GENETIC STUDIES ON THE BRACTIOLE CHARACTERS IN AN
INTERSPECIFIC CROSS BETWEEN GOSSYPIUM TOMENTOSUM AND GOSSYPIUM HIRSUTUM

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## TABLE OF CONTENTS

Page
INTRODUCTION ..... 1
REVIEW OF IITERATURE ..... 3
MATERIALS AND METHODS ..... 14
RESULTS AND DISCUSSION ..... 18
Dominances and Heritabilities ..... 18
Population Frequency Distributions and Esti-mates of Minimum Number of Genes Involved
Correlations Between the Characters ..... 2924Recombination of Characters as Shown by
Correlation Diagrams ..... 42
SUMMARY ..... 58
BIBLIOGRAPHY ..... 61

## LIST OF TABLES

I. The means, variances, and ranges of the 14 bractiole characters of the parental populations, G. tomentosum and G. hirsutum19

II. The means, variances, and ranges of the 14
bractiole characters of the $\mathrm{F}_{1}$ and $\mathrm{F}_{2}$ popu
lations of cross between $G$. tōmentosum and
G. hirsutum ..... 20
III. The means, variances, and ranges of the 14 bractiole characters in the backeross to G. hirsutum . . . . . . . . . . . . . . . . . ..... 21
IV. Dominance and heritability estimates for the fourteen characters ..... 22
V. Frequecny distributions for the length of the bractiole ..... 30
VI. Frequency distributions for the width of the bractiole ..... 30
VII. Frequency distributions for the base of the bractiole ..... 31
VIII. Frequency distributions for the number of bractiole teeth ..... 31
IX. Frequency distributions for the length of tooth No. 1 ..... 32
X. Frequency distributions for the length of tooth No. 2 ..... 32
XI. Frequency distributions for the length of tooth No. 3 ..... 33
XII. Frequency distributions for the width of toothNo. 1 . . . . . . . . . . . . . . . . . 33
XIII. Frequency distributions for the width of toothNo. 2 . . . . . . . . . . . . . . . . 34
Table ..... Page
XIV. Frequency distributions for the width of tooth ..... 34
XV. Simple correlation coefficients for the widthof the bractiole with the other nine charac-ters in the parental, $\mathrm{F}_{1}, \mathrm{~F}_{2}$ and backerosspopulations . . . . . . . . . . . . . .37
XVI. Simple correlation coefficients for the base of the bractiole with the other nine charac- ters in the parental, $\mathrm{F}_{1}, \mathrm{~F}_{2}$ and backcross populations ..... 38
XVII. Simple correlation coefficients for the length of tooth No. l with the other nine charac- ters in the parental, $\mathrm{F}_{1}, \mathrm{~F}_{2}$ and backeross populations ..... 39
XVIII. Simple correlation coefficients for the length of tooth No. 2 with the other nine charac- ters in the parental, $\mathrm{F}_{1}, \mathrm{~F}_{2}$ and backeross populations ..... 40
XIX. Simple correlation coefficients for the length of tooth No. 3 with the other nine charac- ters in the parental, $F_{1}, F_{2}$ and backeross populations ..... 41

## LIST OF FIGURES

## Figure

## Page

I. Diagram of a cotton bractiole ......... . . 15
II. Correlations between the base of the bractiole and the width of the bractiole of the two parental and the $F_{2}$ populations48
III. Correlations between the base of the bractiole and the leng th of tooth No. 1 of the two parental and the $F_{2}$ populations . . . . . . .49
IV. Correlations between the base of the bractiole and the length of tooth No. 2 of the two parental and the $F_{2}$ populations .......50
V. Correlations between the base of the bractiole and the leng th of tooth No. 3 of the two parental and the $F_{2}$ populations
VI. Correlations between the width of the bractiole and the length of tooth No. 1 of the two parental and the $F_{2}$ populations . . . . . . 52
VII. Correlations between the width of the bractiole and the length of tooth No. 2 of the two parental and the $F_{2}$ populations . . . . . .53
VIII. Correlations between the width of the bractiole and the length of tooth No. 3 of the two parental and the $F_{2}$ populations
IX. Correlations between the leng th of teeth No. 1 and 2 of the two parental and the $F_{2}$ populations.55
X. Correlations between the length of teeth No. 1 and 3 of the two parental and the $\mathrm{F}_{2}$ populations . . . . . . . . . . . . . . . .56
XI. Correlations between the length of teeth No. 2 and 3 of the two parental and the $F_{2}$ populations . . . . . . . . . . . . . . . . . .

## INTRODUCTION

The taxonomic keys developed by Hutchinson, Silow and Stephens(9) place great emphasis on the characteristics of the bractiole as critera for separating species within the genus Gossypium. Various species within the genus differ greatly in the morphological characteristics of the bractioles developed around the floral parts. Similiarly, the bractioles of the three tetraploid species of Gossypium recognized by Hutchinson et al. are very different. The bractioles of $G$. tomentosum Nuttal are ovate-oblong and are serrated along the upper margin into 8 to 10 coarse teeth, the teeth rarely being as much as thrice as long as broad. The bractioles of $G$. hirsutum Linnaeus are longer than broad and the upper margin is gashed into 7 to 12 long, acuminate teeth which are more than thrice as long as broad. The bractioles of $G$. brabadense are very similar to those of $G$ 。hirsutum. In general, the average bractiole of $G$. hirsutum and $G$. barbadense is about two to three times larger than those of $G$. tomentosum (3).

The firat objective of this investigation was to study the inheritance of fourteen quantitative characters of bractioles in an interspeciric cross between $G$. tomentosum and $\mathrm{G}_{\mathrm{G}}$. hirsutum. The second objective was to determine the genetic and developmental relationships of these characters by correlating the fourteen characters in order to better understand
the relationships between these two species. Attempts were made to determine whether correlations are the result of physiological effects, pleiotrophic genes, or closely linked blocks of genes.

## REVIEW OF LITERATURE

Interspecific crosses have been studied intensively in several genera, primarily in studies to the transfer of certain genes from one species to another by a combination of hybridization, backcrossing, and selection, Allard(1) lists four generalizations on segregation in wide interspecific crosses:
(a) Tremendous diversity of types appear in the $F_{2}$ and later generations as a result of the extreme heterozygosity of interspecific $F_{1}$ hybrids. Each individual in an $F_{2}$ progeny is likely to be different from each other individual in a large number of characters.
(b) Great difficulty is encountered in attempting to account in precise Mendelian terms for inheritance in species crosses. The meiotic processes rarely function with complete normality in interspecific hybrids, so that the segregation of ten does not fit classical Mendelian patterns.
(c) Although segregation in the Fr and later generations produces extremely heterogeneous recombination types, the recombinations that actually appear are by no means a random sample of the total possible recombinations of parental characteristics.
(d) Male gametogenesis is more easily upset by chromosomal or genic disharmonies than female gametogenesis. For this reason, the propagation of hybrids of ten depends on backerossing the $\mathrm{F}_{1}$
as the seed parent to one or the other of the parental species. Skovsted(18) has placed the species of Gossypium into three groups: (a) species with $2 n=26$ from America and the Pacific Islands, (b) species with $2 \mathrm{n}=26$ from Africa, Asia, and Australia, and (c) New World tetraploid species with $2 n=52$ from America and the islands in the Pacific Ocean. Subsequent studies have served to elaborate the relations suggested by Skovsted. However, compared to certain other genetically well known genera, interspecific crosses within the genus Gossypium have not been studied extensively.

Silow(13) reported different degrees of specific divergence within the Asiatic diploid section of the genus Gossypium. Silow found that hybrids between $G$. arboreum and $G$. herbaceum are fully fertile in the $F_{1}$, but showed breakdown in viability in the $F_{2}$. Hybrids between these species and $G$. anomalum are almost sterile.

Gerstel and Phillips(6) studied the allotetraploid segregations of red lethal, red plant, yellow pollen, yellow petal, and leaf shape in the following species combinations: (a) $4 n-$ G. arboreum $\times$ G. herbaceum, (b) $4 n-\underline{G}$. thurberi $\times \underline{G}$. raimondii, (c) Amphiploids between 0ld world cotton and G. anomalum, and (d) G. arboreum $x$ G. thurberi. The general conclusions drawn from the results of these studies were that genetic ratios of a series of synthetic allotetraploids widen rapidly with decreasing cytotaxonomic affinity of the component species. No recognizable tendency of the chromosomes of $G$. arboreum $\times \mathbb{G}$. herbaceum to associate preferentially was observed. This could be interpret-
ed as meaning that the chromosomes of $\underline{G}$. arboreum and $\underline{G}$. herbaceum have remained homologous cytologically.

The amphiploids which were used as the material in this experiment did not produce functional homogenic gametes(RR and rr as ppposed to Rr gametes) with equal frequency. Amphiploids sythesized from the wild American species G. thurberi and G. raimondii, which are very different in morphology and in origin, but both with D genomes, gave approximately a 13 : 1 backcross ratio for the one locus studies. The differences between segregation ratios of the 4 A and the 4 D amphiploids show that amphiploid segregation is much more sensitive to differences in chromosome homology than is $F_{1}$ pairing, since pairing of the chromosomes at metaphase is normal in both $\underline{G}$. arboreum $\times \mathbb{G}$. herbaceum and $\mathbb{G}$. thruberi x G. raimondii hybrids. Amphiploids containing the A and B genomes both from the 0ld World and with high $\mathrm{F}_{1}$ affinity, gave very wide ratios whereas the 2(AD) amphiploid type were almost completely stable.

The New World tetraploid species are differentaiated into thre species between which genetic isolation barriers exist(9). The center of origin of $\underline{G}$. barbadense appears to have been in South America and that of $G$. hirsutum in Southern Mexico and Guatemala. The third species, G. tomentosum, is endemic to the Hawaiian islands. The three tetraploid species intercross freely, giving fully fertile $F_{1}$ hybrids which exhibit considerable hybrid vigour. Skosvted(15) explained meiosis in the $\mathrm{F}_{1}$ 's of crosses involving the tetraploids and found it normal. In the $F_{2}$, however, extensive genetic breakdown occurs, giving rise to unbalanced
low viability. According to Hutchinson(8), Harland has discussed the nature of the species differentiation in the three species and concluded that threre is no evidence for processes other than gene substitution being involved in differentiation of these tetraploids. In crosses involving G. tomentosum, heavy losses in the seeding stage are the rule, and the raising of large progenies in $F_{2}$ and later selfed generations is usually a matter of considerable difficulty. In an $F_{2}$ of $G$. hirsutum var. punctatum X G. tomentosum germination and seedling development were as follows(9):
(a) Seeds with small embryos that failed to germinate.
(b) Seeds with apparently normal embryos that failed to germinate.
(c) Seedlings that failed to expand the cotyledons.
(d) Seedlings that died within three weeks.
(e) Unthrifty seedlings at three weeks old.
(f) Strong seedlings at three weeks old.

The genetic breakdown in the G. tomentosum and G. hirsutum cross began much earlier and was much more serious than in $\underline{G}$. hirsutum $x$ G. barbadense; consequently $G$. tomentosum must be genetically further removed from $G$. hirsutum than is G. barbadense. Comparable data are not available for $G$ 。 barbadense X G. tomentosum, but according to Hutchinson(9), Harland considered G。tomentosum to be nearer to Gobarbadense than to G. hirsutum, and it is possible that breakdown in that hybrid might not be so severe as in the Go hirsutum cross.

Stephens (16) reported that there is considerable selective elimination of the donor parental genotype in interspecific backcrosses involving $G$. hirsutum and G. barbadense. In the fixst
backcross, the elimination, primarily gametic, is operative both in pollen and ovules. The selective elimination can be detected by the significant skewness of specific monofactorial segregation and also by the cumulative tendency for the recurrent parental genotype to be recovered more rapidly than expected as a result of random segregation and recombination. Of four loci which showed selective elimination, two are suspected on independent grounds to be carried on structurally differentiated chromosomes. The results are not explicable by interspecific differentiation based on freely assorting modfier systems, but require some form of internally balanced polygenic complexes. It is considered that the so called polygenic complexes may be structurally differentiated chromosome segments.

From studies of chromosomal translocations in hybrids of the Old World and New World cottons, Gerstel and Sarvella (7) point out that all representatives of $G$. arboreum carry the same chromo-
 mental interchange involving a major portion of a chromosome arm. These data indicate that the chromosomal arrangements of the tetraploids are closer to that of $G$. herbaceum than to that of $G$. arboreum. These cytological results suggest $G$. herbaceum as a common ancester of all three New World species but are by no means conclusive.

Several studies have been made of the inheritance of quantitative characters in interspecific crosses. Worley(18) studied the inheritance of fiber strength in an interspecific cross be-
tween G. hirsutum and G. barbadense. He reported on the $F_{1}$ and first and second segregating generations of a interspecific cross between DPL(G. hirsutum) and Sea Island(G. barbadense). In Worley's material, fiber strength behaved as a quantitative character. Partial dominance of low Pressley index occurred; however, fiber strength at 0.125 inch index lacked dominance. Attempts were made to estimate the number of genes segregating for fiber strength. Parental means differed by 2.81 units of Pressley index and 2.27 units of 0.125 inch strength index. Three methods for estimating minimum number of genes indicated that fiber strength was conditioned by a relatively small number of genes. There appeared to be more genes segregating for 0.125 inch streng th index than for Pressley index. The reliability of the estimates of heritability varied. The third generation $\left(F_{3}\right)$ results were found most reliable in the estimation of heritability. Fifty to sixty per cent of the high strength $\mathrm{F}_{2}$ plants produced high streng th $\mathrm{F}_{3}$ lines.

Kamel(10) studied the inheritance of fiber fineness in the interspecific hybrid $G$. hirsutum $x$ G. barbadense. The material consisted of the parents, $F_{1}, F_{2}$ and $F_{3}$ populations for the interspecific hybrid DPL(G. hirsutum) x Sea Island(G. barbadense). The characters analyzed were fiber wall thickness and perimeter which are the two major components of weight fineness. The arealometer was used in measuring these characteristics. The three fiber properties behave as quantitative characters, although not typical of such characters in all respects. Abnormal segregates with extra fine and thin walled fibers were encounter-
ed in the two segregating generations.
In studying species crosses, mutual association of characters are of interest to the geneticist for understanding the species differences. Collins(4) has divided the mutual relations of characters into three main groups to which he applied the names "physical", "physiological" and "genetic". Physical correlations are those in which the relation is obviouly causal. In many instances correlations of this kind are little more than different names for the saim phenomenon or parts of the same phenomenong as when increased weight is correlated with increased height. In physical language, one of the characters would be dew scribed as a function of the other. Physiological correlations are those where both characters are the result of the same physiom logical tendency as when long internodes in the main stalk are correlated with long internodes in the branches. This may be looked upon as general a tendency to elongated growth that is manifested in different parts of the plants. Genetic correlations cover the large residue of correlations, the nature and caused of which are questions of controversy, but which are associated with the method or mechanism of heredity. An example of this kind correlation is shown in the association of yellow petals and deeply lobed leawes in Egyptian x Upland cotton hybrids.

Anderson(2) in his analysis of recombination products prow duced by the hyorid between Nicotiana alata $x$ N. langsdorfei pointed out that if the recombinations of any two characters are considered, the ones actually observed form, more or less,
an ellipse running diagonally across the correlation rectangle from one parental combination to the other. From his data, Anderson concluded that even in an infinitely large $F_{2}$ population the combinations being studied would fall far short of reaching the upper left-hand and lower right-hand corners of the correlation diagrams, which indicated restrictive segregation.

Kearney(11) studied the inheritance of 39 quantitative characters or grading characters in the parental, $F_{1}, F_{2}$ generations of a cross between Pima, an Egyptian cotton variety, and Holdon, an Upland type. Comparisons of the coefficients of variation for the graded characters showed Holdon to be decidedly the more variable of the parental populations. In a large majority of the characters, the $F_{1}$ was less variable than the parental populations which gave the higher coefficient of variation or standard deviation for the character in question. The $F_{2}$ was more variable than the respective more variable parental population for most of the characters and was significantly more variable than the $F_{1}$ in all but one character. Relatively few bimodal segregations were noted in the $F_{2}$ most characters showing distributions approaching the normal. Kearney concluded that segregation was taking place and that the apparent nonoccurrance of definite ratios in the $F_{2}$ indicated that the characters were each conditioned by several factors. He also pointed out that the relatively small size of the population may have played a part.

Kearney (11) studied the correlations of 39 characters in an Upland-Egyptian cotton hybrid(Pima x Holdon). The coefficients
of correlation were determined for 703 pairs of characters in the second generation of the hybrid of which 93 were probably significant. Many of the correlations are undoubtedly physical or physiological or are of a secondary nature, resulting from the mutual correlation of several characters. Of the 92 paixs of characters which showed a presunably significant correlation in the $F_{2}$, the sign in 66 cases indicated coherence or expression of the characters in the hybrid in the same relation as they were received from the parents. In 27 of the significant correlations, the opposite tendency, disherence, was shown. A few of these disherent correlations obviouly were of a physical or physiological nature. The occurrance of disherent correlations also noted by Collins and Kempton(5) in their study of a hybrid between toesinte and maize, seems to be contrary to any generally recognized principle of heredity.

In a study of the inheritance of fiber strength in an interspecific cross, Worley(18) demonstrated that there were no relationships between fiber strength and seed index, lint density index, lint per cent, and immaturity or shape factor in either in $\mathrm{F}_{2}$ or $\mathrm{F}_{3}$ population. The 0.125 inch strength index showed a significant negative association with wall thickness and perimeter, and highiy significant but low correlation with weight fineness. The correlations between fiber strength and these fiber fineness components were interpreted as being physical in nature. Similiar values were obtained among plants of the parental populations. In the $\mathrm{F}_{2}$, the correlation coefficient between the two measurements of fiber strength was 0.74 and among means of $\mathrm{F}_{3}$ lines
0.62. Both ryalues are highly significantindicating relatively close association between the two strength measurements. However, there were several exceptions to this association among the $80 \mathrm{~F}_{3}$ lines.

A low but significant correlation was found for wall thickness and perimeter by Kamel(10) in his study of the inheritance of fiber fineness in the interspecific hybrid $G$. hirsutum $X$. barbadense, implying little difficulty wauld be encountered in combining the high or low expressions of the two characters, except for large perimeters. High positive and significant corre lations were obtained for weight fineness and its two components. Desirable expressions of weight fineness could be reached through selection of one of its two components or both.

Lewis(12) reported that in a hybrid involving three species of Gossypium the correlation between $F_{2}$ plants and the mean values of their $F_{3}$ progenies was highly significant for leaf index, seed index, and lint strength, length, fineness, and shape, but not significant for lint perimeter and lint index. A high positive correlation between lint fineness and lint shape was found in both the $\mathrm{F}_{2}$ and $\mathrm{F}_{3}$ generations, Which appears to be a developmental correlation.

In summary, segregations in the interspecific crosses within the genus Gossypium are similiar to those reported in other genera. Some differentiation has occurred between the chromosomes as shown by allotetraploid segregations, but the chromosomes of the various species are remarkabiy similiar. In
the $F_{2}$, there is considerable breakdown even in the interspecific crosses between the most closely related species. As part of this breakdown, there is considerable selective elimination, so that all possible combinations are not likely to be recovered even in large populations.

In those instances where genetic studies have been carried out on quantitative characters, the inheritance seems similiar to that in intraspecific crosses; but qualitative characters of ten give skewed ratios in interspecific crosses compared to those obtained in the intraspecific crosses.

Correlations between characters in segregating populations resulting from interspecific crosses are difficult to interpret. They may be due to physical or physiological phenomena or they can be genetic in nature. Even when the correlations are shown to pe genetie, they can be the result of either linkage or pleiotropism. The distinguishing of linkage from pleiotropism could be difficult in an interspeicfic cross if the linkage were close, considering the breakdown that occurs.

MATERIALS AND METHODS

## (1) Strains used:

This investigation was undertaken to obtain a statistical degcription of fourteen characteristics of the bracm tioles in one variety of Gossypium hirsutum, of a collection of the species Gossypium tomentosum and of the $F_{1}$ and $F_{2}$ generations resulting from a cross between these two species and to study the inheritance of these fourteen characters when the two species are crossed. In addition, a population of the backeross to hirsutum was includea. The backeross to tomentosum could not be included because of the difficulty of obtaining flowers of tomentosum.

The seed of the $F_{1}, F_{2}$ and backdross generations used in this study were obtained from Dr. James Meyer of stoneville, Mississippi。 These seed resultec from a cross between a tomentosum plant that Dr. Meyer grew in the greenhouse and 8948, a double haploid plant developed from Deltapine 14.
G. tomentosum rarely flowers outside Hawaii and a population of g. tomentosum comld not be grown in Oklahoma. The plant material of $G$. tomentosum used in this study was collected in its native habitat in Hawiil by Dr. Jimmie B. Smith of the University of Hawail.

## (2) Collection of material:

The bractioles on which the measurements were made were collected on the day the flowers opened, removed from the flowers and mounted on papers.

Wherever possible, the six bractioles from two flowers of each plant were collected and measured in all populations. In some cases only the three bractioles from one flower were used.
(3) Definition of characters under study:

In order to obtain quantitative descriptions of the bractioles, measurements on 14 characters were made on the bractioles. These 14 characters are diagramed in Figure $I$ and described as follows:


Figure I :- Diagram of a cotton bractiole, showing location of the measurements: length of bractiole ( $a-b$ ), width of bract. $(d-e)$, base of bract. $(b-c)$, leng th of tooth (No. 1, $\mathrm{a}-\mathrm{c}$, No. 2, $\mathrm{j}-\mathrm{k}$ ), width of tooth(No. 1, h-i, No. 2, f-g).

The length of bractiole: the distance from the top of tooth $l$ to the bottom of the bractiole ( $a$ to $b$ in Figure I).

The width of bractiole: the width of the bractiole at its
widest point(d to e in Figure I).
The length of the base of bractiole: the distance from the base of tooth 1 to the bottom point of the bractiole ( $c$ to $h$ in Figure I).

The number of teeth: the total number of teeth on the bractiole.

The length of the teeth: the distance from the top of the tooth to the center of the tooth where it connects with the bractiole( $\mathbf{j}-\underline{k}, \quad \underline{a}-\underline{c}$, in Figure I).

The width of the teeth: the distance across the widest part of the tooth where it connects to the bractiole.
the length and width of five teeth, as shown in Figure I, were studied.
(4) Statistical analysis of quantitative characters:

The total number of plants used in the study were 30 in both of the parental species, 16 in $\mathrm{F}_{1}, 158$ in $\mathrm{F}_{2}$ and 38 in the backcross to hirsutum. The total number of bractioles measured was 100 in both tomentosum and hirsutum, 87 in the $F_{1}$, 925 in the $\mathrm{F}_{2}$ and 228 in the backcross.

Since the characters under investigation are quantitative in nature, the genetic segregation was studied in terms of heritability and estimation of minimum number of genes, as determined by the formula presented by Sinnott et al.(17). The method used here to estimate the heritability is simply to divide the average variance of the non-segregating generations $\left(F_{1}, P_{1}\right.$ and $\left.P_{2}\right)$ by the variance of the $F_{2}$ generation and sub-
tract this ratio from 1.00. The formula is as:

$$
\text { Heritability }=1-\frac{\delta_{E_{1}}^{2}+\delta_{P_{1}}^{2}+\delta_{P_{2}}^{2} / 3}{\delta_{F_{2}}^{2}}
$$

The relative dominance values were calculated here as being:

$$
\text { Dominance }=\frac{\mathrm{F}_{1}-\left(\mathrm{X}_{\mathrm{p}_{1}}+\mathrm{X}_{\mathrm{p} 2}\right) / 2}{\left(\mathrm{X}_{\mathrm{p} 1}+\mathrm{X}_{\mathrm{p} 2}\right) / 2} .
$$

This method of calculation expresses dominance in terms of a decimal fraction, which may be positive or negative depending on which parent shows dominance. This estimation may not be entirely accurate since the tomentosum plants were grown on the arid shores of Hawaii and the other populations were grown on fertile farm land in Oklahoma.

Correlation coefficients were calculated on all possible combinations of the fourteen characters studied in order to determine whether the same genes or closely linked blocks of genes affect more than one character of the bractiole. In order to see the extent of recombination, correlation diagrams were made for 10 combinations of characters for which the parental species were most clearly distinguished from each other.

RESULTS AND DISCUSSIONS

In order to describe the nature of the inheritance of the fourteen bractiole characters under study, the degrees of dominance, hertiabilities, and the frequency distributions were studied, and the minimum number of genes involved were estimated. The means, variances, coefficients of variation, and ranges are presented in Tables I- III.

These data show that all parts of the bractiole of hirsutum are larger than those of tomentosum. On the basis of the variances, the strain of hirsutum appears to be much more variable than tomentosum. However, when the differences in the sizes of the characters are taken into consideration, by use of coefficient of variability, the difference between the relative variabilities of the two species is somewhat different. For the characters that describe the size of the bractiole, namely, length of bractiole, width of the bractiole, base of the bractiole, and number of teeth, hirsutum remains the more variable parent. On the other hand, tomentosum is much the more variable parent for the length and width of all bractiole teeth except tooth 1. The coefficient of variability for the length of tooth 1 is very similiar in both species.

## (1) Dominances and Heritabilities:

The estimates of the dominances and heritabilities of

TABLE I
THE MEANS, VARIANGES AND RANGES FOR 14 BRACTIOLE
CHARACTERS OF THE PARENTAL POPULATIONS, G. TOMENTOSUM AND G. HIRSUTUM

| Characters | Tom. |  |  |  | Hir. |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Means | $\delta^{2}$ | C.V. | Ranges | Means | $\delta^{2}$ | C.V. | Ranges |
| Length of bract. | 14.31 | 2.89 | 11.8 | 1.1-1.9 | 41.31 | 17.89 | 10.2 | 2.9-5.9 |
| Width of bract. | 11.47 | 1.71 | 11.4 | 0.9-1.4 | 32.29 | 7.72 | 8.6 | 1.2-3.4 |
| Base of bract. | 11.67 | 1.73 | 20.0 | 0.9-1.6 | 26.32 | 5.75 | 9.1 | 1.5-3.0 |
| Number of teeth | 8.26 | 2.43 | 18.8 | 5-13 | 12.15 | 2.19 | 12.2 | 9-15 |
| Leng th of tooth No. 1 | 2.56 | 0.56 | 28.3 | 0.1-0.4 | 24.86 | 9.54 | 12.4 | 1.1-2.8 |
| No. 2 | 1.00 | 0.21 | 46.1 | 0.0-0.2 | 14.29 | 13.17 | 25.4 | 0.6-1.2 |
| No. 3 | 0.25 | 0.21 | 118.4 | 0.0-0.1 | 7.47 | 10.82 | 4.0 | 0.2-1.8 |
| No. 4 | 1.12 | 1.02 | 90.1 | 0.0-0.1 | 15.05 | 11.90 | 22.9 | 0.5-2.1 |
| No. 5 | 0.36 | 1.14 | 297.0 | 0.0-0.2 | 7.71 | 14.51 | 49.4 | 0.0-1.6 |
| Width of tooth No. 1 | 2.82 | 0.85 | 100.0 | 0.1-0.5 | 7.37 | 1.12 | 14.4 | 0.0-1.6 |
| No. 2 | 1.53 | 0.75 | 57.0 | 0.0-0.3 | 6.59 | 1.93 | 21.1 | 0.2-0.8 |
| No. 3 | 0.41 | 0.77 | 214.0 | 0.0-0.3 | 5.29 | 1.93 | 26.3 | 0.2-1.0 |
| No. 4 | 1.38 | 0.62 | 57.2 | 0.0-0.4 | 6.38 | 1.29 | 17.9 | 0.2-0.9 |
| No. 5 | 0.30 | 0.29 | 180.0 | 0.0-0.3 | 5.01 | 1.41 | 23.8 | 0.2-0.6 |

TABLE II
THE MEANS, VARIANCES AND RANGES FOR 14 BRACTIOLE CHARACTERS OF THE F $\mathrm{F}_{1}$ AND $\mathrm{F}_{2}$ POPULATIONS OF CROSS BETWEEN G. TOMENTOSUM AND G. HIRSUTUM

| Characters | $\mathrm{F}_{1}$ |  |  |  |  | F2 |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Means | $5^{5}$ | $\mathrm{C} \mathrm{V}^{2}$ | Ranges | Means | $\delta^{2}$ | C.V. | Ranges |
| Length of bract. | 34.23 | 11.28 | 10.6 | 2.8-4.2 | 33.82 | 34.29 | 17.5 | $2.4-5.7$ |
| Width of bract. | 21.59 | 6.96 | 12.2 | 1.7-2.8 | 20.46 | 12.61 | 17.4 | 1.4-2.9 |
| Base of bract. | 21.59 | 7.96 | 12.9 | 1.5-2.6 | 20.57 | 13.69 | 18.0 | 1.4-3.0 |
| Number of teeth | 12.25 | 3.24 | 14.7 | 9-16 | 11.08 | 9.73 | 28.2 | 5-20 |
| Leng th of tooth No. 1 | 12.69 | 7.34 | 21.4 | 0.9-1.8 | 13.12 | 16.72 | 31.1 | 0.1-3.4 |
| No. 2 | 5.78 | 3.06 | 30.3 | 0.1-0.9 | 5.31 | 11.83 | 64.8 | 0.1-2.6 |
| No. 3 | 1.26 | 2.43 | 123.8 | 0.0-0.5 | 1.36 | 3.06 | 127.8 | 0.0-1.2 |
| No. 4 | 5.71 | 4.62 | 37.7 | 0.0-1.0 | 5.50 | 11.32 | 60.2 = | $0.0-2.2$ |
| No. 5 | 1.11 | 5.58 | 218.0 | 0.0-0.5 | 1.39 | 4.00 | 143.8 | 0.0-1.9 |
| Width of tooth No. 1 | 4.95 | 0.65 | 14.3 | 0.3-0.8 | 4.61 | 1.87 | 29.7 | 0.2-0.8 |
| No. 2 | 3.67 | 1.27 | 30.8 | 0.1-0.6 | 3.23 | 2.46 | 46.7 | 0.0-0.9 |
| No. 3 | 1.20 | 1.61 | 105.8 | 0.0-0.5 | 1.15 | 1.87 | 119.1 | 0.0-0.5 |
| No. 4 | 3.76 | 1.84 | 36.2 | 0.1-0.7 | 3.20 | 2.68 | 51.3 | 0.0-0. 5 |
| No. 5 | 0.82 | 0.96 | 119.5 | 0.0-0.4 | 0.99 | 1.27 | 114.1 | 0.0-0.5 |

## TABLE III

THE MEANS, VARIANGES AND RANGES OF THE 14 BRACTIOLE CHARACTERS IN THE BACKCROSS TO G. HIRSUTUM

| Characters | Means | $8^{2}$ | C.V. ${ }_{\text {R }}$ Ranges |  |
| :---: | :---: | :---: | :---: | :---: |
| Length of bract. | 40.73 | 41.91 | 15.9 | 2.0-5.6 |
| Width of bract. | 25.08 | 13.23 | 14.7 | 1.2-3.6 |
| Base of bract. | 23.40 | 11.12 | 14.2 | 1.1-3.2 |
| Number of teeth | 13.30 | 6.12 | 18.6 | 5-20 |
| Length of tooth No. 1 | 17.32 | 24.48 | 28.8 | 0.0-3.4 |
| No. 2 | 8.84 | 10.25 | 40.0 | 0.0-0.2 |
| No. 3 | 2.33 | 6.59 | 112.0 | 0.0-1.3 |
| No. 4 | 9.07 | 10.57 | 45.0 | 0.0-2.2 |
| No. 5 | 2.16 | 6.73 | 120.4 | 0.0-1.3 |
| Width of tooth No. 1 | 5.11 | 1.25 | 23.5 | 0.2-0.9 |
| No. 2 | 4.19 | 1.45 | 30.3 | 0.1-0.7 |
| No. 3 | 1.79 | 2.48 | 88.3 | 0.0-0.5 |
| No. 4 | 4.21 | 2.34 | 36.3 | 0.0-0.8 |
| No. 5 | 1.26 | 1.12 | 88.1 | 0.0-0.4 |

the fourteen characters are presented in Table IV.

TABLE IV
DOMINANCE AND HERITABILITY ESTIMATES
FOR THE FOURTEEN CHARACTERS

| Characters | Herit. (\%) | Dominance |  |
| :---: | :---: | :---: | :---: |
|  |  | Degree | Dom. ${ }^{\text {P }}$ |
| Length of bract. | 0.694 | 0.2666 | Hir. |
| Width of bract. | 0.567 | -0.0132 | Tom. |
| Base of bract. | 0.746 | 0.1367 | Hir. |
| Number of teeth | 0.755 | 0.2060 | Hir. |
| Length of tooth |  |  |  |
| No. 1 | 0.781 | -0.0740 | Tom. |
| No. 2 | 0.534 | -0.1209 | Tom. |
| No. 3 | -0.461 | -0.6500 | Tom. |
| No. 4 | 0.452 | -0.1772 | Tom. |
| Width of tooth | -0.790 | -0.6407 | Tom. |
| No. 1 | -0.740 | -0.0980 | Tom. |
| No. 2 | 0.464 | -0.0960 | Tom. |
| No. 3 | 0.326 | -0.5780 | Tom. |
| No. 4 | 0.534 | -0.0300 | Tom. |
| NO. 5 | 0.224 | -0.6910 | Tom. |

That considerable genetic segregation is occuring in the $F_{2}$ is shown by the ranges in the $F_{2}$ compared to the $F_{1}$. As shown the $F_{1}$ has a range of 0.0 to 0.5 for the leng th of tooth 3 while the $\mathrm{F}_{2}$ ranges from 0.0 to 1.5 .

The formula used to detect the presence of dominance results in a positive value if the larger parent is dominant and negative value if the smaller parent is dominant. As shown by the data in Table IV, tomentosum exhibited some degree of dominance for eleven of the 34 characters measured. Characters associated with the bractiole and not the teeth were the only ones for which hirsutum showed dominance. Tomentosum shows a degree of dominance for the length and
width of all teeth. Since no replication could be carried out on these measurements, no statements of significance can be made. However, the strong similarity of teeth occupying equivalent positions on the bractiole suggests that tooth 4 might serve as a replicate for tooth 2 and that tooth 5 might serve as a replicate for tooth 3. The high degree of dominance exhibited by tomentosum for length and width of teeth 3 and 5 and for length of teeth 2 and 4 are undoubtedly highly significant.

An interesting aspect of these data is the progressively increasing dominance from the apex to the base of the bractiole. For instance, as shown in Table IV, the dominances for length of teeth 1,2 , and 3 are $-0.0740,-0.1209$ and -0.6500 respectively. The behavior of teeth 4 and 5 is similiar to teeth 2 and 3 respectively.

These data show that except for the length of teeth 3 and 5, all characters considered are highly heritable. The heritability values for the other characters indicate that these characters are highly heritable and that they offer excellent material for studying quantitative inheritance in interspecific crosses. The consistancy of the heritabilities for characters occupying comparable positions on the bractiole adds reliability to the estimates. Because of the similiarities of tooth 2 with tooth 4 and of tooth 3 with tooth 5 and because teeth 2 and 3 occupy positions on the bractiole complementary to those of teeth 4 and 5 respectively, teeth 4 and 5 appear to be controlled by the
same processes as teeth 2 and 3 and will not be given further consideration.

The negative heritability of the width of tooth 1 is due to the extreme variability of tomentosum for this character, for which no explaination is offered. On the other hand, the negative heritabilities of the length of teeth 3 and 5 can probably be explained on the basis of the high degree of dominance exhibited by the tomentosum and the tendency of variances to be proportional to the magnitude of the means. The G. hirsutum parent has a rather large mean and a large variance as shown in Table I. This large component of variation results in an excessively large estimated environmental variance and a negative genetic variance. If the variance of the $G$. hirsutum is omitted and the calculation of the heritability is carried out on the $\mathrm{F}_{1}$ and $\mathrm{F}_{2}$ variances, then the heritabilities for the leng th of tooth 3 and 5 become 0.21 and -0.46 respectively, which is probably more realistic.
(2) Population frequency distributions and estimates of minimum number of genes involved:

In order to estimate the number of genes controlling each character, frequency distributions for each character are presented in Tables $V$ - XIV, and discussed in the following sections.
a. Length of bractiole:

The frequency distributions presented in Table $V$ show that the two parental populations are well separated for this character and that no overlapping occurs between the populations. The hirsutum parent has much larger bractioles but is much more
variable than tomentosum. The position of the $F_{1}$ is somewhat intermediate between the two parents, although it is entirely within the range of the hirsutum parent. However, the mode of the $F_{1}$ is toward the lower part of the hirsutum parent; and the low dominance value presented in Table IV indicates an intermediate position of the mean.

The $F_{2}$ distribution is typical for a quantitative character. The mode is approximately the same as that of the $F_{1}$ and the curve is rather smooth across its distribution. Calculation of the number of gene controlling this character by the formula presented by Sinnott et al.(17) indicates that not fewer than 4 pairs are involved. If this estimation is correct then at least 256 individuals would normally be necessary for a tomentosum parental type segregant to occur.
b. Width of bractiole:

As shown in Table VI, the frequency destributions of the two parental populations are similiar to those for the length of the bractiole. However, the width of the frequencymistribution curve for the $\mathrm{F}_{2}$ is much narrower than that for the length of the bractiole, indicating that a larger number of genes are involved for this characters. In fact, the curve is no wider than that of the $F_{1}$, but there is a higher frequency of the extreme classes of the $F_{1}$ in the $F_{2}$. Using the formula of Sinnott et al., it appears that at least 10 pars are controlling bractiole width in this cross. c. Base of bractiole:

As shown in Table VII, there is a small amount of overlapping
between the two parents. The $F_{1}$ distribution appears to be similiar to that of the hirsutum parent except the entire curve is shifted about 0.5 units to the left, indicating the $F_{1}$ is somewhat intermediate between the two parents. The $F_{2}$ curve is somewhat wider than that of the other populations, but the apparent tomentosum-parent-type segregants are most likely environmental variants of an intermediate type. The least estimate of the numbers of genes involved is five pairs. However, this estimate is undoubtedly low because of the apparent dominance exhibited by the hirsutum parent.
d. Number of teeth:

As shown in Table VIII, tomentosum tends to have fewer teeth than hirsutum, although the two parental populations overlap strongly. The $F_{1}$ is similiar to the hirsutum parent for this character, as indicated by both the frequency distributions and the dominance value presented in Table IV. Types similiar to both parental types are found among the segregants. The formula presented by sinnott et al. indicates less than one pair distinguishes the two species. However, the $F_{2}$ curve suggests that transgressive segregation has taken place and that tomentosum has genes for number of teeth that hirsutum does not carry even though hirsutum seems to have a higher number of teeth than tomentosum.
e. Length of tooth 1 :

The two species appear to be well separated on the basis of the length of tooth 1 . However, there is considerable varia-
tion within each species and hirsutum is particularly variable. The distribution of $F_{I}$ is clearly intermediate, substantiating the small dominance value presented in Table IV. These data indicate that at least 7 pair of genes are controlling the length of tooth 1 .
f. Length of tooth 2:

As shown in Table $X$, the two species are well separated for length of tooth 2. The $F_{1}$ seems to be approxmately interm mediate but overlaps both parents. The comparison of the $\mathrm{F}_{1}$ mean with the two parental means substantiates the dominance estimate presented in Table IV. The distribution of the $F_{2}$ population substantiates also the dominance estinate since there is a clustering of $F_{2}$ individuals about the tomentosum parental class. With this degree of dominance, any estimate of gene number will be low. However, on the basis of the formula used, a minimum of three pairs are involved. Considering the dominance involved, several more than three pairs must be involved.
g. Length of tooth 3:

The two parental species are not as clearly distinguished on the basis of the length of tooth 3 as they are for the other characters. Furthermore; the high degree of dominance calculated by a comparison of the $F_{1}$ mean with the parental means is substantiated by the preponderance of the $F_{2}$ population falling into the same classes as the tomentosum parent. This high degree of dominance invalidates any estimates of gene number made by the formula of Sinnott, et al.(17). On the other hand, the data from both $\mathrm{F}_{2}$ and the backeross populations suggest that two genes
probably control the length of tooth 3 . One of these genes appears to have a high degree of dominance and to be epistatic to the second one. The second gene appears to have more of a modifying effect and to give a general reduction to the tooth of individuals carrying two recessive alleles for the first gene.
h. Width of tooth 2:

As shown in Table XII, there is hlgh degree of overlapping between the two parents; and the $F_{1}$ distribution seems to approgimate being intermediate between the two parental populations. The extreme overlapping between the parents here makes this character less desirable than the length of the teeth for studying quantitative inheritance in an interspecific cross. Since the width of the distribution curve of the $\mathrm{F}_{2}$ is only slightly wider than the $F_{1}$, it appears that the two parents differ by a number of genes for this character. on the basis of the data presented here, it appears two and three pairs of genes are involved.
i. Width of tooth ? :

The data presented in Table XIII, show that the two parents overdap concideralby and that the $F_{1}$ is approximately intermediate between the two parents. The frequency distribution of the $F_{2}$ extends completely across those of both parents, indicating a rather small mumex of genes. The small gene number hypothesis Is substantiated by an estimate of between 2 and 3 genes, which is very close to the estimates for several of the other charac-
ters.
j. Width of tooth 3:

As shown by the data in Table XIV, the two parents overlap considerably and both are rather variable for this character. The relative positions of the $F_{1}$ and $F_{2}$ frequency distributions in Table XIV substantiate the dominance of tomentosum presented in Table IV. The rather narrow $\mathrm{F}_{2}$ frequency distribution indicates that a relative large number of partially dominant genes are controlling this character.
(3) Correlations between the characters:

Generally, the evolutionary change in one character is associated with a change in other. The association of the change in one character with others is both interesting in itself and significant for the interpretation of many evolutionary phenomena. Pleiotropy and gene association are the best known genetic mechanisms by which correlated changes in different characters of the same organism may be conditioned. The presence or absence of segregation between two correlated characters would provide good criteria for distinguishing between these two phenomena. Linked genes could give rise to recombinant types. If the correlation were due to pleiotropy, no recombinant types would be possib]

Since several striking differences distinguish the bractioles of $G$. hirsutum and $G$. tomentosum, a study of the correlations of some of these differences would be important to an understanding of the genetic differences and evolution of $G$. hirsutum and G. tomentosum.

TABLE V
FREQUENCY DISTRIBUTIONS FOR THE IENGTH OF BRACTIOIE

| $\begin{aligned} & 1.0-1.6-2.1-2.6-3.1-3.6-4.1-4.6-5.1-5.6- \\ & 1.5 \quad 2.02 .5 \\ & 1.0 \\ & \hline \end{aligned}$ |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Tom. | 66 | 34 |  |  |  |  |  |  |  |  | 100 |
| Hir. |  |  |  | 1 | 5 | 18 | 36 | 28 | 8 | 5 | 100 |
| $\mathrm{F}_{1}$ |  |  |  | 8 | 47 | 25 | 5 | 3 |  |  | 87 |
| $\mathrm{F}_{2}$ |  | 1 | 8 | 25 | 46 | 56 | 13 | 6 | 2 | 1 | 158 |
| B.C. |  |  | 1 | 1 | 5 | 8 | 16 | 6 | 1 |  | 38 |

TABLE VI
FREQUENCY DISTRIBUTIONS FOR THE WIDTH OF BRACTIOLE

|  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Tom. | 56 | 44 |  |  |  |  |  |  |  |  | 100 |
| Hir. |  |  | 2 | 8 | 20 | 31 | 19 | 11 | 9 | 2 | 100 |
| $\mathrm{F}_{1}$ |  | 3 | 24 | 40 | 16 | 4 |  |  |  |  | 87 |
| $\mathrm{F}_{2}$ |  | 26 | 54 | 50 | 24 | 4 |  |  |  |  | 158 |
| B.C. |  | 2 | 3 | 9 | 12 | 8 | 3 | 1 |  |  | 38 |

TABIE VII
FREQUENCY DISTRIBUTIONS FOR IHE BASE OF BRACTIOIE


TABLE VIII
FREQUENCY DISTRIBUTIONS FOR THE NUMBER OF TEETH OF BRACTIOLE

|  | $\begin{aligned} & 5- \\ & \hline \end{aligned}$ | 7- | $\begin{array}{r} 9- \\ 10 \\ \hline \end{array}$ | $\begin{array}{r} 11- \\ 12 \\ \hline \end{array}$ | $\begin{array}{r} 13 \\ 14 \\ \hline \end{array}$ | $\begin{aligned} & 15- \\ & 16 \\ & \hline \end{aligned}$ | $\begin{aligned} & 17- \\ & 18 \end{aligned}$ | $\begin{array}{r} 192 \\ 20 \\ \hline \end{array}$ | Total |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Tom. | 2 | 49 | 21 | 4 | 2 |  |  |  | 100 |
| Hir. |  |  | 25 | 51 | 19 | 5 |  |  | 100 |
| $\mathrm{F}_{1}$ |  |  | 12 | 32 | 32 | 11 |  |  | 87 |
| $\mathrm{F}_{2}$ | 8 | 24 | 39 | 41 | 25 | 15 | 5 | 1 | 158 |
| B.C. |  |  | 3 | 8 | 13 | 8 | 4 | 1 | 38 |

## TABLE IX

FREQUENCY DISTRIBUTIONS FOR THE LENGTH OF TOOTH 1

| $\begin{aligned} & 0.0-0.4-0.7-1.0-1.3-1.6-1.4-2.2-2.5-2.8-3.1 \\ & 0.30 .6 \quad 0.21 .21 .5 \quad 1.8 \\ & \hline \end{aligned}$ |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Tom. | 88 | 12 |  |  |  |  |  |  |  |  |  | 100 |
| Hir. |  |  |  |  | 1 | 2 | 19 | 35 | 25 | 17 | 3 | 100 |
| $\mathrm{F}_{1}$ |  |  | 8 | 29 | 32 | 13 |  |  |  |  |  | 87 |
| $\mathrm{F}_{2}$ | 2 | 5 | 18 | 52 | 38 | 33 | 5 | 4 | 0 | 1 | 1 | 158 |
| B.C. | 1 | 0 | 2 | 4 | 7 | 8 | 10 | 4 | 2 | 1 |  | 38 |

## TABLE X

FREQUENCY DISTRIBUTIONS FOR THE LENGTH OF TOOTH 2

|  | $0.0-0.3-0.6-0.9-1.2-1.5-1.8-2.1-2.4$ |  |  |  |  |  |  |  |  |  |  |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
|  | 0.2 | 0.5 | 0.8 | 1.1 | 1.4 | 1.7 | 2.0 | 2.3 | 2.6 | Total |  |
| Tom. | 100 |  |  |  |  |  |  |  |  |  |  |
| Hir. |  | 1 | 3 | 22 | 26 | 20 | 16 | 11 | 1 | 100 |  |
| F $_{1}$ | 5 | 26 | 37 | 4 |  |  |  |  |  | 87 |  |
| $\mathrm{~F}_{2}$ | 16 | 54 | 63 | 12 | 3 | 1 | 1 | 1 | 1 | 158 |  |
| B.C. | 1 | 6 | 10 | 12 | 5 | 3 | 1 |  |  | 38 |  |

## TABIE XI

FREQUENCY DISTRIBUTIONS FOR THE LENGTH OF TOOTH 3

|  | $\begin{aligned} & 0.0- \\ & 0.1 \\ & \hline \end{aligned}$ | $\begin{aligned} & 0.2 \\ & 0.3 \\ & \hline \end{aligned}$ | $\begin{array}{r} 0.4 \\ 0.5 \\ \hline \end{array}$ | $2.7$ | $0.2$ | $\begin{aligned} & 0 \\ & 0 \\ & \hline \end{aligned}$ |  |  |  | TO. |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Tom. | 100 |  |  |  |  |  |  |  |  | 100 |
| Hir. |  |  | 16 | 29 | 25 | 18 | 4 | 5 | 3 | 100 |
| $\mathrm{F}_{1}$ | 63 | 15 | 9 |  |  |  |  |  |  | 87 |
| $\mathrm{F}_{2}$ | 90 | 49 | 12 | 4 | 2 | 2 | 1 |  |  | 158 |
| B.C. | 18 | 10 | 6 | 2 | 1 | 0 | 1 |  |  | 38 |

TABLE XII
FREQUENCY DISTRIBUTIONS FOR IHE WIDIH OF TOOTH 1

|  | 0.0 | 0.1 | 0.2 | 0.3 | 0.4 | 0.5 | 0.6 | 0.7 | 0.8 | 0.9 | 1.0 |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| Tom. | 9 | 39 | 52 | 6 | 4 |  |  |  |  | 100 |  |
| Hir. |  |  | 7 | 12 | 41 | 15 | 3 | 2 |  | 100 |  |
| F $_{1}$ |  |  | 1 | 10 | 60 | 14 | 2 | 1 |  | 87 |  |
| $F_{2}$ | 2 | 22 | 30 | 53 | 32 | 15 | 4 |  | 158 |  |  |
| B.C. | 1 | 4 | 10 | 14 | 6 | 4 | 2 | 1 | 38 |  |  |

TABLE XIII
FREQUENCY DISTRIBUTIONS FOR THE WIDTH OF TOOTH 2

|  | 0.0 | 0.1 | 0.2 | 0.3 | 0.4 | 0.5 | 0.6 | 0.7 | 0.8 | 0.2 | Total |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| Tom. 13 | 36 | 39 | 12 |  |  |  |  |  |  | 100 |  |
| Fir. |  |  | 6 | 14 | 27 | 24 | 20 | 6 | 3 | 100 |  |
| $\mathrm{~F}_{1}$ | 12 | 12 | 17 | 36 | 16 | 5 |  |  |  | 87 |  |
| $\mathrm{~F}_{2}$ | 2 | 4 | 20 | 46 | 54 | 24 | 4 | 1 | 2 | 1 | 158 |
| BiC. | 1 | 3 | 5 | 14 | 10 | 4 | 1 |  |  | 38 |  |

TABLE XIV
FREQUENCY DISTRIBUTIONS FOR THE WIDTH OF TOOTH 3

|  | 0.0 | 0.1 | 0.2 | 0.3 | 0.4 | 0.5 | 0.6 | 0.7 | 0.8 | 0.2 | 1.0 TO. |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| Tom. 76 | 14 | 9 | 1 |  |  |  |  |  |  |  |  |
| His. |  |  | 6 | 15 | 38 | 10 | 6 | 5 | 4 | 3 |  |
| $\mathrm{~F}_{1}$ | 32 | 28 | 13 | 7 | 5 | 2 |  |  |  |  |  |
| $\mathrm{~F}_{2}$ | 11 | 57 | 53 | 33 | 2 | 2 |  |  |  |  |  |
| B.C. 12 | 6 | 7 | 8 | 4 | 1 |  |  |  |  |  |  |

All possible combinations of simple correlations were computed for the 14 characters measured. However, from the standpoint of recombination of characters, interpretation of most of the correlation pairs seemed highly speculative because of the tendency for slight overlapping between the two parental populations. Consequently, the correlations presented here are limited to all combinations of the base of the bractiole, width of the bractiole, and the length and width of teeth 1 , 2 and 3.

These correlation coefficients are complicated in that nearly as many characters were correlated in the hirsutum parent as were correlated in the $F_{2}$ generation, which indicates environment must play a substantial role in the development of the bractioles.

## a. Width of the bractiole:

As shown in Table XV, the width of the bractiole is correlated with all characters in the $F_{2}$ except the width of tooth 3 . Essentially the same correlations are found for the hirsutum parent. However, in the hirsutum parental population, the width of the bractiole is correlated with the width of tooth 3 , is not correlated with the width of tooth 2 .

In the tomentosum parental population, the length of tooth 2 is the only character with which the width of the bractiole is correlated.

## b. Base of the bractiole:

As shown on Table XVI, the base of the bractiole shows a significant positive correlation with only 4 characters in the $\mathrm{F}_{2}$. Likewise, there are only a few significant correlations in the $F_{1}$ and tomentosum-parental populations. On the other hand, most of the characters were significantly correlated in the hirsutum parent, making any intrepretation of the $F_{2}$ difficult. In the $\mathrm{F}_{2}$ generation, the base of the bractiole was negatively correlated with the number of teeth. The base of the bractiole was correlated with the length of the bractiole and with the width of the bractiole.

## c. Length of tooth 1:

As shown in Table XVII, the length of tooth 1 is highly correlated with all other characters in the $\mathrm{F}_{2}$ except the number of teeth. The length of tooth 1 was negatively correlated with length of tooth 3 in the tomentosum parent. In the hirsutum population, these two characters showed a significantly positive correlation. These results show that the length of tooth 1 is associate with big bractioles and big teeth. However, in hirsutum the size of tooth 3 apparently is not associated with the size of tooth 1 . These results show that the cross has induced variables into the population that were not in the parental populations and that these variables affect the whole bractiole except tooth number in the same direction as they do the leng th of tooth 1 . d. Length of tooth 2:

Except for the base of the bractiole and the width of

## TABLE XV

SIMPIE CORRELATION COEFFICIENTS FOR THE WIDTH OF THE BRACTIOLE WITH THE OTHER NINE CHARACTERS IN THE PARENTAL, $F_{1}, F_{2}$ AND BACKCROSS POPULATIONS

| Correlated pairs | Tom. | Hir. | $\mathrm{F}_{1}$ | $\mathrm{F}_{2}$ | B.C. |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Length of Bract. | .213* | .551** | .402** | .447** | .633** 1/ |
| Base of Bract. | . 167 | .324** | .197** | . $430 * *$ | .183** |
| Number of teeth | .386** | .374** | . 175 | . $304 * *$ | .566** |
| Length of tooth No. 1 | . 177 | .443** | . 101 | .270** | .396** |
| No. 2 | .211** | .491** | . 144 | .180** | .307** |
| No. 3 | . 054 | . 127 | . 109 | .115** | .292** |
| Width of tooth No. 1 | -. 077 | . 4 +7** | . 170 | .378** | .480** |
| No. 2 | .160 | . 158 | . 102 | .270** | . $493 * *$ |
| Na. 3 | . 040 | . 212 * | . 034 | . 017 | .175* |

1/ $\begin{aligned} & * \\ & * * \text { significant at } \\ & \text { significant at } \\ & \text { 1\% }\end{aligned}$ level

SIMPLE CORRELATION COEFFICIENTS FOR THE. BASE OF THE BRACTIOLE WITH THE OTHER NINE CHARACERS IN THE PARENTAL, $\mathrm{F}_{1}, \mathrm{~F}_{2}$ AND BACKCROSS POPULATIONS

| Correlated pairs | Tom. | Hir. | $\mathrm{F}_{1}$ | $\mathrm{F}_{2}$ | B.C. |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Length of Bract. | . 900 ** | .698** | .630** | .676** | . $705 * *$ |
| Width of Bract. | . 213* | . $324 * *$ | . $197 *$ | . $430 * *$ | . $184 * *$ |
| Number of teeth | -.195* | .197* | . 168 | -. 088 * | .106 |
| Length of tooth No. 1 | . $347 * *$ | . 182 | .134 | .117** | .294** |
| No. 2 | .107 | .245* | .206* | . 009 | .227** |
| No. 3 | --. 122 | . 151 | .148 | . 030 | .139* |
| Width of tooth No. 1 | . 088 | .290** | . 203 | . $115 * *$ | . 307** |
| No. 2 | -. 004 | . 415 ** | . 014 | . 052 | .340** |
| No. 3 | -. 019 | . 197* | .054 | -. 019 | .146 |

## TABIE XVII

SIMPLE CORRELATION COEFFICIENTS FOR THE IENGTH OF TOOTH NO: 1 WITH THE OTHER NINE CHARACTERS IN THE PARENTAL, FI, $F_{2}$ AND BACKCROSS POPULATIONS

| $\begin{gathered} \text { Correlated } \\ \text { pairs } \end{gathered}$ | Tomen | Hir. $\mathrm{F}_{1}$ | $\mathrm{F}_{2}$ | B.C. |
| :---: | :---: | :---: | :---: | :---: |
| Length of Bract. | .661** | .817** .568* | . 729** | . $776 * *$ |
| Width of Bract. | . 177 | . 44 3** . 101 | .270** | . 369 ** |
| Base of Bract. | . 347 ** | .182 .134 | .117* | . 294 |
| Number of teeth | . 001 | . $017-.150$ | . 037 | .133 |
| Length of tooth No. 2 | . 028 | . 415 **.361** | . 447 ** | . $442 * *$ |
| No. 3 | -.270** | . $212 * *-.019$ | . 225 ** | .164* |
| Width of tooth No. 1 | . 003 | .491** . 059 | .254** | . 443 ** |
| No. 2 | . 008 | . 124 .311** | .102** | .268** |
| No. 3 | -. 174 | $.143-176$ | .107** | . 126 |

## TABIE XVIII

SIMPLE CORRELATION COEFFICIENTS FOR THE IENGTH OF TOOTH NO. 2 WITH THE OTHER NINE CHARACTERS IN THE PARENTAL, FI, $F_{2}$ AND BACKCROSS POPULATIONS

| Correlated pairs | Tom. | Hir. $\mathrm{F}_{1}$ | $\mathrm{F}_{2}$ | B.C. |
| :---: | :---: | :---: | :---: | :---: |
| Length of Bract. | . 075 | . 443 ** .323** | . 340** | . $468 * *$ |
| Width of Bract. | .211** | . $491 * * .144$ | . 180 ** | . $307 * *$ |
| Base of Bract. | . 107 | .245**.206** | . 009 | .227** |
| Number of teeth | . 136 | . $234 * *-.114$ | .256** | .319** |
| Length of tooth No. 1 | . 028 | .415**/.361** | . $447 * *$ | . $442 * *$ |
| No. 3 | . 046 | . $234 * * .032$ | .389** | . $292 * *$ |
| Width of tooth No. 1 | -. 226** | . $223 * *-.074$ | . 018 | .272** |
| No. 2 | . $517 * *$ | . 593**.095 | .301** | .269** |
| No. 3 | -. 072 | $.106-.025$ | .264** | . $247 * *$ |

TABLE XIX
SIMPLE CORRELATION COEFFICIENTS FOR THE LENGTH OF TOOTH NO. 3 WITH THE OTHER NINE CHARACTERS IN THE PARENTAL, F ${ }_{1} 9$
$\mathrm{~F}_{2}$ AND BACKCROSS POPULATIONS

| Correlated pairs | Tom. | Hir. | $\mathrm{F}_{1}$ | $\mathrm{F}_{2}$ | B.C. |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Length of Bract. | - . 22s* | . 24 ** | . 081 | . $133 * *$ | . $195 * *$ |
| Width of Bract. | . 054 | . 127 | . 109 | . 715 ** | .292** |
| Base of Bract. | -. 122 | . 151 | . 148 | -. 030 | . $139 *$ |
| Number of teeth | . 485 ** | .234* | . 385 ** | .302** | . 489 ** |
| Length of tooth No. 1 | -.270** | .212* | . 019 | .225** | .164* |
| No. 2 | . 046 | .234* | . 032 | . 389 ** | . 292** |
| Width of tooth No. 1 | -. 038 | . 760 * | -. $237^{*}$ | -.099* | . .064 |
| No. 2 | .044 | . 149 | -. 118 | . 036 | . 133 |
| No. 3 | . 540* | .406** | .673** | . $547 * *$ | .652** |

tooth 1, the length of tooth 2 was highly correlated with all characters in the $\mathrm{F}_{2}$. Only the width of the bractiole and the width of tooth 1 were correlated in hirsutum. Here it appears that segregation in the $F_{2}$ has resulted in added variation, which affects most of the parts of the bractiole but not the base of the bractiole and the width of tooth 1 .
e. Length of tooth 3:

As shown in Table XIX, the length of tooth 3 is correlated with all characters except the base of the bractiole, and the widths of teeth 2 and 4. In the hirsutum population, the same relationships were found except the leng th of tooth 3 was not correlated with the width of the bractiole. These results show that tooth 3 must develop rather independent of tooth 2 .
(4) Recombination of characters as shown by correlation diagrams: Gossypium tomentosum and $G$. hirsutum are considered to be the most distantly related of the tetraploid species of gossypium. Consequently, in order to get additional information on the comparative genetics of these distantly related species, studies were made of the amount of recombination occuring between five of the quantitative characters under consideration. The characters studied in this section are the five for which the parents appear to be most distinct. These characters are the width of the bractiole, base of the bractiole, and the lengths of teeth 1,2 and of 3 . The correlation diagrams for all combinations of these characters are presented in Figures II to XI and the results are considered in the following sections.
a. Base of the bractiole and width of the bractiole:

As shown by the data diagramed in Figure II, G. hirsutum the G. tomentosum are well distinguished on the basis of both the base and the width of the bractiole. The $\mathrm{F}_{2}$ population is rather intermediate for the base of the bractiole, but like the $F_{1}$ many of the $F_{2}$ individuals are similiar to the hirsubum parent for the base of the bractiole size. From the data presented in figure II and the distribution of the $F_{I}$ data on the characters in Tables VI and VII, a few $\mathrm{F}_{2}$ individuals with a base of the bractiole greater than would be expected for the hirsutum population can be distinguished. Considering the number of genes estimated to be involved, recombination of the genes appears to be rather free. However, the number of genes involved is so large that the new recombinant types, particularly the extrene, occur in low frequency. In addition to gene number restricting recombination, linikage also may be involved.
b. Base of bractiole and length of tooth 1:

As shown by the data presented in Figure III, the recombination between these two characters is similiar to that between the two just discussed, although somewhat leas restrictive. As shown by these data, the $\mathrm{F}_{2}$ population is intermediate between the two parental species, but overlaps buth parental populations considerably fox base of the bractiole and overlaps hirsutum for the length of tooth 2. A comparisor of the distributions and variances of the $F_{2}$ with those of the parents and the $F_{1}$ indicates recombination occur more freely between these two characters than it dows between the base of the bractiole and the width
of the bractiole. The greater freedom of recombination between these characters might indicate less linkage. On the other hand, the length of tooth $l$ appears to be controlled by fewer genes than is the width of the bractiole, thus allowing more freedom of recombination. Another possible explanation is that several of the genes controlling the base of the bractiole size are also involved in controlling the width of the bractiole resulting in a certain degree of physiological correlation. However, since the length of tooth $l$ is an expression of the degree of serration of the outer edge of the bractiole, tooth length might be expectec to show less physiological association than would be expected for the width of the bractiole with base of the bractiole.
c. Base of the bractiole and length of tooth 2 :

As shown by the data presented in Figure IV, Table VII and Table X , recombination between these two characters is similiar to that between the base of the bractiole and the length of tooth 1. However, the two populations are less widely separated on the basis of the length of tooth 2 than on the length of tooth 1. A few of the individuals which fell in the lower right of the correlation diagram appear to represent recombinations.
d. Base of the bractiole and length of tooth 3:

The recombination between the base of the bractiole and the length of tooth 3 is similiar to that between the base of the bractiole and the length of tooth 2, as shown by the data dia-
gramed in Figure V. Considering the number of genes involved, these results show rather clearly that recombination of genes controlling these characters is rather free. However, the number of genes controlling length of tooth 3 appears to be smaller which may partially explain the apparently greater recombina* tion between these two character.
e. Width of the practiole and length of tooth 1:

As shown by the data in Figure VI, recombination is simiw liar to that between the base of the bractiole and the length of tooth 1 .
f. Width of bractiole and length of tooth 2 :

The $\mathrm{F}_{2}$ and parental populations are presented in Figure VII. The pattern of recombination between these two characters is similiar to that between the base of the bractiole and the lengt of tooth 2. The hirsutum population does not overlap the tomentosum population for these two characters. The $F_{2}$ is intermediate between the two parents, no individual overlaps the to mentosum parental population for these two characters and only one individual overlaps the hirsutum population. A few individuals in the upper left corner of the graph and a few in the lower right corner of the figure may represent recombinants. These data indicate that recombination between these characters is small but that it does occur.
g. Width of the practiole ang length of tooth 3:

As show in Figure VIII, the $F_{2}$ population is approximately intermediate between the two parents. It is difficult to determ
mine whether recombination is occuring for these two characters. However, again there are a few individuals falling in the lower right and a few in the upper left corners of the diagram that appear to represent recombinant types.
h. Length of tooth 1 and length of tooth 2 :

As shown by the arrangement of the data diagramed in Figure IX, recombination between the length of tooth 1 and length of tooth 2 is rather limited when the frequency distributions for the length of these teeth in the $F_{1}$ (table IX to $X$ ) are taken into consideration. Only one individual in the upper left can be suspected as being a recombinant type rather than some intermediate for both characters. The arrangement of these three populations in an ellipse diagonally across the figure indicates strongly that recombination between these two characters is very limited. It appears that either many of the same genes control these characters or that the genes controlling these two characters are very closely linked.
i. Length of tooth 1 and length of tooth 3:

From the data presented in Figure $X$ and the distribution of the $F_{1}$ and parental populations which were shown in Tables $X$ and XI, the genes controlling the lengths of teeth 2 and 3 are similiar to those controlling the lengths of teeth 1 and 3 . However, the variability in hirsutum for these characters makes the detection of recombinant types difficult.
j. Length of tooth 2 and length of tooth 3:

As shown by the arrangement of the data in Figure $X I$, the
dominance of the tomentosum parent for the length of tooth 3 is evident. These data indicate the amount of genetic recombination occruing between these two characters is rather limited, although certain individuals show that there has been a certain degree of recombination.

In summary, the data diagramed and discussed in this section indicate that a large number of gene pairs distinguish $G$. hirsutum from Ge tomentosum for bractiole characteristics and that although recombination is restricted, it does occur. The apparent recome bination between the characters indicates that at least some of the parts of the bractiole are affected by different genese On the other hand, the correlations and diagrams show that rew combination is not completely free and indicates that at least some genes may affect more than one part of the bractiole. The minimum numbers of genes estimated to be controlling the various characters and the recombination involved indicates that $G$. tomentosum and $G$. hirsutum differ by a large number of gene pairs for these bractiole characters.

FIGURE II
CORRELATIONS BETWEEN THE BASE OF THE BRACTIOLE AND THE WIDTH OF THE BRACTIOLE OF THE TWO PARENTAL AND THE $F_{2}$ POPULATIONS


[^0]FIGURE III
CORRELATIONS BETWEEN THE BASE OF THE BRACTIOLE AND THE LENGTH OF TOOTH NO. 1 OF THE TWO PARENTAL AND THE $\mathrm{F}_{2}$ POPULATIONS

Length of tooth No. 1

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| $3.4-3.5$, $\Delta$ |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 3.2-3.3 $\Delta$ |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 3.0-3.1 $\Delta$ - $\Delta$ |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 2.2-2.3 (1) (1) (1) (9) (8) (6) (3) (3) (1)3 8 - |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 2.0-2.1 (1) (2) (6) (12) (9) (2) (5) (2) (2) $^{\text {(2) }}$ (2) |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1.8-1.9 (7) (2) (2) (3) (8) (5) (3) (3) (1) (1) |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1.6-1.7 (1) (1) (1) (4) (3) (3) (2) (1) |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1.4-1. 5 <br> 2 <br> 4 <br> (1) <br> (1) <br> (1) <br> (4) <br> (2) <br> (1) |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1.2-1.3 4 41 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1.0-1.1 20 23 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 0.8-0.9 4 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

FIGURE IV
CORRELATIONS BETWEEN THE BASE OF THE BRACTIOLE AND THE LENGTH OF TOOTH NO. 2 OF THE TWO PARENTAL AND THE $\mathrm{F}_{2}$ POPFFATIONS


FIGURE V
CORRELATTONS BETWEEN THE BASE OF THE BRACTIOIE AND THE LENGGTH OF TOOTH NO. 3 OF THE TWO PARENTAL AND THE $\mathrm{F}_{2}$ POPULATIONS


FIGURE VI
CORRELATIONS BETWEEN THE WIDTH OF THE BRACTIOLE AND THE LENGTH OF TOOTH NO. 1 OF THE TWO PARENATAL AND THE $\mathrm{F}_{2}$ POPULATIONS


FIGURE VII
CORRELATIONS BETWEEN THE WIDTH OF THE BRACIIOLE AND THE LENGTH OF TOOTH NO. 2 OF THE TWO PARENTAL AND THE $F_{2}$ POPULATIONS


FIGURE VIII
CORRELATIONS BETWEEN THE WIDTH OF THE BRACTIOLE AND THE LENGTH OF TOOTH NO. 3 OF THE TWO PARENTAL AND THE $\mathrm{F}_{2}$ POPULATIONS


FIGURE IX
CORRELATIONS BETWEEN THE LENGTH OF TOOTH NO． 1 AND THE LENGTH OF TOOTH NO． 2 OF THE TWO PARENTAL AND THE F2 $\quad$ POPULATIONS

Length of tooth No． 2

| Length of 0.0 tooth $\mathrm{HO}_{2} 2$ | O．1－0 0.2 0.2 | ．3－0．5 $0.4 \quad 0.6$ | $.5-0.7-$ <br> $.6 \quad 0.8$ | 0．9－ | $1.1-1$. 1.2 1.3 | 1.5 1.6 | 1.7 1.8 | $1.9-$ 2.0 | 2.1 | －2．3 | 2.5 2.6 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 3．1－3．2 |  |  |  |  |  |  | A |  |  | $\triangle$ |  |
| 2．9－3．0 |  |  | $\triangle$ |  | $\triangle$ | B | Q | $\triangle$ | $\triangle$ |  | $\triangle$ |
| 2．7－2．8 |  |  |  |  | （ ${ }^{\text {B }}$ | $\triangle$ | 今 | 合 | $\triangle$ |  |  |
| 2．5－2．6 |  | $\triangle$ | 2 | 13 | 2 8 | （20） | 金 | 会 | $\triangle$ |  |  |
| 2．3－2．4 |  | $\triangle$ | $\triangle$ B |  | 今 0 | － 4 | B | $\triangle$ |  |  |  |
| 2．1－2．2 |  |  |  | （1）$\lambda$ | （2）5 | $\triangle$ | $\triangle$ |  |  |  |  |
| 1．9－2．0 | （1） |  |  | （1）2 | （1）${ }^{\text {d }} \triangle$ | $\triangle$ | $\triangle$ |  |  |  |  |
| 1．7－1．8 |  | （1）（4） | （4）（6） | （2） |  |  |  |  |  |  |  |
| 1．5－1．6 |  | （7）（10） | （c）（b） | （2） |  |  |  |  |  |  |  |
| 1．3－1．4（1） | （3）（3） | （8）（17） | （7）（8） | （4） |  |  |  |  |  |  |  |
| 1．1－1．2 | （6） | （4）（4） | （4） （4）$^{4}$ |  |  |  |  |  |  |  |  |
| 0．9－1．0（1） | （3） | （8）（4） | （4）（2） | （1） |  |  |  |  |  | \} |  |
| 0．7－0．8 | （2） | （5）（2） | （2） |  |  |  |  |  |  |  |  |
| 0．5－0．6 | （1） | （2）（1） | （1） |  |  |  |  |  |  |  |  |
| 0．3－0．4 8 | 48 |  |  |  |  |  |  |  |  |  |  |
| 0．1－0．2 4 |  |  |  |  |  |  |  |  |  |  |  |

FIGURE $X$
CORRELATIONS BETWEEN THE LENGTH OF TEETH NO. 1
AND 3 OF THE TWO PARENTAL AND THE $F_{2}$ POPULATIONS
Length of tooth No. 1


## FIGURE XI

CORRELATIONS BETWEEN THE LENGTH OF TEETH NO. 2 AND 3 OF THE TWO PARENTAL AND THE $F_{2}$ POPULATIONS


## SUMMARY AND CONCIUSIONS

A study was made of the inheritance of fourteen morphological characters of the bractiole in an interspecific cross between $G$. tomentosum and $G$. hirsutum. The fourteen characters are designated as the length, width, and base of the bractiole, the number of teeth, and the lengths and widths of teeth 1,2 , 3, 4 and 5. The data presented show that for the characters that discribe the size of the practiole, namely, the length, width and base of the bractiole, and the number of teeth, hirsutum is the more variable parent. On the other hand, tomentosum is much the more variable parent for the lengths and widths of all bractiole teeth except tooth 1 .

Tomentosum exhibited dominance for the width of the bractiole and for both the lengths and widths of all teeth. Characters associated with the bractiole and not the teeth were the only ones for which hirsutum showed dominance. The data also show a progressively increasing dominance from the apex to the base of the bractiole.

The data show all the characters considered are highly heritable, except the length of teeth 3 and 5 which showed a negative heritability. However, considerable genetic segregation did occur for these two characters in the Fi as shown by the variability of the $F_{2}$ compared to the $F_{1}$. The nega-
tive heritability is probably due to the extreme variability of hirsutum for these characters.

The data on the segregation of the bractiole characters indicate that at least 4 pairs of genes control the length of the bractiole, that at least 10 pairs control the bractiole width, and that at least 5 pairs control the base of the bractiole. The data indicateless than one pair of genes distinguish the two species for the number of teeth, but transgressive segregation for this character indicates that the two species must be distinguished by more than a single pair of genes. The data also show at least 7 pairs of genes control the length of tooth 1, that at least 3 pairs control the length of tooth 2, that at least two pairs control the leng th of tooth 3 , and that at least 2 to 3 pairs control the widths of teeth 1 and 2. The data indicate that a relatively large number of partially dominant genes control the width of tooth 3 .

All possible combinations of simple correlations were computed for the 14 characters in order to estimate the degree of genetic differentiation between the two species. The correlation coefficients are complicated in terms of heredity in that nearly as many characters were correlated in the hirsutum parent as were correlated in the $\mathrm{F}_{2}$ generation, which indicates the environment must play a substantial role in the development of the bractioles.

For additional information on the comparative genetics of these two related species, studies of recombination were made
between the following five characters: the width of the bractiole, the base of the bractiole, and the lengths of teeth 1, 2 and 3. In view of the numbers of genes estimated to be involved, these data show that recombination of the genes appears to be rather free but that the number of genes involved is so large that the new recombinant types occur in low. frequency. In some cases, it is difficult to determine whether recombination is occurring between the two characters. In addition to gene number restricting recombination, linkage may also be involved, since the number of genes is so large.

In conclusion, all characters studied appear to be controlled by several pairs of genes. Since some recombination of characters does occur, at least part of the genes concerned with the bractiole characters affect only part of the bractiole characters. These observations show that many different pairs of genes controlling the bractiole characters separate $G$. hirsutum and $G$. tomentosum. Therefore, the bractiole characters appear to be reliable taxonomic criteria.

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[^0]:    $\square$ represents the $G$ tomentosum parent, $\triangle$ represents the Ge hirsutum parent and represents the $\vec{F}_{2}$ population.

