were reduced in size and were wrinkled. These plants developed a few flowers which were mostly sterile. The pollen grains were empty and the stigmas were undeveloped. The plants were found to be free from insect pests or attack of any disease. Three plants out of 85 gave two small pods. This type of plants was obtained in the F_2 of the crosses in which Corientes-3 was crossed with the spreading varieties.

The F_2 plants showed a ratio of 15 normal to 1 abnormal suggesting the coming together of two factors from each of the two parents. The genetic constitution of Corientes-3 may be assumed as $N_1N_1n_2n_2$ and that of the other parent as $n_1n_1N_2N_2$. Hayes (1933) mentions sterility caused by a two factor difference segregating in F_2 in 15 : 1 ratio. It is possible that the abnormal plant mentioned here and his sterile plant are identical. Unfortunately he has not given a detailed description of his plants.

When Small Japan and Gudiyattam Bunch, the two bunch varieties are crossed with the spreading varieties, no abnormal plants are found in F_2. This indicates that these varieties are genotypically either $N_1N_1n_2n_2$ or $N_1N_1N_2N_2$. But when either of these two bunch varieties is crossed with

TABLE III.

Inheritance of abnormality.

Parents	F_1 Phenotypes	F_2 Phenotypes	
		Normal	Abnormal
$n_1n_1N_2N_2$ $N_1N_1n_2n_2$			
Philippine white × Corientes-3 ..	Normal	1332	73
Saloum × Corientes-3	Normal	237	12
Observed		1569	85
Expected on 15 : 1 ratio ..		1551	103
$\frac{\text{Dev.}}{\text{S. E.}} = 1 \cdot 84$			

Corientes-3, no abnormal plants are obtained in F_2. It may, therefore, be concluded that the Small Japan and Gudiyattam Bunch have in their genetic make up $N_1N_1N_2N_2$.

3. *Growth habit.*—The habit of growth of the plant influences considerably the agronomic practices. The optimum spacing and the mode of harvest in groundnut largely depend upon the habit of growth. The commonly cultivated variety may be resolved according to the habit into two groups, *viz.*, spreading and bunch. In the spreading varieties, the main axis grows erect, the two pairs of primary branches which take off from the main axis almost at right angles, grow along the ground and give a spreading or procumbent appearance to the plant. A few internodes, however, towards the growing top show a tendency to grow obliquely. In the bunch type the main axis grows erect and the primary branches which are usually four in number grow obliquely from the base of the main axis.

Seven crosses were made between the bunch and the spreading varieties, 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 the spreading groups. The bunch habit in F_2 plants varied from typically erect to the ordinary bunch type, while the plants in the spreading group varied from the ordinary spreading to the trailing plants with completely prostrate branches. Repeated attempts to further classify the bunch and spreading groups at different stages of the growth of the plant did not give any intelligible ratios. This variation may be due to the presence of minor modifying factors or due to the differential effect of the factors in the homozygous or heterozygous condition. We have yet no evidence for either of these two assumptions. The counts obtained in the F_2 are set down below :—

TABLE IV.

Inheritance of habit.

Cross number	Parents	F_1 phenotypes	F_2 phenotypes	
	$S_1 S_1 S_2 S_2$ $s_1 s_1 S_2 S_2$		Spreading	Bunch
25 (*a*)	Philippine white × Corientes–3	Spreading	162	49
25	Philippine white × Corientes–3	,,	1019	334
28	Philippine white × Gudiyattam (bunch)	,,	797	245
28 (*a*)	Philippine white × Gudiyattam (bunch)	,,	181	64
30 (*a*)	Saloum × Corientes–3 ..	,,	36	11
32	Saloum × Small Japan ..	,,	376	124
34	Saloum × Gudiyattam (bunch)	,,	250	87
35	Madagascar × Gudiyattam (bunch) ..	,,	271	89
26 (*a*)	Philippine white × Small Japan	,,	368	111
	F_2 hybrids		692	225
	Observed		4152	1339
	Expected on 3 : 1 ratio ..		4119	1372
	P between 0·2 and 0·3 x^2/m		0·264	0·879
	Expected on 13 : 3 ratio ..		4461	1030
	P less than 0·01 x^2/m ..		2·162	9·270

It is seen from the above figures that the bunch type is recessive. That the spreading type is probably the result of two complementary factors is evident from the data of another cross mentioned below. H.G.1 bunch variety when crossed with Spanish-10, another bunch variety, gave an F_1

spreading type and in the F_2 the spreading and the bunch types occurred in the ratio of 9 : 7.

TABLE V.

Inheritance of habit.

Parents		F_1 phenotypes	F_2 phenotypes	
$s_1s_1S_2S_2$	$S_1S_1s_2s_2$		Spreading	Bunch
Spanish-10 (bunch) × H. G. 1 (bunch) ..		Spreading	235	173
	Expected on 9 : 7 ratio		230	178
	$\frac{\text{Dev.}}{\text{S.E.}} = 0 \cdot 15$			

The data show that two dominant factors are necessary to produce the spreading type of habit. The genetic constitution of H.G.1 may be taken as $S_1S_1s_2s_2$ and that of Spanish-10 as $s_1s_1S_2S_2$. S_1s_2, s_1S_2 and s_1s_2 phenotypes are bunch in habit and S_1S_2 phenotype is spreading in habit. The constitution of the spreading variety may be taken as $S_1S_1S_2S_2$. This explains 3 : 1 ratio obtained in the crosses between the bunch and the spreading varieties.

The findings are in agreement with the observation made by Badami (1928) that erect is recessive to spreading with the bifactoral difference. Hayes (1933) has, however, reported that the segregation for habit is on the basis of 15 : 1 ratio. He found considerable difficulty in grouping the intermediate plants and, in addition, there were seventeen plants which were abnormal out of the total of 141 plants which he studied. It may be mentioned here that the classification of F_2 population has to be done between six to eight weeks after sowing, otherwise some of the bunch habit plants may, later on, be mistaken for spreading plants. When the bunch plants are sown on a ridge they may, with age, appear spreading in habit. It is, also, essential to sow the seeds at a uniform depth in order to avoid trouble in grouping.

4. *Branching.*—On the basis of branching, the groundnut varieties can be classified into branching and non-branching types. The branching type has two pairs of opposite primary branches developing in the axils of the cotyledons. Each of them has a number of secondary and tertiary branches. Flowers are produced on all these branches. Two or three single primary branches may also appear higher up on the main axis. The non-branching varieties, on the other hand, have only two pairs of primary

branches. In the non-branching type secondary or tertiary branches are not met with, but occasionally a small branch at the junction of the main axis and the primary may appear. Most of the spreading varieties are branched and most of the bunch varieties are not branched. The F_1 of the crosses between the branched and non-branched types were very profusely branched. In F_2 a ratio of three branched to one unbranched was obtained. The data are tabulated below :—

TABLE VI.

Inheritance of branching.

Cross number	Parents	F_1 phenotypes	F_2 phenotypes	
			Branched	Non-branched
25	Branched (BB) Philippine white × Non-branched (bb) Corientes–3	Branched	1050	352
	Expected		1051	351

It is obvious that there is a single factor difference between branching and non-branching. The genetic constitution of the branched and non-branched varieties should be BB and bb respectively. This character has not received the attention of the previous workers.

Linkage between branching and habit.

Since the parents in cross 25, were spreading branched type and bunch non-branched type, the F_2s were tabulated into four groups, *viz.*, spreading-branched, spreading-non-branched, bunch-branched, and bunch-non-branched. The data are tabulated in Table VII.

TABLE VII.

Linkage between branching and habit (30·8 *per cent. crossing over*).

Cross number	F_2 phenotypes			
	Spreading-branched	Spreading-non-branched	Bunch-branched	Bunch-non-branched
25	876	192	174	160
Expected on 9 : 3 : 3 : 1 ratio	788	263	263	88

The figures indicate the absence of 9 : 3 : 3 : 1 ratio. The frequency of the parental combination is more than the expected on the basis of random assortment of gametes : about 30 per cent. crossing over is obtained. This shows that the genes for the habit and branching are different but are located on the same chromosome.

5. *Duration.*—When the groundnut plant matures, the flowering stops and the stem and the branches turn yellow and the leaves are shed, but still some of the pods may remain immature. The early varieties mature within 3 to 3½ months after sowing and the late varieties mature in about 4½ to 5 months. In the crosses between the early and the late types, F_1s seem to be intermediate in duration and F_2s segregate into fairly clear groups of early, medium and late duration plants. By the time when the early plants wither, the medium duration plants have pale yellowish leaves and yellow stems, and the late plants are green. The plants were classified when they were 3½ months old and the classification was not difficult. The actual counts obtained in the F_2 are tabulated below.

TABLE VIII.

Inheritance of duration.

Parents	F_2 phenotypes		
Late LL × Early ll	Early	Medium	Late
Philippine white × Corientes-3 ..	313	734	358
Reciprocal	54	119	47
Philippine white × Small Japan ..	95	247	114
Philippine white × Gudiyattam (bunch) ..	242	538	274
	704	1638	793
Expected on 1 : 2 : 1 ratio ..	784	1567	784

Badami's (1928) finding that earliness is recessive will be true if medium and late plants are grouped together. It is apparent, however, that there is a single factor difference between early (ll) and late (LL).

6. *Pubescence.*—In the groundnut, the stem is generally covered with hairs, the degree of hairiness differing with the variety. Among the varieties under study, two groups were met with. In the first group which is termed hairy, the stem is rather thickly covered throughout with hairs. In

the second type—sparsely hairy—the distribution of hairs is sparse and it is largely confined to the young portions of the stem. The variety, Philippine white, is a typical example of the sparsely hairy types and Corientes-3 is a typical hairy type. In a cross between these two varieties F_1 plants resulted which showed more hairiness than Corientes-3 and in F_2 different gradations of hairiness were met with, but there was no instance of the complete absence of hairiness. The F_2 classification was made on the basis of very hairy, hairy, and sparsely hairy and the figures tabulated in Table IX fit 1 : 2 : 1 ratio. The hairy parent would, therefore, be HH and the sparsely hairy hh. Badami (1928) has also reported that hairiness is dominant over sparsely hairy condition.

TABLE IX.

Inheritance of hairiness.

Parents		F_2 segregation		
Sparsely hairy hh	Hairy HH	Very hairy	Sparsely hairy	Slightly hairy
Philippine white × Corientes-3		300	771	324
Expected on 1 : 2 : 1 ratio..		349	697	349

7. *Seed-coat colours.*—Until very lately only two testa or seed-coat colours, *viz.*, brown or rose, and red, were known to the botanists. The authors were able to obtain in 1932, a sample of kernels having purple coloured testa from Brazil, the home of the groundnut, and a sample from Gambia having white or yellowish grey coloured testa. The last named white variety is supposed to have originated as a mutation in Gambia from the imported Philippine red variety and it is accordingly named Philippine white. The black colour of the seed-coat and the various patterns on the seed-coat, common in many members of the *Papilionaceæ* are absent in the groundnut. It is likely that these homologous characters may be found in some of the wild varieties of the groundnut if a search is made. Vavilov (1922) after a comprehensive study of a large number of genera has enunciated the law of homologous variation. On the basis of homologous characters, the variations in seed-coat colours of the groundnut can be expected.

There are four distinct testa colours in the groundnut, *viz.*, white, rose, red and purple. What is termed here rose is equivalent to the pink or buff or tan or brown of other workers. In Plate IV testa colours obtained in five varieties are shown. For calculating the ratios only four main colours, *viz.*, rose, red, purple and white were taken into consideration. Different shades of rose colour were grouped under rose, and other colour groups were treated similarly. The following are the seed-coat colours of different varieties used in the crosses mentioned below.—

Variety.	*Testa colour.*
Corientes-3	Dark purple
Small Japan	Red
Saloum	Rose
Gudiyattam bunch	Rose
Philippine white	White

With a view to study the inheritance of testa colours all the possible crosses among the above were made.

Rose colour.—In the crosses 27 and 28 (*vide* Table X) two rose-coloured varieties were separately crossed with Philippine white, the F_1 plants were rose and in F_2 the plants having rose and white testa were in the ratio of 15 : 1. The difference between the white testa and the rose testa is due to two factors R_1 and R_2, either of which produces rose colour in the testa. The constitution of the two rose varieties is, therefore, $R_1R_1R_2R_2$ and that of the Philippine white $r_1r_1r_2r_2$.

TABLE X.

Inheritance of rose testa.

Cross number	Parents	F_1 phenotype	F_2 phenotypes		
	Female (white) $r_1r_1r_2r_2$ × Male (rose) $R_1R_1R_2R_2$		Rose	White	$\frac{\text{Dev.}}{\text{S. E.}}$
27	Philippine white × Saloum ..	Rose	314	20	
	Expected on 15 : 1 ratio..		313	21	0·23
28	Philippine white × Gudiyattam (bunch)	Rose	996	58	
	Expected on 15 : 1 ratio..		988	66	1·01

Red colour.—In crosses 32 and 33 (*vide* Table XI), rose-coloured varieties were crossed with red-coloured variety—Small Japan. In F_1, red testa was dominant and in F_2 the segregation occurred in 3 : 1 ratio. This is in agreement with the finding of Stock (1910), Badami (1928), Stokes and Hull (1930), and Hayes (1933).

TABLE XI.

Inheritance of red testa.

Cross number	Parents	F_1 pheno-type	F_2 phenotypes			
	Rd.Rd. Red — rd.rd. Rose		Red	Rose	White	
32	Small Japan × Saloum	Red	49	13		
33	Small Japan × Gudiyattam (bunch)	Red	224	79		
	Observed		273	92		
	Expected on 3 : 1 ratio ..		274	91		
	Expected on 13 : 3 ratio ..		297	68		
	x^2/m		1·939	8·47		P below 0·01
26	rd.rd.$r_1r_1r_2r_2$ × Rd.Rd.$R_1R_1R_2R_2$ / Philippine white × Small Japan (white) (red)	Red	298	91	19	
	Expected on 45 : 15 : 4 ratio		287	96	25	
	x^2/m		0·420	0·261	1·44	P between 0·5 & 0·3
	Expected on 12 : 3 : 1 ratio		306	77	25	
	x^2/m		0·209	2·555	1·440	P between 0·2 & 0·1

Crosses 32 and 33 indicate that there is a single factor difference between red and rose. In cross 26 (Small Japan × Philippine white) we find that rose-coloured kernels appear in F_2, indicating that Small Japan carries the factors for both the rose and the red colours. The number of factors for rose, present in Small Japan, is a point for consideration. The F_2 segregation of the progeny of cross 26 is either according to 45 : 15 : 4 ratio or 12 : 3 : 1 ratio. There are two hypotheses possible, *viz.*, (i) that the red colour in the testa develops only in the presence of one of the rose factors, and (ii) that the expression of the red factor is independent of the presence of a rose factor.

Taking the first hypothesis, there are two possibilities according to the number of rose factors present in Small Japan.

	Small Japan	× Philippine White	F_1	F_2 Red Rose White
(*a*)	$Rd.Rd.R_1R_1R_2R_2$	× $rd.rd.r_1r_1r_2r_2$	$Rd.rd.R_1r_1R_2r_2$	45 : 15 : 4
(*b*)	$Rd.Rd.R_1R_1r_2r_2$	× $rd.rd.r_1r_1r_2r_2$	$Rd.rd.R_1r_1r_2r_2$	9 : 3 : 4
	or			
	$Rd.Rd.r_1r_1R_2R_2$	× do.	$Rd.rd.r_1r_1R_2r_2$	

Since 9 : 3 : 4 ratio is not obtained, the proposition under (*b*) is ruled out.

Under the second hypothesis, there are the following two possibilities :—

	Small Japan	× Philippine White	F_1	F_2 Red Rose White
(*c*)	$Rd.Rd.R_1R_1R_2R_2$	× $rd.rd.r_1r_1r_2r_2$	$Rd.rd.R_1r_1R_2r_2$	48 : 15 : 1
(*d*)	$Rd.Rd.R_1R_1r_2r_2$	× do.	$Rd.rd.R_1r_1r_2r_2$	12 : 3 : 1
	or			
	$Rd.Rd.r_1r_1R_2R_2$	× do.	$Rd.rd.r_1r_1R_2r_2$	

The proposition under (*c*) is ruled out since the ratio obtained is far from 48 : 15 : 1. The choice is between the propositions (*a*) and (*d*). If the correct ratio is 12 : 3 : 1, the assumption should be that Small Japan carries one rose factor but its presence is not necessary for the development of the red colour. On the other hand, if the ratio 45 : 15 : 4 is the correct one it will have to be assumed that the rose factor is necessary for the development of red and that Small Japan carries both the rose factors. From the analogy of the results obtained for the purple testa and from the inheritance behaviour of the pigment in the vegetative portions of the plant, the latter assumption appears to be the more plausible one.

Purple colour.—In crosses 30 and 31 (*vide* Table XII) the plants having purple testa were crossed with those having rose testa. F_1 was purple and in F_2 the segregation was in the ratio of 3 purples and 1 rose. This indicates a single factor differences between the rose-coloured varieties and the purple, and that Corientes–3, the variety having purple testa, carries factors for rose also.

That purple is dominant over red and that there is a bifactorial difference between the red and the purple is evident from cross 29, where segregation in F_2 occurs in the ratio of 12 purples, 3 reds and 1 rose. PRd.R and Prd.R phenotypes are purple, PRd.R are red, and p.rd.R are rose. The cross 25 shows the absence of the factor Rd. in Corientes–3.

The interpretation of the F_2 results of cross 25 will depend upon what we assume about the relationship between the purple and the rose factors. If it is assumed that purple carries one of the rose factors and that purple

TABLE XII.

Inheritance of purple testa.

Cross number	Parents	F_1 phenotype	F_2 phenotypes			
	PP Purple × pp Rose		Purple	Rose		
30	Corientes–3 × Saloum ..	Purple	195	81		
31	Corientes–3 × Gudiyattam (bunch)	Purple	71	21		
	Total observed		266	102		
	Expected on 3 : 1 ratio ..		276	92		
	x^2/m		0·362	1·086		P between 0·2 & 0·3
	Expected on 13 : 3 ratio ..		299	69		
	x^2/m		3·642	15·79		P. below 0·01
	PPrd.rd. Purple × pprd.rd Red		Purple	Red	Rose	
29	Corientes–3 × Small Japan ..	Purple	280	66	25	
	Expected on 12 : 3 : 1 ratio..		278	70	23	
	x^2/m		0·014	0·229	0·174	P between 0·8 to 0·9
	Expected on 45 : 15 : 4 ratio		261	87	23	
	x^2/m		1·384	5·069	0·174	P between 0·05 & 0·02
	PPrd. rd. $R_1R_1R_2R_2$ (Purple) × pprd. rd. $r_1r_1r_2r_2$ (white)		Purple	Rose	White	
25	Corientes–3 × Philippine white	Purple	1056	364	99	
	Expected on 45 : 15 : 4 ratio		1061	354	94	
	x^2/m		0·024	0·282	0·266	P between 0·8 & 0·7
	Expected on 12 : 3 : 1 ratio		1140	285	94	
	x^2/m		6·190	2·190	0·266	P between 0·3 & 0·2

can show only in the presence of the latter factor, the F_2 ratio should correspond to 9 : 3 : 4 of purple : rose : white, but the actual ratio obtained obviously does not represent this. The F_2 ratio can be taken as either 12 : 3 : 1 or 45 : 15 : 4 of purple : rose : white. If we accept the former ratio as the correct one, we should assume that Corientes-3 carries one rose factor but its presence is not necessary for the expression of purple factor. On the other hand, if the ratio 45 : 15 : 4 is taken as correct, it is necessary to assume that the rose factor is necessary for the development of purple and that Corientes-3 carries both the rose factors. The latter assumption appears to be the more plausible one.

8. *Anthocyanin pigment.*—The presence of purple pigment on the stem in varying intensity is a common occurrence in the groundnut varieties. Even though the stem may show slight traces of the pigment, it may be noticed very much more intensified on the tender developing gynophores. Among 100 varieties collected so far, there is only one variety, namely, Philippine white with kernels having white testa and which shows complete absence of purple pigment and the plants are green throughout. In crosses involving a purple pigmented parent and a green parent, the F_1 is purple pigmented. In F_2 the segregaation occurs into purples and greens in 15 : 1 ratio (*vide* Table XIII). Among the purples, different degrees of pigmentation

TABLE XIII.

Inheritance of anthocyanin pigment.

Cross number	Parents	F_1 phenotype	F_2 phenotypes		
	$r_1r_1r_2r_2$ × $R_1R_1R_2R_2$ Green Purple		Purple	Green	
25	Philippine white × Corientes-3 ..	Purple	1295	98	
26 (*a*)	Do. × Small Japan ..	,,	432	24	
27	Do. × Saloum ..	,,	315	21	
28	Do. × Gudiyattam (bunch) ..	,,	996	58	
	Observed		3038	201	
	Expected on 15 : 1 ratio		3037	202	
			F_3 segregation		
	F_2 Genotypes of cross 26 (*a*)		Purple	Green	$\frac{\text{Dev.}}{\text{S.E.}}$
	$R_1r_1r_2r_2$ and $r_1r_1R_2r_2$ ..		201	52	
	Expected on 3 : 1 ratio		190	63	1·59
	$R_1r_1R_2r_2$ Dihybrids ..		183	9	
	Expected on 15 : 1 ratio		180	12	0·88

are observed. Hayes has reported a single factor difference between purple and slight purple.

Anthocyanin pigment and seed-coat colours.—The plants which were studied for testa colours were also observed for the purple pigment in the plant. It was found that only plants having white testa showed the absence of purple pigment on the gynophores and branches. The plants having purple pigment had invariably coloured or pigmented testa. Even in the F_3 plants with purple pigment on the vegetative parts white or colourless testa could not be found. All plants lacking in anthocyanin pigment had invariably white coloured seed-coats.

The interpretation of the results would depend upon what we assume about the relationship between the factors for seed-coat colours and the anthocyanin pigment in the plant. In the absence of even a few crossovers among the large population studied, it cannot be readily postulated that the factors for plant colour are linked with the seed-coat colour factors, and that too with all the four factors P, Rd, R_1 and R_2. Even though the assumption that the two factors for plant colour are absolutely linked with two seed-coat colour factors R_1 and R_2 is adequate to explain the results, it appears unnecessary in view of the observations recorded in other species. Emerson (1921) has found in maize that the factors A, C and R affect both the plant colour and the aleurone colour. The factor A develops anthocyanin pigment in the plant and in the aleurone also. On analogy with the relationship between plant colour and aleurone colour factors in maize, it might be assumed that the factors R_1 and R_2 produce purple pigment in the plant and rose colour in the seed-coat. Since the plant colour and the seed-coat colours are doubtless anthocyanin pigments, it seems to be natural to expect close inter-relationship between them. Consistently with this hypothesis it must be assumed that the varieties with coloured seed-coats which were investigated, carry both the rose factors and that only in the presence of a rose factor P or Rd. is expressed. On this basis the genetic constitution of the varieties studied is summed up below :—

Colour of seed-coat	Variety	Genotype
White	Philippine white	pprd.rd.$r_1r_1r_2r_2$
Rose	Gudiyattam bunch	pprd.rd.$R_1R_1R_2R_2$
Rose	Saloum	Do.
Red	Small Japan	ppRd.Rd.$R_1R_1R_2R_2$
Purple	Corientes–3	PPrd.rd.$R_1R_1R_2R_2$

Discussion.

Waldron (1919) has suggested that *Arachis hypogæa* may be divided into two sub-species, *viz.*, *fastigiata* for the bunch type and *procumbens* for the spreading type. He postulates that "the cultivated bunch varieties are derived from such species as *A. pusilla*" a wild Brazilian species, erect in habit, and that "the prostrate varieties are derived from *A. prostrata*," another wild species in Brazil which is spreading in habit. The varieties Gudiyattam bunch, Small Japan, and Spanish-10 would come under the sub-species *fastigiata*; and the spreading varieties Philippine white, Saloum and Madagascar would come under the sub-species *procumbens*. In tracing the phylogeny of the sub-species *fastigiata* and *procumbens*, a comparison of the genetic complex of each of these two sub-species would be valuable. One of the objects of the geneticist's enquiry is to discover, if possible, what the distinctions between species are in terms of genetic constitution.

TABLE XIV.

Genetic analysis of the sub-species procumbens *and* fastigiata.

Characters	Gene complex		Characters
	Procumbens	*Fastigiata*	
Spreading habit ..	$S_1S_1S_2S_2$	$s_1s_1S_2S_2$	Erect or bunch habit
Branching habit ..	BB	bb	Non-branching habit
Chlorophyll deficiency factors	$G_1G_1g_2g_2$	$g_1g_1G_2G_2$	Chlorophyll deficiency factors
Long duration	LL	ll	Short duration
Abnormality factors ..	$N_1N_1n_2n_2$	$N_1N_1N_2N_2$ $n_1n_1N_2N_2$	Abnormality factors Do. in some varieties
Basic testa colour—factors for rose and for anthocyanin pigment in plant	R_1R_1	R_1R_1	
Do. in one variety..	r_1r_1	..	
Red testa factors ..	Rd. rd.	Rd. rd.	
Purple testa factors ..	P	P p	

The tabulation of the genic analysis of the two sub-species shows that the differences between them are not wide. Similar differences are found among the varieties in many species, and generally no attempts are made to group such varieties into sub-species or to suggest their origin from two different species. The so-called sub-species *fastigiata* and *procumbens* cross very readily, and the number of chromosomes in both the sub-species is the same. Until it is proved that the behaviour of the chromosomes of these two sub-species is different, the necessity for postulating separate origin for these two species is doubted.

A reference to the literature dealing with the studies regarding the inheritance of characters in the different members of *Leguminosæ* shows that in most of the species studied branching forms are dominant over non-branching forms and that erect or bunch habit is recessive to the spreading. The parallel behaviour of these characters is suggestive of true homology.

Summary.

In an attempt at a genetic analysis of the several characters—chlorophyll deficiency, abnormality, habit, branching, duration, hairiness, anthocyanin pigment in the plant and four seed-coat colours—of the groundnut, data accumulated during a period of five years, involving an examination of not less than 10,000 individual plants are reported. As an interpretation of the results obtained, thirteen genetic factors are assumed and the following conclusions are drawn :—

1. When a bunch ($g_1g_1G_2G_2$) variety is crossed with a spreading ($G_1G_1g_2g_2$) variety the segregation occurs in F_2 in the ratio of 15 green to one albino plants.

2. Abnormal dwarf plants which are mostly sterile, were obtained in a cross between the spreading varieties and the bunch variety Corientes-3. There are two factors for abnormality which give 15 : 1 ratio in F_2.

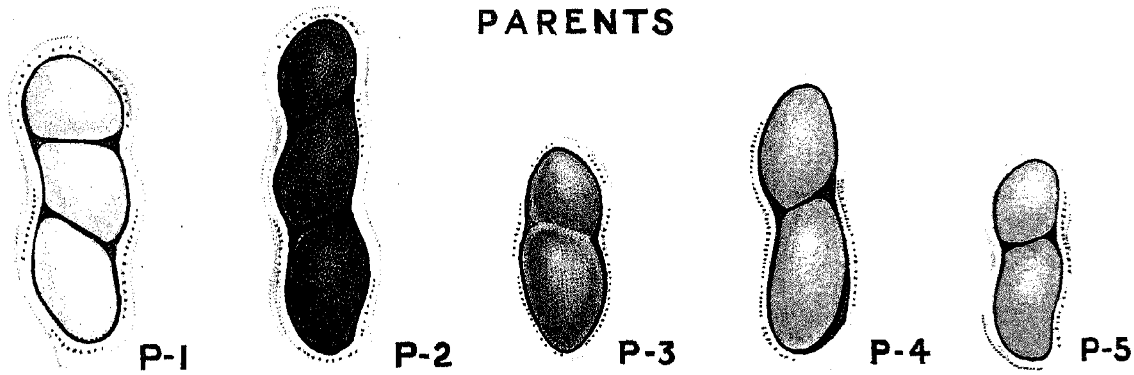
3. The spreading habit is met with when the dominant factors (S_1S_2) are present. In the absence of either one or both of them the progeny is bunch in habit.

4. The character—branching is dominant over non-branching and is inherited in simple Mendelian ratio of 3 : 1 in F_2. The branching is linked with the spreading habit with 30 per cent. of crossover.

5. Late duration is dominant over early. The F_1 is intermediate in duration and F_2 segregation is in the ratio of 3 non-early and one early plants.

6. Hairiness is dominant over sparse hairiness and is caused by a single gene difference.

PARENTS



7. There are four distinct seed-coat colours, in groundnut, *viz.*, dark purple, red, rose and white. There are two duplicate factors for the rose colour. The factor for red and the factor for purple are dominant to rose. But they (red and purple factors) are expressed only in the presence of the rose factor. The purple is dominant to red. The white seed coat colour ($pprd.rd.r_1r_1r_2r_2$) is recessive to the coloured seed-coats.

8. The purple pigment in the plant is produced by duplicate genes which give in F_2 15 : 1 ratio. It is suggested that the two factors which produce the rose coloured testa might also produce the purple pigment in the plant.

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EXPLANATION OF PLATE IV.

P-1 : Philippine white ; P-2 : Corientes-3 ;
P-3 : Small Japan ; P-4 : Saloum ; P-5 : Gudiyattam bunch.