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INTRA-SPECIFIC DIFFERENTIATION IN *GOSSYPIUM HIRSUTUM*

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1. INTRODUCTION

THE taxonomy of the lint-bearing cottons has been greatly simplified in the past twenty-five years, and only five species are now recognised in this section of the genus *Gossypium*. Much of the variation formerly regarded as inter-specific has consequently been included within the species. While some of this variation is no more than random heterogeneity within the lowest recognisable taxonomic units, an important part of it is not randomly distributed, but so assorted between different parts of the range as to give rise to distinct geographical races. Some of these are readily identified, and have been given varietal names, but the less distinct are only recognisable with confidence in extensive collections of material representative of the whole range of the species. Such a representative range has been studied in *G. arboreum* by Silow (1944). He concluded that geographical factors had dominated intra-specific differentiation, but that the geographical races so formed were generally highly variable, and consequently not sufficiently distinct to justify a formal taxonomic sub-classification. Recently (Hutchinson, 1950), Silow's interpretation of intra-specific differentiation has been shown to be applicable to *G. herbaceum* as well as to *G. arboreum*, and it is now apparent that in all the cultivated species of *Gossypium*, sub-specific differentiation is best treated in terms of geographical distribution.

Sub-specific differentiation in the cottons is small relative to that between species. There is good evidence that it is of recent origin, and the barriers between the races are rarely complete, and usually allow of some gene interchange between them. Hence morphological differences are generally small, and it is often impossible to assign a single specimen to a particular race unless its place of origin is known. Nevertheless, when a large collection is assembled and is grouped according to localities, the relationship between types from the same area is clear, and it is possible to divide the range into areas between which there are consistent distinctions.

It has long been accepted that the centre of variability of *G. hirsutum* is in Central America, but in the absence of adequate collections from that region, classification has perforce been based on material from the peripheral areas of its distribution. The species is at present divided into the typical form and two varieties. Accounts of the typical form are heavily weighted by data from the commercial Upland stocks of the American Cotton Belt. The description of var. *punctatum* was based on West African material, and until recently the New World *punctatums* have been regarded as of only secondary interest. The separation of var. *marie-galante* followed studies of West Indian cottons, with some reference to collections from Ecuador, the Spanish Main and Brazil. In no recent discussion save that of Mauer (1930) has any range of Central American material been considered. This can now be remedied, as extensive collections have recently been made in Mexico and Guatemala by Richmond (in 1945-46), Stephens (in 1946-47) and Ware and Manning (in 1948). The area traversed by these collectors lies between the Mexican States of Guerrero and Puebla to the west, and the Republic of El Salvador to the east. The Pacific coast was better covered than the coast of the Gulf of Mexico, but a small collection of Gulf coast types was provided by Dr I. Kelly. Collections from north of Mexico City would be of interest, and material from Honduras, Nicaragua and Panama is desirable to link up the Central American cottons with the *marie-galantes* of Colombia, but the Mexican and Guatemalan accessions cover the most important part of the Central American range. A very large proportion of the material collected belongs to *G. hirsutum*. Forms of *G. barbadense* were found occasionally throughout the area, but they showed little variability apart from the distinction between free and kidney seed, and they will not be considered further in this paper.

The system of collection was in general to take seed from any distinct lot of cotton that was observed. A few accessions from coastal Guatemala represent small samples of seed from ginneries, and a few more were obtained in country markets. A considerable number were from pickings of representative plants in small field crops. The great majority, however, were obtained from occasional plants or groups of plants in house yards, field margins, or hedgerows. In general, therefore, an accession may be taken to represent the interest in cotton of a single household, rather than any particular unit of the cotton population. The number of accessions available from an area, in fact, reflects the time spent by the collectors in the area, and only indirectly the density of its cotton population.*

The new material is of great taxonomic interest. It exhibits on

* Dr Stephens comments : " This is definitely incorrect in my case at least. There was absolutely no correlation. I collected more in a single day from certain regions, than in many days in others. In Salvador one really had to comb to find any cottons at all. Quite the opposite situation in Yucatan. I think one could say that the number of collections was definitely proportional to the density of the population in the sampled area ; even more—that the relatively small areas sampled were representative of the larger natural regions in which they occurred."

the one hand a diversity that is not contemplated in the current classification of the species (Hutchinson, 1947), and on the other, an orderly differentiation that is not discernible among the multiplicity of species proposed in earlier works. A reassessment of the species is therefore necessary, and division into seven geographical races is proposed. The perennial varieties *punctatum* and *marie-galante* as at present understood constitute two of these races. Four of the others are also perennials, and to these the names *yucatanense*, *morrilli*, *richmondi*, and *palmeri* will be given. The seventh, and most important, is made up of the generally annual group to which the Upland cottons belong. To this the name *latifolium* (from *G. latifolium* Murray) seems appropriate. Three of the races, *punctatum*, *marie-galante* and *latifolium*, have spread further than the rest, and have undergone further differentiation, but apart from the consequences of their wider distribution and greater agricultural success, they are in no way different in rank from those that are confined to Central America.

The intra-racial differentiation of *latifolium* is of the greatest agricultural importance. It commenced in Central America, where the early fruiting forms spread through areas occupied by previously differentiated perennial races, and has continued in the vast extensions of range which *latifolium* has enjoyed in post-Columbian times. It can now be seen in progress in the United States Cotton Belt, and in India and Africa. This most recent, and continuing, differentiation is the process with which the plant breeder is concerned, and an understanding of it, and of the conditions by which it is governed, will make possible better planning of his work.

2. THE GEOGRAPHICAL RACES OF *G. HIRSUTUM*

The classification of the races of *G. hirsutum* is based on three seasons' observations on living material grown in the Sudan and Uganda. Richmond's and Stephens' collections were grown at Shambat (near Khartoum in the Sudan) in the 1947-48 season, when a preliminary classification was made. In the 1948-49 season they were grown again, one complete set of plots being sown early (beginning of July), and a second set late (mid-August). Seed of the Ware-Manning collection was received in August 1948, and sown immediately after the second sowing of the other series. The whole of the *latifolium* section of the C.R.S. collection * was grown at Namulonge in Uganda in the 1949-50 season, and the discussion on the distribution of variability given later in this paper was developed with constant reference to this material in the experimental plots.

As the classification proceeded it became evident that the collections made on the three separate expeditions gave a remarkably consistent

* The C.R.S. collection is the world collection of cottons and cotton relatives maintained by the research stations of the Empire Cotton Growing Corporation. It is now located at Shambat, near Khartoum, in the Sudan.

picture of the distributions of the seven races. Each of the six perennial races has its own distinct area in which it is practically the sole perennial type to be found, and outside which it occurs rarely if at all. A certain amount of overlap, with consequent blurring of the racial distinctions by intercrossing, occurs at the margins, but the areas of overlap are only a small proportion of the whole. The annual *latifolium* has spread widely in recent years, but when the regions in which it is known to be a recent introduction are omitted, the presumably primitive area of the race fits into the pattern formed by the rest. The distributions of the races are discussed in more detail later, but they may be summarised here for convenience.

The most northerly race is *morrilli.* It is dominant on the Mexican plateau in Oaxaca, Puebla and Morelos, and from earlier collections (Cook and Hubbard, 1926) is known to extend as far north as Sonora and Sinaloa. *Palmeri* is the sole perennial race in the State of Guerrero and in the neighbouring coastal region of western Oaxaca, and has only been collected occasionally elsewhere. *Richmondi* is confined to a small area on the south coast of the Isthmus of Tehuantepec, with a few outliers on the edge of the plateau in Oaxaca, and in Chiapas. To the east, *marie-galante* is the native perennial of coastal Guatemala and El Salvador eastwards from Escuintla, presumably linking through Costa Rica and Panama with its better known area of distribution on the Spanish Main.

TABLE 1

Distribution by Races of Accessions of G. hirsutum *from Central America*

Area	Race						
	morrilli	*richmondi*	*palmeri*	*punctatum*	*yucatan-ense*	*marie-galante*	*lati-folium*
Sonora and Sinaloa	3	...	...	...	...	...	...
Puebla and Morelos	9	...	1	...	...	...	...
Oaxaca	71	5	...	...	...	...	11*
Guerrero and W. Oaxaca	...	...	49	...	...	...	20*
Salina Cruz (Isthmus of Tehuantepec)	...	8	...	...	...	...	...
Chiapas	...	4	2	6	...	...	31
Peten (N. Guatemala)	...	...	...	23	...	...	...
Yucatan and Campeche	...	...	2	29	12	...	...
Central Guatemala	...	...	...	8	...	...	90
S. Coastal Guatemala	...	...	...	...	...	...	29
E. Guatemala and El Salvador	...	...	...	...	...	30	...

On the north coast of Central America, race *punctatum* is distributed in British Honduras and northern Guatemala, and in all the Gulf coastal states of Mexico, particularly in Yucatan. The specialised race *yucatanense* is confined to coastal sand dunes in north Yucatan.

Race *latifolium* is the cotton of central Guatemala and the Motagua valley, spreading west into Chiapas, and (in recent years) into Oaxaca and Guerrero.

These distributions are summarised in table 1, and are outlined in the map given in fig. 1. Extensions of the range of race *latifolium* that are known to have taken place recently are starred in the table, but are omitted from the map.

Plant habit characters provide the most important distinguishing features of the races of *G. hirsutum*. As they were almost always obscured in the old and often mutilated house yard and hedgerow

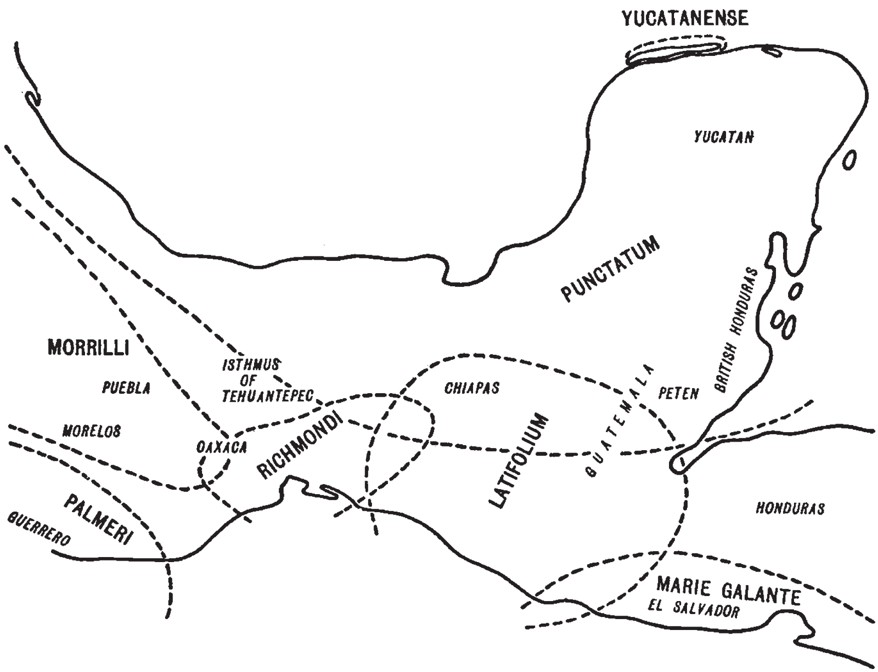

Fig. 1.—The Central American Distribution of Races of *G. hirsutum*.

plants * which provided seed of most of the accessions, field notes were of no assistance in classification, and the account given below is based entirely on observations on young and well-grown plants in the experimental plots. Though this material was strictly comparable, it did not, of course, represent anything more than response of the genotypes to the climates of the northern Sudan and Uganda. The morphological differences between races were much the same in these two widely different climates, however, and the comparisons may therefore be regarded as valid.

* Dr Stephens comments: "This is quite correct as regards Upland and *punctatum* types. . . . I do not feel happy at the placement of *marie-galante* as an equal subdivision with the other races. A novice can easily pick out *marie-galante* from the rest—he would be hard put to it to distinguish the others in the field."

Habit is a complex of many correlated characters, and it is not easy to sum up. An attempt was made to assess its more important components under size and general growth form, nature and development of vegetative branches, type of stem (rigidity and internode length), and node at which the first sympodial fruiting branch arose. An important, but less easily distinguished, habit character is the photoperiodic control of fruiting. This has been studied by Konstantinov (1934), who has summarised his conclusions as follows : " . . . the cotton plant should be ranked among plants of the short day. . . . The earliest and early forms do not answer to shortening of the day ; intermediate forms exhibit a slight reaction. The shortening of the day exerts the strongest effect upon the perennial arboreous cottons ; there are forms belonging to this group, however, which nevertheless do not react or react slightly to the shortening of the day. The basic change that is produced in the cotton plant by shortening of the period of illumination consists in lowering of the level at which the first fructiferous branch is formed." The node number of the first fruiting branch, and the number of vegetative branches formed were recorded on all material, and an estimate of photoperiodic response was obtained by comparing data from plots sown in early July with those from plots sown in mid-August (1948-49 crop at Shambat). The latitude of Shambat is about 16° N., about the same as that of central Guatemala, and the difference in day length was not large. Other environmental differences were small also. There was very little rain in July, and none thereafter, and the irrigation rotation was the same for both sowings. Humidity dropped from August onward, but there was no great drop in temperatures until November. Nevertheless, very striking differences were recorded between the two sowings in both node number and number of fruiting branches (see table 4). The difference between early and late sowings is simply termed sowing date response, but in view of Konstantinov's findings it is probable that the causative factor was in fact day length.

Information on seed cotton and lint characters was collected as opportunity offered, having regard to the first requirement from plots of all collections, which was the provision of adequate self-bred seed for future use. In the 1948-49 season, fuzz type and fuzz colour were recorded on all types, and lint colour and lint length (measured as halo length in mm.) on most. Ginning outturn was determined on those that gave sufficient seed cotton, either selfed or open pollinated. Since self pollination reduces the number of seeds per boll in some strains, the weight of seed cotton per boll was only determined on types from which sufficient naturally pollinated bolls were picked. The characteristics of the seven races are summarised in tables 2 and 3. Habit characters, as being most important, are given first, followed by leaf, stem and boll characters that often provide useful ancillary distinguishing marks. Mean values for lint and seed characters are also included, though their range of variation is in general so great as to provide little of value in distinguishing the races. Detailed data on sowing date response are given in table 4, and on lint and seed characters in tables 5-8.

TABLE 2

The characteristics of the races of G. hirsutum
(*Central American accessions only*)

Character	*morrilli*	*richmondi*	*palmeri*
Habit characters			
Size and general growth form	large, upright, perennial shrubs	large, lax, sprawling perennial shrubs	compact, upright, perennial shrubs
Vegetative branches	10-20, ascending, often overtopping the main stem	10-20, long lax, spreading	15-20, ascending, considerably shorter than the main stem
Stems . . .	stiff and erect	flexible, internodes long	stiff and erect, internodes short
1st sympodial node	17-32	13-22	20-30
Sowing date response (see table 4)	strong	considerable	considerable
Leaf, stem and boll characters			
Stem tip and leaf hairiness	densely hairy, hairs short	glabrous or nearly so	glabrous or nearly so
Leaves . .	$\frac{1}{2}$ to $\frac{2}{3}$ cut	$\frac{1}{2}$ to $\frac{2}{3}$ cut	palmatifid, rarely lanceolate entire
Leaf lobes . .	divergent, tapering	divergent, tapering	divergent, lanceolate acuminate
Stem anthocyanin	weak or absent	weak or absent	strong
Bolls . . .	round, not opening widely	round, opening widely	round, opening widely
Seed cotton per boll	*c.* 1·5 gm.	*c.* 3·0 gm.	*c.* 1·5 gm.
Lint and seed characters			
Mean lint length .	*c.* 27 mm.	*c.* 30 mm.	*c.* 27 mm.
Lint colour . .	white, creamy, grey or brown	creamy	creamy, rarely brown
Ginning outturn (per cent.)	*c.* 26	*c.* 26	*c.* 30
Seed type . .	fuzzy	fuzzy	fuzzy
Fuzz . . .	green	green, greenish or brownish	green, rarely brown

The differences between the early and late sown progenies in both node number and number of vegetative branches (table 4) are very striking. The two characters are strongly correlated, and there are also strong correlations between the data from the same strains at the two sowing dates. Differences between sowing dates are small in the low node number types, and large in those with high node numbers, thus matching the day length effect reported by Konstantinov (1934).

The range of lint length and ginning outturn is large in all races. In the whole series of collections the upper limit of lint length is low, only 42 plants (10 per cent. of the whole) having given mean lengths over 30 mm. In ginning outturn on the other hand, high values are common. Even in the perennial races ginning outturns of 32 per

TABLE 3

The characteristics of the races of G. hirsutum (*Central American accessions only*)

Character	*punctatum*	*yucatenense*	*marie-galante*	*latifolium*
Habit characters				
Size and general growth form	bushy perennial shrubs	small, slow-growing perennial sub-shrubs	large perennial shrubs or small trees	annual sub-shrubs, sometimes persisting for 2 years
Vegetative branches	8-15, spreading or prostrate	many, prostrate	8-20 spreading or slightly ascending, not overtopping the main stem	0-5, spreading or ascending
Stems	flexible, bowing under the crop	prostrate	stout and upright	usually upright, sometimes sprawling
1st sympodial node	14-20	...	20-30	8-10
Sowing date response (see table 4)	considerable, except in early Chiapas form	...	strong	slight or absent
Leaf, stem and boll characters				
Stem tip and leaf hairiness	sparse or nearly glabrous	nearly glabrous	glabrous, sometimes moderately hairy	glabrous, sparsely or densely hairy
Leaves	very shallowly cut	very shallowly cut	½ to ⅔ cut	½ cut or less
Leaf lobes	parallel-sided	parallel-sided	divergent, tapering	divergent, broadly triangular
Stem anthocyanin	moderate to strong	slight	usually slight, sometimes strong	usually slight
Bolls	oval or round, opening widely	very small, round, opening widely	round or oval, opening widely	round, oval or long, opening widely
Seed cotton per boll	*c.* 1·8 gm.	...	*c.* 1·7 gm.	2·0-6·3 gm.
Lint and seed characters				
Mean lint length	*c.* 27 mm.	*c.* 20 mm.	*c.* 25 mm.	*c.* 27 mm.
Lint colour	white, often brown in Yucatan	grey or medium brown	white, dull, grey, or light brown	white, creamy, light or rusty brown
Ginning outturn (per cent.)	*c.* 28	*c.* 20	*c.* 32	28-38
Seed type	fuzzy or tufted	fuzzy	fuzzy, tufted or naked	fuzzy or tufted
Fuzz	white, brown on brown linted types	brownish	green, sometimes brownish	white, green or brown

cent. and upwards were not uncommon, and in *latifolium* the Oaxaca, Guerrero and Chiapas field crop series almost all exceeded 32 per cent. Ginning outturn was only measured on one sample of *yucatanense*, but all accessions were similar in this respect, and something of the order

TABLE 4

G. hirsutum. *Central American accessions*
Node number and number of vegetative branches

Race and source	No. of accessions	Node number		Vegetative branches	
		Early sown	Late sown	Early sown	Late sown
1. *morrilli*					
Oaxaca	*4*	24·0	16·8	15·0	9·8
Puebla and Morelos	*6*	31·8	20·0	22·0	9·7
2. *richmondi*					
Salina Cruz	*6*	22·0	15·3	17·5	9·8
Chiapas	*1*	13·0	13·0	10·3	4·0
3. *palmeri*					
Guerrero	*3*	29·3	21·1	19·7	13·4
Chiapas	*2*	27·5	19·4	21·4	15·4
4. *punctatum*					
Yucatan and Campeche	*13*	20·5	15·7	13·9	7·8
Peten	*20*	20·7	14·4	13·2	8·6
Chiapas	*3*	12·3	11·7	10·3	6·7
6. *marie-galante*					
Guatemala and El Salvador	*15*	34·4	21·2	19·8	6·9
7. *latifolium*					
Central Guatemala	*12*	11·5	9·2	4·8	1·5
Chiapas (house yard)	*13*	9·8	8·2	4·9	2·2
Chiapas (field crop)	*15*	8·6	8·1	4·3	3·4
Coastal Guatemala	*29*	9·7	8·4	4·4	2·2

of 20 per cent. may be accepted as a representative figure. The low staple length of *yucatanense* may be noted. Its lint is as poor in quality as any produced in the New World, but it is quite spinnable, and is in fact, superior in length and fineness to that of some commercial Asiatic cottons of the present day. Data on lint length and ginning outturn are given in tables 5 and 6.

Boll size data are given in table 7. Except in race *richmondi*, the bolls of the perennial races rarely contain more than 2·4 gm. of seed cotton. In *richmondi* there are types with 3·0 to 4·8 gm. of seed cotton per boll. In *latifolium*, a much wider range of boll size is to be found, running in general from 1·0 to 4·5 gm. of seed cotton, except in the Chiapas field crop series. This group is remarkable for its very large bolls, with contents ranging from 4·7 to 8·4 gm. of seed cotton.

Data on seed fuzz type and lint colour are given in tables 8 and 9.

TABLE 5

G. hirsutum. *Central American accessions. Lint length*

Race and source	No. of accessions	Halo length (mm.)																	Mean
		18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	
1. *morrilli*																			
Oaxaca	*68*	...	...	2	1	7	4	13	8	11	5	8	5	...	4	...	...	...	25·5
Puebla and Morelos	*8*	...	...	...	...	...	...	...	...	...	...	1	3	...	1	1	1	1	30·6
2. *richmondi*																			
Salina Cruz	*8*	...	...	...	...	...	...	...	...	...	...	1	2	...	1	3	1	...	30·8
Oaxaca	*5*	...	...	...	...	...	...	1	1	1	...	1	...	1	...	...	...	...	26·6
Chiapas	*3*	...	...	...	...	...	...	...	...	...	...	1	...	1	1	...	...	...	29·7
3. *palmeri*																			
Guerrero and W. Oaxaca	*49*	...	...	1	...	...	...	3	3	13	10	9	4	2	4	...	...	...	27·1
Chiapas and Yucatan	*4*	...	...	...	...	1	...	1	...	1	1	...	...	...	...	...	...	...	24·8
4. *punctatum*																			
Yucatan and Campeche	*28*	...	...	1	...	1	4	5	6	4	6	1	...	...	...	...	...	...	24·9
Peten	*23*	...	...	...	...	...	...	...	1	1	1	3	5	5	4	2	1	...	29·3
Motagua Valley	*8*	...	...	...	...	1	1	1	1	2	1	1	...	...	...	...	...	...	25·1
Chiapas	*6*	...	...	...	...	...	...	...	...	1	3	...	1	1	...	...	...	...	27·7
5. *yucatanense*																			
Yucatan Coast	*9*	3	...	2	2	...	1	...	1	...	...	...	...	...	...	...	...	...	20·4
6. *marie-galante*																			
Guatemala and El Salvador	*28*	...	...	...	3	2	2	4	3	4	5	5	...	...	...	...	...	...	25·1
7. *latifolium*																			
Central Guatemala	*89*	1	1	1	2	2	3	8	12	15	11	12	11	4	3	3	...	...	26·5
Chiapas (house yard)	*14*	...	...	...	...	...	...	...	1	1	3	2	3	2	...	2	...	...	28·5
Chiapas (field crop)	*16*	...	...	...	...	...	...	...	...	1	1	...	1	7	4	2	...	...	30·0
Coastal Guatemala	*29*	...	...	...	1	...	...	2	3	4	4	8	2	...	3	1	...	1	27·5
Oaxaca (*morrilli* region)	*11*	...	...	...	...	1	...	1	2	1	1	1	1	3	...	...	...	...	26·9
Guerrero (*palmeri* region)	*20*	...	...	...	...	2	1	2	4	4	5	2	...	...	...	...	...	...	25·5

TABLE 6

G. hirsutum. *Central American accessions. Ginning outturn*

Race and source	No. of accessions	Ginning outturn (per cent.)																											Mean
		18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	
1. *morrilli*																													
Oaxaca	*67*	...	...	...	2	1	2	3	6	11	10	10	7	4	4	4	2	1	...	...	...	...	...	...	...	...	...	...	27·5
Puebla and Morelos	*6*	...	...	...	2	1	1	...	...	1	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	23·3
2. *richmondi*																													
Salina Cruz	*8*	...	...	...	...	...	...	1	...	3	...	2	...	1	1	...	...	...	...	...	...	...	...	...	...	...	...	...	27·4
Oaxaca	*5*	...	...	...	1	...	...	...	3	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	24·6
Chiapas	*3*	...	...	...	...	...	...	...	1	...	1	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	27·3
3. *palmeri*																													
Guerrero and W. Oaxaca	*47*	...	...	...	...	...	...	...	...	1	3	6	6	19	11	...	1	...	...	...	...	...	...	...	...	...	...	...	29·6
Chiapas and Yucatan	*4*	...	1	...	...	...	...	...	...	...	...	1	...	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	26·8
4. *punctatum*																													
Yucatan and Campeche	*28*	...	...	...	...	...	...	1	2	9	9	2	2	1	1	...	1	...	...	...	...	...	...	...	...	...	...	...	27·1
Peten	*23*	...	...	...	...	...	...	...	1	1	...	4	5	8	2	1	...	1	...	...	...	...	...	...	...	...	...	...	29·4
Motagua Valley	*8*	...	...	...	...	...	...	...	1	1	1	2	2	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	27·8
Chiapas	*6*	...	...	...	...	...	1	...	3	1	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	25·2
5. *yucatanense*																													
Yucatan Coast	*1*	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	18·0
6. *marie-galante*																													
Guatemala and El Salvador	*22*	...	...	...	...	...	...	...	...	1	2	1	1	2	2	...	2	5	5	1	...	...	...	...	...	...	...	...	32·1
7. *latifolium*																													
Central Guatemala	*36*	...	...	...	...	...	...	1	2	3	6	5	1	4	3	2	1	...	2	2	...	1	...	...	1	...	1	1	30·9
Chiapas (house yard)	*14*	...	...	...	...	...	...	...	1	1	...	1	2	4	...	1	3	...	...	...	...	...	...	1	...	...	...	...	30·6
Chiapas (field crop)	*16*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	2	1	2	1	2	4	...	2	...	1	1	38·1
Coastal Guatemala	*29*	...	...	...	...	...	2	...	1	3	3	...	...	...	3	...	5	3	4	1	1	1	2	...	...	...	...	...	31·7
Oaxaca (*morrilli* region)	*11*	...	...	...	...	...	...	...	...	...	...	...	1	1	...	1	1	1	3	1	1	1	...	...	...	...	...	...	34·0
Guerrero (*palmeri* region)	*20*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	3	2	6	6	...	2	1	...	...	...	...	...	...	34·4

TABLE 7

G. hirsutum. *Central American accessions. Seed cotton per boll*

Race and source	No. of accessions	Seed cotton per boll (gm.)																				Mean
		0·9 1·0	1·1 1·2	1·3 1·4	1·5 1·6	1·7 1·8	1·9 2·0	2·1 2·2	2·3 2·4	2·5 2·6	2·7 2·8	2·9 3·0	3·1 3·2	3·3 3·4	3·5 3·6	3·7 3·8	3·9 4·0	4·1 4·2	4·3 4·4	4·5 4·6	4·7 4·8	
1. *morrilli*																						
Oaxaca	*4*	...	1	1	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1·4
Puebla and Morelos	*6*	1	...	3	...	1	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1·4
2. *richmondi*																						
Salina Cruz	*6*	...	...	...	1	1	...	...	1	...	...	...	1	...	...	1	...	...	...	...	1	2·9
3. *palmeri*																						
Guerrero and W. Oaxaca	*3*	...	...	...	2	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1·7
Chiapas	*2*	...	...	1	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1·4
4. *punctatum*																						
Yucatan and Campeche	*9*	...	...	2	5	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1·5
Peten	*17*	...	...	...	2	9	4	1	...	...	...	1	...	...	...	...	...	...	...	...	...	1·9
Chiapas	*3*	...	...	...	...	1	1	...	1	...	...	...	...	...	...	...	...	...	...	...	...	2·0
6. *marie-galante*																						
Guatemala and El Salvador	*15*	...	...	2	5	4	3	1	...	...	...	...	...	...	...	...	...	...	...	...	...	1·7
7. *latifolium*																						
Central Guatemala	*12*	...	1	...	1	2	3	2	2	...	...	...	...	1	...	...	...	...	...	...	...	2·0
Chiapas (house yard)	*13*	...	...	...	...	...	...	...	2	...	1	2	...	4	1	1	1	...	1	...	...	3·3
Coastal Guatemala	*29*	...	...	...	1	...	1	1	2	3	...	2	2	3	2	4	2	3	3	...	...	3·3
Oaxaca and Guerrero	*3*	...	...	...	...	...	...	...	1	1	...	...	...	1	...	...	...	...	...	...	...	2·8
		4·7 4·8	4·9 5·0	5·1 5·2	5·3 5·4	5·5 5·6	5·7 5·8	5·9 6·0	6·1 6·2	6·3 6·4	6·5 6·6	6·7 6·8	6·9 7·0	7·1 7·2	7·3 7·4	7·5 7·6	7·7 7·8	7·9 8·0	8·1 8·2	8·3 8·4		
7. *latifolium*																						
Chiapas (field crop)	*15*	1	...	2	1	1	...	2	1	1	...	...	1	2	...	2	...	...	...	1	...	6·3

Fuzzy seed is the commonest condition, tufted seed being rare or absent in *yucatanense*, *morrilli*, *richmondi*, *palmeri*, and *marie-galante*. Between 15 and 20 per cent. of the *latifoliums* were tufted, and about two-thirds of the *punctatums*. Fuzz colour and lint colour go together.

TABLE 8

G. hirsutum. *Central American accessions*

Fuzz type and fuzz colour

Race and source	Fuzz type				Fuzz colour				
	Fuzzy	Semi-fuzzy	Tufted	Mixed fuzzy-tufted	White	Greenish	Green	Brownish	Brown
1. *morrilli*									
Oaxaca	63	...	3	2	...	...	66	1	1
Puebla and Morelos	7	1	...	...	...	...	6	...	...
2. *richmondi*									
Salina Cruz	8	...	...	...	...	2	1	5	...
Oaxaca	5	...	...	...	...	...	5	...	...
Chiapas	4	...	...	...	...	3	...	1	...
3. *palmeri*									
Guerrero and W. Oaxaca	48	...	1	1	...	...	49	1	...
Chiapas and Yucatan	2	...	2	...	...	...	...	...	4
4. *punctatum*									
Yucatan and Campeche	12	7	8	1	14	...	1	1	12
Peten	2	2	19	...	23	...	...	...	...
Motagua Valley	...	...	8	...	8	...	...	...	...
Chiapas	6	...	...	...	...	5	...	1	...
5. *yucatanense*									
Yucatan coast	9	...	...	...	...	...	...	9	...
6. *marie-galante*									
Guatemala and El Salvador	28	...	...	...	...	...	24	3	1
7. *latifolium*									
Central Guatemala	68	...	19	2	65	11	4	8	1
Chiapas (house yard)	13	1	...	...	3	3	4	3	1
Chiapas (field crop)	16	...	...	...	11	3	2	...	...
Coastal Guatemala	26	1	3	1	28	3	...	...	...
Oaxaca (*morrilli* region)	11	...	...	...	...	1	10	...	...
Guerrero (*palmeri* region)	4	...	5	11	12	...	...	3	2

Brown lint is associated with brown fuzz, or sometimes with green fuzz. Bright white lint, which is only found on types with white fuzz, is commonest in *punctatum* and *latifolium*. Green fuzz and off-white lint are characteristic of *morrilli*, *palmeri* and *marie-galante*. Brown fuzz and brown lint are the rule in *yucatanense*.

3. NOTES ON THE RACES

(1) *Race* morrilli

Cook and Hubbard (1926) described a wild plant from the coast of Sonora, Mexico, as *G. morrilli*. Their Sonora plant is indistinguishable from a large group of perennial shrubby cottons from the central Mexican plateau in the States of Oaxaca, Morelos and Puebla.

TABLE 9

G. hirsutum. *Central American accessions*
Lint colour

Race and source	Bright	Creamy	Dull	Grey	Pale Brown	Medium Brown	Dark Brown	Rusty Brown
1. *morrilli*								
Oaxaca	1	33	10	11	...	3	3	7
Puebla and Morelos	5	...	1	...	...	...	...	...
2. *richmondi*								
Salina Cruz	2	4	1	...	...	...	...	...
Oaxaca	...	3	1	1	...	...	...	...
Chiapas	2	1	...	...	...	...	...	...
3. *palmeri*								
Guerrero and W. Oaxaca	6	41	1	...	...	1	...	...
Chiapas and Yucatan	...	...	...	...	...	2	2	...
4. *punctatum*								
Yucatan and Campeche	8	4	1	1	...	10	3	...
Peten	16	5	2	...	...	...	...	...
Motagua Valley	2	3	3	...	...	...	...	...
Chiapas	2	3	1	...	...	...	...	...
5. *yucatanense*								
Yucatan Coast	...	...	...	2	...	7	...	...
6. *marie-galante*								
Guatemala and El Salvador	...	4	2	16	6	...	...	...
7. *latifolium*								
Central Guatemala	12	7	7	...	...	1	...	...
Chiapas (house yard)	8	...	...	1	...	1	...	1
Chiapas (field crop)	10	1	2	...	1	1	...	...
Coastal Guatemala	4	10	3	...	...	...	...	...
Oaxaca (*morrilli* region)	1	4	6	...	...	...	...	...
Guerrero (*palmeri* region)	2	14	2	...	1	...	...	1

Outstanding features are their stout upright habit, and profuse development of vegetative branches. The latter soon equal or overtop the main stem, giving a rounded bush. Leaves and stems are usually densely hairy. The bolls are small and round, and do not open widely. The Puebla and Morelos types are generally taller and more open than those from Oaxaca, and have rather longer lint and a lower ginning outturn. In other respects the race is morphologically uniform.

Seed was obtained from the United States Department of Agriculture of four of the Sonora and Sinaloa types described by Cook and Hubbard as distinct species, and living material was compared with that in the new Central American collections. Cook and Hubbard's *G. morrilli* and *G. dicladum* are within the range of the group here described as race *morrilli*. Their *G. patens* resembles *morrilli* in habit, but it is nearly glabrous. The fourth type, *G. contextum*, is nearer race *punctatum*.

The area of race *morrilli* is sharply delimited to the south. It does not occur in the extensive series from Guerrero nor is it found south of the edge of the plateau in Oaxaca, and it has not been recorded from Chiapas. Cook and Hubbard's collections provide the only information on the extent of its distribution to the north.

(2) *Race* richmondi

This very distinct type does not appear to be covered by any of the numerous names that have been applied to the cottons of Central America. The first, and most characteristic, material was that collected by Richmond in the region of Salina Cruz, Mexico. When well grown, *richmondi* plants are large, lax, much branched shrubs with flexible stems that tend to sprawl on the ground when carrying a crop. They are generally without much anthocyanin pigmentation, and are glabrous or only slightly hairy. The bolls are usually larger than those of *morrilli* and *palmeri*. The distribution is limited. It was the only type collected by Richmond in the region of Salina Cruz on the south coast of the Isthmus of Tehuantepec. It was also found among the highly variable cottons of the State of Chiapas (Richmond's collection), and among the dominant *morrilli* in Oaxaca as far inland as Ocotlan and Ejutla (Ware and Manning's collection). In Oaxaca and Chiapas intermediates occur between *richmondi* and other races, but in the region of Salina Cruz it is morphologically uniform. Its area is evidently small, since at Pochutla (on the south coast of Oaxaca) on the west, Ware and Manning found *latifolium* only, and on the east it does not reach the *latifolium* tract of the Guatemala coast.

(3) *Race* palmeri

The *palmeri* cottons all have deeply laciniated leaves, and have therefore caught the eye of plant collectors. Watt (1907) has described laciniate-leaved cottons from Central America under four specific names. All four are forms of *G. hirsutum*. Three of them (*G. palmeri*, *G. fructiculosum*, and *G. lanceolatum*) belong to this race, and the fourth (*G. schottii*) includes both this type and laciniate-leaved Uplands.

Palmeri is the name most used, and is therefore adopted. Besides their laciniate leaves the *palmeri* cottons are distinguished by their habit. They are sturdy, upright shrubs with short internodes and many ascending vegetative branches. The latter do not equal the main stem in height and a typical shrub is consequently pyramidal in outline. They are glabrous, usually with strong anthocyanin pigment in the stems and petioles, and bear a prolific crop of small, widely opening bolls. *Palmeri* is the only perennial cotton in collections from the Mexican State of Guerrero, and from the neighbouring coastal region in western Oaxaca. A collection of 49 types from this area was extremely uniform. Elsewhere it has only been found rarely (once in 10 collections in Puebla and Morelos, twice in 43 in Yucatan, and twice in 43 in Chiapas). The four Chiapas and Yucatan types have brown lint, but from the main area, brown lint was only present in one out of 49 collections. Mauer (1930), reporting on Bukasov's collections, stated that it was wild, but from field notes by Richmond and Ware and Manning, it is evident that it does not occur in natural vegetation, but in house yards, hedgerows and abandoned clearings. In field cultivation it has been replaced by *latifolium* in recent years.

(4) *Race* punctatum

G. punctatum Sch. et Thon., *G. hirsutum* var. *punctatum* J. B. H. This is the best known of the perennial races of *G. hirsutum*. It was originally described from West Africa, where it has been established since the end of the eighteenth century (Hutchinson, 1949). The *punctatums* are slender-stemmed shrubs with a number of spreading vegetative branches. Under favourable conditions they crop heavily, and the slender main stem becomes decumbent, while the spreading vegetative branches lie prostrate on the ground. Anthocyanin pigment is generally well developed. Stems and leaves are glabrous or nearly so. The leaves are characteristic, being usually very shallowly cut into three obtuse lobes, the lateral lobes ascending so that the leaves have a parallel-sided appearance. Bolls are medium to small, the lint is short and the ginning outturn low, so that in spite of prolific bolling, the crop is not large and is expensive to pick and gin. Hence, in spite of a wide adaptability, the race is of little use as a commercial cotton.

In Central America, *punctatum* is extremely common in Yucatan, where it is very variable, in the Peten region of Guatemala, where Stephens reports that the whole process of establishment of house yard types in the wild can be seen, and in neighbouring British Honduras. An early fruiting form occurs in Chiapas, and intermediates are there to be found between *punctatum*, *richmondi* and *latifolium*. The typical form occurs round the coasts of the Gulf of Mexico to Florida and the Bahamas. It was the first cotton to be cultivated in what is now the United States of America (Hopi and Moqui Indian cotton). In the Greater Antilles a xerophytic form is to be found wild in scrubby vegetation on the dry leeward sides of some of the larger islands.

Punctatum has been widely distributed in the Old World (see Hutchinson, 1947). It has been very successful in house yards and small cultivations throughout the West African and Sudan savannah regions from the Gambia and Senegal to the Red Sea. Here, further differentiation has taken place. In West Africa an early annual form has been developed which is grown in small field plots, and in Egypt, a specialised type has become established as a weed in crops of the more valuable Egyptian cotton. In response to the requirements of this habitat the " Hindi weed," as it is called, has developed the quick germinating, rapid growing, and early fruiting characteristics necessary for survival in an annual crop.

Punctatum has played a most important part in the development of resistance to blackarm disease in New World cottons acclimatised in Asia and Africa. Knight and Hutchinson (1950) have shown that one or more genes for resistance to blackarm disease occur commonly in *punctatum* in the Bahamas, and there can be little doubt that the existence of blackarm resistance in the introduced stock has contributed greatly to its widespread success in the Old World. In West Africa, among both annuals and perennials, lines are to be found with varying degrees of resistance up to virtual immunity, and resistance has been found in types acclimatised in India and northern Australia. Moreover, where *latifolium* has been introduced in the Old World, it has almost always been preceded or accompanied by *punctatum*, and Knight and Hutchinson (1950) have shown that the blackarm resistance now commonly to be found in the acclimatised forms of *latifolium* can be traced to hybridisation with *punctatum*.

(5) *Race* yucatanense

This race has not previously been described. It was collected by Stephens, who reported that it was growing wild in natural vegetation on coastal sand dunes in the region of Progreso, Yucatan. The sand dune region is cut off from the mainland by a swampy tract, so these cottons probably enjoy a fair degree of isolation. The plants are small, much branched, procumbent or prostrate, and glabrous or nearly so. Anthocyanin pigmentation is usually slight, The leaves resemble those of *punctatum* in being very shallowly divided into ascending lobes, giving a parallel-sided appearance. The bolls are small and open widely. The lint is brown, short and scanty, and the seeds have hard seed coats and delayed germination. Variability is low.*

* Dr Stephens comments: " In respect of habit, no doubt, but the population I collected was segregating for simple mendelian genes, anthocyanin, corolla colour, lint colour, hairiness. Presumably the uniformity only applies to characters of high selective value."

Punctatum has given rise in many parts of its range to forms which have become established in natural vegetation. *Yucatanense*, which is obviously closely related to *punctatum*, is the most extreme of these, having developed the specialised procumbent habit, but " algodon brujo " of Cabo Rojo in Puerto Rico (Hutchinson, 1944), " *G. ekmanianum* " of Haiti, and " *G. taitense* " of the Polynesian Islands all resemble it in their small bolls, poor and scanty lint, and small hard seeds. This last is a characteristic of the truly wild species of *Gossypium*, and since it spreads germination over more than one season, it has obvious advantages for a wild plant in a xerophytic environment.

(6) *Race* marie-galante

G. hirsutum var. *marie-galante* J. B. H. This race includes the largest and most tree-like of all the cottons. The Guatemalan and Salvadorean types, however, are shrubby,* and no larger than the other Central American races, to which they are evidently closely related. The *marie-galantes* are highly photoperiodic, much branched shrubs. One of the chief characteristics of the race is the dominance of the main stem, and in the large West Indian and Brazilian types this results in the development of a small tree with a trunk that may be 5 or 6 inches in diameter. This is in strong contrast to *morrilli*, *richmondi* and *punctatum* in which the lateral branches soon equal or exceed the main stem, and an old plant develops into a bushy thicket and not a tree.

The Central American types have small bolls and small seeds, with short but copious, usually greyish, lint. In the Stephens and Ware-Manning collections there were two rather distinct types, one glabrous with strong anthocyanin pigmentation, and the other bearing a coat of short hair, and having little anthocyanin pigment.

Marie-galante was originally described from the West Indies. It was first recorded from Central America by R. A. Silow (personal communication), who noted that two specimens from the Pacific Coast of Costa Rica in the Gray Herbarium might well belong to this race. From his description they appear to be similar to those collected by Stephens in coastal Guatemala and El Salvador. Stephens obtained a considerable series, and Ware and Manning added to it, but the race seems to be confined to the Pacific slopes from Escuintla eastwards. There is every reason to believe that the distribution is continuous from Guatemala to Colombia, where larger, better quality forms provide the commercial crop of the Atlantico Province. The race is common throughout the Caribbean region and in north Brazil, and on the west coast of South America it extends southwards from

* Dr Stephens comments : " This is not completely true. I did find tree types 15 ft. high or more but they were not bolling when I collected. I remember 3 of the finest specimens I have seen in a garden in Santa Lucia, Guatemala. These were larger and taller than any I have seen in the West Indies. However, on the whole, the *marie-galantes* were small and shrub-like but with a pronounced main stem."

Colombia to Ecuador. It has undergone considerable differentiation in response to the demands of perennial cultivation. The cultivated forms are large and tree-like, and include a great range of types in respect of such characters as plant hairiness, boll size, seed type, staple length, and lint quantity. Moreover, in the open vegetation of xerophytic habitats on the coasts and islands of the Caribbean, it has become established in the wild, and there are now to be found types with the scanty lint, hard seed coats, and delayed germination that characterise the wild cottons of many races.

Further differentiation has occurred following hybridisation. In the North Brazilian States of Rio Grande de Norte and Ceara, Harland (1939) reported that the introduction of Upland (*latifolium*) has resulted in the development in the commercial crop of a hybrid stock almost to the exclusion of pure *marie-galante*. On the Gold Coast, where the race is well established in house yards in the southern forest region, spread into the northern savannahs has been made possible by the acquisition of blackarm resistance by introgressive hybridisation with *punctatum* (Hutchinson, 1949).

(7) *Race* latifolium

From *G. latifolium* Murray (see Watt, 1907). Sub-shrubs growing as annuals in field crops, or persisting for a few years as house yard plants. These include the most advanced products of man's selection as crop plants. Many of the Central American forms have enough photoperiodic response to prevent satisfactory fruiting in more northern latitudes (Ware, 1936), but types capable of crop production in long days have been selected and have given rise to the commercial cottons of the American Cotton Belt, commonly known as Uplands, and thence to crops in many other parts of the world. *Latifolium* includes a great range of types with medium large to very large bolls, and copious lint of fair to good quality.

The centre of the race is in central and northern Guatemala and the neighbouring State of Chiapas in Mexico. It is now established as a commercial crop on the south coast of Guatemala, where it was collected by Richmond and Stephens. Ware and Manning found it in small field crops in Oaxaca and Guerrero also, but were informed that it had been introduced there within living memory.

The Guatemalan collections are highly variable in plant habit, hairiness, anthocyanin pigmentation, boll size, productivity and other characters. In Chiapas the Guatemalan type is to be found in house yards, differing little from that of central Guatemala except in the frequency of larger bolls. In small field crops, on the other hand, a very distinct form is grown. This is a rather lax and sprawling, glabrous plant, with large leaves. It has very large bolls, outside the range of all other Central American forms of the species. Moreover, it is uniformly high in ginning outturn, and is one of the few Central

American groups to reach a mean lint length of 30 mm. It is of considerable agricultural importance, as types collected in the vicinity of Acala in Chiapas gave rise to the Acala variety and its derivatives in the United States Cotton Belt.

Further west in the *morrilli* and *palmeri* areas *latifolium* is generally to be found in small field plots, whereas the perennial races are house yard cottons. In both areas the influence of the old-established perennial on the immigrant *latifolium* is very evident. In Oaxaca the Uplands have developed, doubtless following hybridisation with *morrilli*, the characteristic upright habit and ascending vegetative branches of the latter, and the dense coat of long hairs on both upper and lower surfaces of the leaves. In Guerrero, the laciniated leaf of *palmeri* has not been transferred, doubtless because it forms such a ready index of contamination and would therefore be eliminated. The transfer of *palmeri* genes is evident, however, in the strong stem and petiole pigmentation and the comparatively glabrous stem tips and leaves of Guerrero accessions. In both areas some differentiation in seed cotton and lint characters is evident. Ginning outturn is high, and boll size is above that of the central Guatemalan type. In the *morrilli* region all accessions had the green fuzz characteristic of *morrilli* itself, whereas in Guerrero the white fuzz more usual in *latifolium* predominated, though *palmeri* has green fuzz.

Latifolium has spread over vast areas in post-Columbian times, having been carried to the United States Cotton Belt, where it gave rise to the Upland cottons, and to most of the cotton-growing countries of the world. The race was established in Carolina at the beginning of the eighteenth century (Watt, 1907), but did not become a major crop until the ginning problem was solved by the invention of the saw gin by Whitney in 1793. Thereafter the American Upland crop rapidly achieved a dominant place in the world's cotton markets, and other cotton-growing countries, both actual and potential, began introducing Upland seed. The development of the crop, first in America and later in India and Africa, has been discussed elsewhere (Ware, 1936; Hutchinson, 1938 and 1947; Hutchinson and Silow, 1947; Knight and Hutchinson, 1949). Suffice it to say that acclimatisation in the United States Cotton Belt involved selection for long day fruiting and early and prolific cropping, and was accompanied by the development of high quality in some lines. Success in India and Africa, on the other hand, depended primarily on the spread of genes for resistance to the jassid pest and blackarm disease.

Though most of the acclimatised *latifolium* stocks of the Old World are derived from the Uplands of the United States Cotton Belt, the important south Indian Cambodia can be traced by way of Cambodia and other parts of southeast Asia (Main, 1912) to direct introductions by the Spaniards from Mexico to the Philippines (Lewton, 1925). In India the Uplands and Cambodias have developed side by side. The Uplands are descended from introductions by the East India

Company in the middle of the nineteenth century. Though initially a failure as a crop, they became established in the Dharwar district of the Deccan, and after a period of natural selection for resistance to jassid and blackarm (see Hutchinson, 1938 and Knight and Hutchinson, 1950), they gave rise to the modern Indian American crops of the Punjab and Sind, and to a less extent of Central India and the northern Deccan. The Cambodias were a late introduction, but had been subject to selection in south-east Asia for a long period, and had developed the highest level of jassid resistance known in the race. Following their success in the Madras Presidency they were widely distributed in more northerly regions. Never having been through the United States Cotton Belt they have not been selected for long day fruiting, and it is probably for this reason that they have failed to compete with the Uplands in northern India.

The distribution of these two *latifolium* stocks is of considerable importance to the plant breeder. When grown together they can be readily distinguished. In an Indian collection grown at Namulonge in 1949-50 the Uplands produced few vegetative branches of little value to the crop, and grew into slender plants with rather small leaves and bolls. The Cambodias produced several stout vegetative branches per plant which contributed considerably to the crop and developed into bushy plants with stout stems, large fleshy leaves and rather large bolls. The sources of accessions of the two types were distributed as follows :—

Locality	Cambodia	Near Cambodia	Near Upland	Upland
Coimbatore (Madras)	5	...	...	...
Dharwar and Parbhani (Deccan)	...	1	2	3
Central India	...	3	1	2
United Provinces and the Punjab	...	...	...	8
Chitral	...	...	...	2

It will be seen that material from the two Deccan stations was predominantly of the Upland type, as might have been expected from the fact that it was at Dharwar in the Deccan that the Upland cottons were first established. In Central India, Coventry distributed a considerable quantity of Cambodia in an area in which Upland was already present as a mixture in the indigenous *arboreum* crop (Hutchinson and Ghose, 1937). In consequence, the two types are now about equally frequent, though the Cambodias show signs, in their rather finer wood and smaller leaves, of gene exchange with the Uplands. Further north, in the Indo-Gangetic plain and in the Himalayan valleys, all the *latifolium* cottons are of the Upland type.

In other parts of Asia, the Cambodia type is only known from Indo-China and the Philippines. A *latifolium* collection from south China and Formosa was more like the Uplands than the Cambodias, and is probably entirely of Upland origin. Russian Uplands appear to be closely related to those of the American Cotton Belt to-day, and those of Persia are similar.

The *latifolium* cottons of Africa are more recent introductions than those of India, little having been done on the crop until the first decade of the present century. They are all Uplands, the early introductions having been of long stapled crop varieties from the American Cotton Belt. The major selective factors in Africa have been similar to those in India. Jassid is a major pest and blackarm a serious disease in most of the rain-fed cotton tracts except the Belgian Congo, and present-day African Uplands contain a high proportion of hairy (jassid-resistant) plants and of plants carrying at least one major gene for blackarm resistance (see Knight and Hutchinson, 1950). In the Congo, on the other hand, where jassid and blackarm are not serious, modern American crop varieties are successfully grown.

The selection pressures exercised by jassid and blackarm have resulted in the development of a type more like the Uplands of northern India than those of the United States. Many points of difference exist, however. The African Uplands were derived from the best quality American varieties of the time, and a higher standard of quality has been maintained than is found in the Indian Uplands and Cambodias. In the East African cottons a tall, leggy type with short fruiting branches is common. It is a slow and rather mediocre cropper, but has the virtue of recovering well from attacks of blackarm and bollworm that would cripple a quick cropping strain. Such a form would never survive in the short season of the Indian cotton tracts. On the other hand, as a result of the breeding work carried on at Barberton in the Eastern Transvaal, a quick cropping, very prolific type (U4) has been isolated and spread in the Transvaal, Portuguese East Africa and Nyasaland.

It will be seen that in race *latifolium*, establishment in the Old World has resulted in the development of highly variable stocks. Rapid communications have made for easy seed exchange, and even types of such widely different histories as the Uplands and Cambodias have not been grown in isolation long enough to have developed such distinctive characteristics as separate the races in Central America. Moreover, differentiation in response to such powerful selective forces as the jassid pest and blackarm disease is as yet in its early stages, susceptible types still being common in all but pedigree stocks from breeding stations.

4. DISCUSSION

The primary object of the Central American expeditions was the collection of material of value for cotton breeding projects. Following Vavilov (1935), it was believed that in the region of origin of a crop plant the variability is at a maximum, and genes are present that are rare or absent from the more recently colonised peripheral areas. From the plant breeder's point of view, the collections have proved somewhat disappointing. Considering the species as a whole, a great range of variability exists in a small area, but a large part of it is assorted between well-defined races, and being largely a matter of diversity in the perennial habit, is of little interest to the breeder of annual cottons. Moreover, even where the intra-racial variability is large—in the perennial race *punctatum* and the annual *latifolium*—almost the whole Central American range in characters of agricultural value lies below that to be found in modern commercial crops and the gene content in respect of resistance to pests and diseases is inferior to that of the acclimatised forms of the Old World. For an understanding of the development of the species, on the other hand, the collections are of the greatest value, since the discovery of the partition of the greater part of the variability between distinct and often very uniform races indicates a more advanced evolutionary status than was anticipated.

Wild forms, which have often been regarded as primitive, are known in four of the seven races of *G. hirsutum*. *Yucatanense* only exists as a wild plant. Wild forms of *punctatum* are to be found in xerophytic scrub on coastal sands in Puerto Rico, in dry areas in Haiti, on the Florida Cays, on numerous islands of the Pacific, and in northern Australia. In *marie-galante*, wild types are known from xerophytic scrub in Jamaica, St Kitts, Nevis, Antigua, Barbados and coastal Colombia. The original type of *morrilli* was collected in the wild on coastal sands in Sonora, Mexico. These forms, wherever they are found, have certain characters in common. They are slow growing, long lived perennials, and they have small bolls and small seeds with hard seed coats and inferior, scanty, and firmly attached, lint. Though they have been regarded as primitive, a little consideration will show that the characters they have in common are at least as readily explained as the consequence of convergent evolution as of common ancestry. This complex of characters is common to all wild species of *Gossypium*, and to the wild forms of the Asiatic cottons and of *G. barbadense*, as well as to those of *G. hirsutum*. All save the inferior and scanty lint are obviously advantageous in the xerophytic scrub vegetation in which wild cottons are found, and scanty lint firmly attached to the seed may well be associated with a hard seed coat.

It should be emphasised that the lint of all wild forms of *G. hirsutum*, though inferior in quality to that of the cultivated forms, is nevertheless spinnable and is in fact superior to that of some current commercial Asiatic cottons. There is therefore no force in the argument that the wild cottons must be primitive because their lint can never have been used.

All the wild forms of *G. hirsutum* listed above are to be found in peripheral areas. On the three Central American collecting expeditions a search was made for truly wild populations growing in natural vegetation. Richmond and Ware and Manning reported, however, that the whole of their collections came from field crops, house yards, hedgerows, and similar man-made habitats.*

Stephens reported that except in two localities, cotton was only to be found in, or close to, villages, in places where it had either been deliberately planted, or to some extent tended directly or in the course of cultivation of more important crops. The two exceptions were on the coastal sands of Yucatan, where *yucatanense* is fully established in the wild, and in the Peten region of northern Guatemala. There he found *punctatum* in all stages of the process of escape from cultivation. At one extreme were house yard cottons receiving a certain amount of care and protection, and at the other were plants fully established in natural vegetation. When grown in culture in the Sudan, those descended from wild plants were indistinguishable from the house yard cottons, and the whole series evidently belonged to the house yard *punctatums* that are widely spread throughout the Yucatan peninsula. No other example of a truly wild cotton was found, and it may therefore be accepted that in eastern Mexico and Guatemala, *G. hirsutum* is entirely a domestic or commensal plant.

It might be argued that the wild prototypes have been supplanted by their cultivated derivatives at the centre of cultivation, and those now found in peripheral areas are the relics of a formerly widespread race. Wild cottons, however, only grow in xerophytic habitats with open vegetation (Hutchinson, 1944) and where cultivated and wild forms are found in neighbouring areas they do not compete with each other, since the habitat of the wild form is unsuitable for cultivation. Hence there is no reason to suppose that a wild prototype of *G. hirsutum* would be extinguished by its derivatives cultivated in more mesophytic situations.

There is thus good evidence from their distribution alone for ignoring the wild forms in the search for the prototype of *G. hirsutum*. The morphological evidence against them is even stronger. The wild forms do not form a homogeneous group, as would be expected in relics of a former widespread race, but bear all the characteristics of the cultivated races of the areas in which they occur. The small house yard forms of *marie-galante* from Guatemala and El Salvador are not very different from the *punctatums* of neighbouring areas. The more tree-like forms that are to be found wild in the Lesser Antilles, on the other hand, are generally similar to the cultivated *marie-galantes* of the same region. They are widely different from the wild *punctatums* of the Greater Antilles, which in turn resemble the cultivated and commensal forms of their own race that are to be found in fields and

* Wild lintless diploid species of *Gossypium* are, of course, indigenous in Mexico, and one of them, *G. gossypioides*, was collected by Richmond and also by Ware and Manning, in natural xerophytic scrub on the Pan-American highway 60-80 m. south of Oaxaca City.

house yards nearby. Similarly, *yucatanense* is obviously related to the variable commensal *punctatums* of Yucatan, rather than to the wild forms of other races, and the wild *morrilli* of Sonora can be matched by cultivated forms of the same race from further south, and not by wild forms from other parts of the Americas. Evidently the development of the wild forms was subsequent to the differentiation of the races, and their possession of a group of characters in common must be the consequence of convergent evolution under the selection pressure of similar ecological situations.

Since the wild forms of *G. hirsutum* throw no light on the differentiation of the species, the problem may be approached from a consideration of the relationships between *G. hirsutum* and its nearest relative. *G. hirsutum* is sufficiently close to *G. barbadense* to give a fully fertile hybrid in F_1, though distinct enough to cause extensive genetic breakdown in F_2 and later generations. Since it has been shown above that the most important inter-racial differentiation in *G. hirsutum* is in habit characters, it is reasonable to regard as primitive those forms of the species that are closest to *G. barbadense* in growth form. Habit differentiation in *G. barbadense* is small compared with that in *G. hirsutum*, and all types, even the wild var. *darwinii*, are rather tall, upright shrubs in which the main stem retains its dominance over the lateral branches. This is the form characteristic of the Central American types of race *marie-galante*, and accepting it as primitive, a consistent pattern of differentiation becomes apparent. Within race *marie-galante*, the size and dominance of the main stem has been intensified, giving rise to the large tree-like forms of the Caribbean region. The dominance of the main stem persists in *palmeri*, which has been differentiated by the shortening of the internodes and the establishment of the laciniate leaf. In *richmondi*, *morrilli* and *punctatum*, lateral development has proceeded at the expense of the main stem. In *richmondi* and *punctatum* the stems are flexible, and the plants tend to sprawl under the weight of the crop, whereas in *morrilli* they are stiff and upright. In *latifolium*, early fruiting has been developed, accompanied by a reduction in lateral growth which reaches the limit in some of the early Upland types, in which vegetative growth is confined to the main stem.

Viewed in this way, the position of *yucatanense* is clear. With its small size, prolific lateral growth, and prostrate habit, it is the farthest removed from the *barbadense* type of plant, and fits naturally into the sequence as a specialised derivative of *punctatum*, adapted to an exacting ecological situation.

The conclusions that cultivated forms of *G. hirsutum* are primitive, and that the present races arose by differentiation in cultivation, have important consequences for the ethnologist. Such sharp distinctions could only have been developed in isolation, and it follows that each of the six cultivated races must have arisen in the fields and gardens of an isolated agricultural community. It should therefore be possible to match the six centres of the cultivated races mapped in fig. 1 with six corresponding foci of civilisation.

As has been noted above, the inter-racial variability is for the most part a matter of differentiation in habit characters that are of little or no value to the breeder of modern annual commercial cottons. From the point of view of the future prospects of the species as a crop plant, it is the intra-racial variability that is important, and particularly that within race *latifolium*. This will now be considered.

In intra-racial variability there is a close relationship between diversity and evolutionary success as measured by population size and recent increases in area occupied. Compare for example *palmeri*, which is one of the primary races, and *yucatanense*, which it is suggested is a secondary derivative of *punctatum*, with *punctatum* and *latifolium*. The two former are small in numbers and occupy strictly limited areas, and are very uniform. The two latter are large in numbers and have spread widely in very recent times, and they are extremely diverse throughout their range. The contrast is parallel to that demonstrated by Hutchinson and Stephens (1947) between the wild lintless species of *Gossypium*, with their small populations, relic status, and low variability, and the cultivated linted species, with large populations, wide distribution, and great diversity. The comparison may be taken further. In a survey of the native cottons of Puerto Rico (Hutchinson, 1944) two forms of *punctatum* were found. The typical house yard form was highly variable, whereas the wild "*algodon brujo*," adapted to the specialised ecological conditions of two small, dry coastal areas, was much more uniform. Diversity, in fact, is associated with evolutionary success at all levels of differentiation from the ecotype to the sub-genus.

Evolutionary success implies the achievement of a favourable balance with the selective forces of the environment. A species cannot multiply and spread unless, either on account of the emergence of a specially well fitted genotype or because of the existence of a particularly favourable environment, selective elimination is low enough to allow an increase in numbers. Under such circumstances an increase in variability may be expected (Fisher, 1930). In fact it is success, and the relatively mild impact of selection that success implies, which permits the development of variability. The effects of success are cumulative, since increasing variability means increasing possibilities of adaptive response, and hence of greater success. Moreover, under the low selection pressures that exist under conditions of success, elimination will continue low, and variability will be maintained or increased. This is the situation characteristic of the cultivated cottons. In the newly colonised areas new genotypes of high adaptive value are to be found, but selective elimination has been moderate, the new material has not excluded the old, and variability is consequently high.

These are the conditions to be found where success has been recent and rapid, and are typical of the circumstances of modern crop plants. They do not represent the conditions when the expanding population fills the available habitats, and a new stable state is established. The achievement of stability comes about by an increase in the pressure of selection until elimination matches population increase, and during this phase a reduction in variability may be expected. The best adapted genotypes will survive to the exclusion of less fit material, and the diversity that remains will be assorted between geographical races, or along clines in a continuous population (see examples of old established, wide-ranging species cited by Mayr, 1949). The extreme case is that provided by the development of a highly adapted, uniform race fitted to survive under special and exacting conditions. Examples in *G. hirsutum* are race *yucatanense* in Yucantan and " *algodon brujo* " in Puerto Rico. These, which may be regarded as relics in the making, are the products of rigorous selection in a difficult environment and not, as Stebbins (1949) has suggested, types which " have survived largely in places where competition has been relatively little, and selection not very rigid."

The spread of *G. hirsutum* in the last few centuries is a good example of development under conditions favouring diversification. Fortunately it is so recent and has been studied so intensively. that it is possible to discuss the development of the variability now present in the newly colonised areas in some detail. The processes involved may be illustrated by a consideration of recent changes in habit characters, disease and pest resistance, and lint quality.

Habit changes have gone on in two directions. In *marie-galante*, under the circumstances of perennial cultivation large and tree-like forms have been developed. In *punctatum* on the other hand, though the Central American perennial shrubby habit is the common form throughout the range of the race, annual forms have been developed to meet the special conditions of field crop culture in the French Sudan, and of persistence as a weed (" Hindi " cotton) in the annual *G. barbadense* crops of Egypt and the Sudan. The whole range of habit is to be found in the same area in both instances, the longer lived, shrubby forms predominating where perennial growth is possible, and the early types where the annual habit is enforced. Among " Hindi " types collected from the Egyptian crop of the Sudan, for instance, a wide range of habit is to be found, from something very close to the shrubby house yard types of the rain fed regions of the country to early cropping forms that match the typical " Hindi " weed of Egyptian literature.

In *latifolium*, the potentialities of annual cropping were present in the Central American stock, though most of the types in the new collections are quite capable of persisting for several years. Truly annual forms are represented, however, by the big bolled form from Chiapas. In respect of habit it is probable that present-day collections are not truly representative of the stock of the race. Before the days of machine-made textiles, the demand for locally grown cotton for hand weaving must have been large, and the amount of cotton grown in field crops considerable. It is a fair presumption that the earlier fruiting types suited to such conditions would be more abundant than the long-lived house yard and hedgerow forms tnat predominate in recent collections. The establishment of the Upland crop in the United States, therefore, involved little but the selection of the early long day forms among those already available in Central America. Subsequent changes in habit have involved little more than the continuation of this early trend. In the development of habit characters, therefore, *marie-galante* and *latifolium* may be contrasted with *punctatum*. In the two former recent developments are the natural continuation of earlier trends, whereas in the latter, the emergence of annual types in the newly colonised areas in Africa is a departure from the general line of development of the race.

Differentiation to meet the conditions of new areas has been very important in the field of disease and pest resistance. The development of blackarm resistance in New World cottons acclimatised in the Old World has been traced by Knight and Hutchinson (1950). The basis of all effective resistance was shown to be the gene B_2, which occurs rarely in *punctatum* in the New World. In the Old World it has spread in *punctatum* and has been transferred by hybridisation to *latifolium*, and there spread under the selective pressure of the disease. Moreover, it has been reinforced until a high degree of resistance is attained, on the one hand by the spread of other major genes in the *punctatums* and *latifoliums* of West Africa, and on the other by minor gene accumulation in the *latifoliums* of India.

A similar situation has arisen in respect of the hairiness that imparts jassid resistance (Parnell *et al.*, 1949). Knight (in press) has shown that resistance depends on a major gene reinforced by minor genes. In the New World major genes for hairiness are commoner than major genes for blackarm resistance, but hairiness adequate for real resistance is confined to race *morrilli*, which does not appear to have contributed to the acclimatised cottons of the Old World. The development of resistance by the synthesis of a gene complex consisting of a major gene and a group of minor genes has gone on in the Old World, probably largely independently in south-east Asia, India and Africa, and has reached its greatest development in the virtually jassid immune Cambodias.

High lint quality in *G. hirsutum* may be traced to the high quality stock of *G. barbadense* that gave rise first to the Sea Island, and later to the Egyptian cottons. The distribution of this stock has been traced by Hutchinson and Manning (1945), who showed that long and fairly fine lint is to be found among the primitive variable *G. barbadense* cottons of western South America, and suggested that the Sea Island cottons were selected in a *G. barbadense* stock brought from western South America to the Greater Antilles by the Spaniards, and thence carried by British colonists to the Sea Islands of South Carolina. The high quality of the modern Egyptian cottons is attributable to the contribution of the Sea Islands to their ancestry (see Hutchinson, 1949). In *G. hirsutum* long lint is to be found in both *marie-galante* and *latifolium*. In *marie-galante* there are long staple types in coastal Columbia, which is on the postulated line of spread of long staple *G. barbadense* from western South America. In the West Indies, the long linted form of *marie-galante* has been identified by Hutchinson and Stephens (1944) with the " French," or " small seeded " cotton of the 18th century, and its source traced to Hispaniola, again on the supposed track of the fine linted *barbadense* cottons. High quality in *latifolium* was developed in a number of lines in the south-eastern United States, where the distribution of Upland and Sea Island overlapped. Some long staple Uplands, *e.g.* Meade, are known to have been derived from Sea Island crosses, and it may be suggested that long staple in all New World cottons is founded on genes derived from the long staple *barbadenses* of western South America.

These examples have been taken to illustrate a process that can be observed in many characters. The great range of variability now to be found in characters of importance in newly colonised areas has arisen by the spread in the population of genes that were formerly very rare. In most cases the source can be traced back to the New World, but in some instances, notably blackarm resistance in West African stocks, there seems reason to believe that the variability has been augmented by gene mutation in the new areas.

Though new gene complexes have arisen under selection, it may be concluded that selection pressure has remained relatively low, since the ancestral characters still persist in all but the most carefully bred populations. Fully blackarm susceptible plants are to be found alongside immunes and high level resistants, jassid susceptibles are common in all but the plant breeder's pedigree stocks, and the range of variation in staple length is an ever-present problem in cotton marketing.

The outstanding feature of recent diversification in *G. hirsutum* is, in fact, the synthesis of new characters in areas where they have a high selective value, on a basis of genes that were formerly very rare in the species. This implies free gene exchange through large parts of the expanding population, and has resulted, contrary to expectation on the Vavilov theory, in the development of high variability in peripheral areas. The key to the distribution of variability in crop plants is, in fact, the rate of gene exchange. Given free gene exchange, the assortment of the available variability into races or clines adapted to local conditions proceeds unhindered. Where gene exchange is limited by self fertilisation, or by excessive fragmentation of the expanding population, the development of new adaptive genotypes by recombination will be retarded. Selective elimination will go on in the existing range, however, and the nett result will be a reduction in variability. Hence the Vavilov condition, of diminishing variability from centre to periphery, will arise where spread outruns gene exchange. In cotton, with considerable natural cross pollination and in many areas repeated introductions of material of more than one race, conditions for gene exchange have been particularly favourable, and there is no evidence of diminishing variability in peripheral areas. In an almost universally self-pollinated crop like wheat, on the other hand, it is easy to see that the speed with which man has spread the crop in recent times has been too great to allow of free assortment of the gene content of the species.

Evidently the pollination system in a crop plant has far-reaching effects on its evolutionary prospects, and merits close consideration. Rick (1950) has demonstrated that the tomato, which is self-pollinated in the recently colonised parts of its distribution, is naturally cross-pollinated in its original home, and has given evidence to show that self-pollination arose in response to selection for fruitfulness in the absence of natural pollinating agents. He thus raises the whole question of the history of self-pollination in crop plants, for where self-pollination was imposed following spread into areas where conditions were unfavourable for cross pollination, the Vavilov type of distribution of variability would naturally arise.

These considerations have an important bearing on plant breeding policy, particularly in new areas such as Africa. It is clear that an understanding of the structure and distribution of variability in a crop plant is of great value in the planning of an efficient breeding scheme. A comprehensive survey of variability makes it possible on the one hand to indicate the best sources of material for particular purposes, and on the other, to decide on the most likely areas in which to search for genes to meet new needs. For example, in the *latifoliums*, West African material is of outstanding importance for blackarm resistance, the hairiness that gives resistance to jassids is best developed in the Cambodia group (Philippines and South India), and high quality should be sought in stocks that have been in contact with the Sea Island-Egyptian group of *G. barbadense*. In more general terms, in breeding for the cotton areas of Asia and Africa, disease and pest resistance and local adaptation giving high cropping capacity are more likely to be found among the acclimatised *latifoliums* of the Old World than in fresh collections from the original area of the species.

For plant breeders concerned with the development of efficient strains in areas to which a crop plant has recently been introduced, the demonstration of the importance of high variability and free gene exchange is very significant. In their analysis of the history of blackarm resistance in New World cottons, Knight and Hutchinson (1950) have shown that if the precautions now considered necessary to safeguard the purity of breeding stocks had been taken by those responsible for the early introductions into the Old World, blackarm resistant Uplands would never have arisen. Random interbreeding is too uncertain a system for use in breeding plots, and considerable progress has been made in substituting planned hybridisation for natural crossing in respect of those characters that have been identified and studied.* In general, however, the plant breeder works with stocks of very limited diversity, and the possibilities inherent in highly variable material have scarcely been explored.

In conclusion, the evolutionary prospects of the races of *G. hirsutum* may be assessed. *Yucatanense* has settled down to relic status already. *Palmeri*, *richmondi* and *morrilli* are little short of it. *Marie-galante* achieved some success on the Spanish Main and in Brazil but has passed its peak, and will probably develop little further. *Punctatum* has been very successful in West Africa, and will probably hold its place on the southern border of the Sahara. In range, population size, and variability, however, race *latifolium* outstrips the whole of the rest of the species, and in it most of the future evolutionary development of the species will proceed.

5. SUMMARY

Extensive new collections from the original area of *G. hirsutum* in Central America have made possible a fresh assessment of differentiation within the species. It is shown that an advanced stage of development has been reached, and that the species can be divided into seven morphologically and geographically distinct races. The greater part of the variability in the Central American material is assorted between races, and in four of the seven, intra-racial variability is low. Six of the seven races—*morrilli*, *richmondi*, *palmeri*, *punctatum*, *yucatanense* and *marie-galante*—are perennials, and one—*latifolium*—is in general annual. Only three races—*punctatum*, *marie-galante* and *latifolium*—extend beyond Central America, and the distributions of all seven are consistent with the view that they arose in Central America, and were originally allopatric.

The spread of the three more widely distributed races is discussed, and it is shown that intra-racial variability is closely related to evolutionary success as judged by population size and recent extensions in range. This relationship holds throughout the genus *Gossypium* from the sub-genus down to the ecotype. Evolutionary success is interpreted as the achievement of so favourable a balance with the environment that selection pressures are moderate. Variability will depend on selection pressure on the one hand, and on the rate of gene exchange on the other. The lower the selection pressure, the less the reduction in variability by selective elimination, and the greater the rate of gene exchange, the greater the opportunity for the synthesis of new and valuable genotypes.

* As for example, in Knight's (1946) systematic work in the transfer of genes for blackarm resistance to commercial Egyptian cottons.

The distribution of variability in the widespread races of *G. hirsutum* is discussed, and illustrations are given of the development of diversity in peripheral areas by the synthesis of new characters on the basis of genes that were formerly rare. It is shown that only under conditions of free gene exchange, such as exist in the cottons, could such high variability be maintained throughout the population. This state of affairs is contrasted with that in self-fertilised crop plants, in which it is shown that distribution by man must have outrun gene exchange, and thus inevitably led to the decay of variability in peripheral areas observed by Vavilov. Reference is made to Rick's demonstration of the change from cross- to self-pollination by the tomato when it was introduced into Europe, and it is pointed out that this alone would lead to the Vavilov type of distribution in newly colonised areas.

Knowledge of population structure and the distribution of variability is of great value to the plant breeder. Examples are given, with special reference to cotton breeding in Africa, of the value of knowledge of the distribution of variability in race *latifolium*, and attention is drawn to the importance of such knowledge for the proper planning of plant breeding policy.

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