

EVIDENCE ON CHROMOSOME HOMOLOGY AND GENE HOMOLOGY IN THE AMPHIDIPOID NEW WORLD COTTONS

By R. A. SILOW,* *Formerly of the Empire Cotton Growing Corporation, Cotton Research Station, Trinidad, B.W.I.*

That the New World tetraploid cultivated cottons (*Gossypium hirsutum* L. and *G. barbadense* L.) arose by amphidiploidy following hybridization between ancestral Asiatic and American diploid species was first suggested by Skovsted (1934, 1937) on the basis of his observations on the extent and nature of chromosome pairing in species hybrids. More recently, colchicine treatment of the sterile hybrids between present-day representatives of these two diploid groups has resulted in the experimental synthesis of similar amphidiploids (Harland, 1940; Beasley, 1940, 1942), and the fact that they give partially fertile hybrids with the New World tetraploids gives strong support to Skovsted's hypothesis. Support from genetic sources has also been adduced by the demonstration that one of the two anthocyanin loci in the New World tetraploids is homologous with the anthocyanin locus in the diploid Asiatic species (R_2) (Harland, 1935), whilst the other is homologous with that in the diploid American species (R_1)† (Silow, 1940; Harland & Atteck, 1941*a*). Phenogenetic developmental studies of the several leaf-shape patterns existent in the genus (Stephens, 1944*a*) also add their weight to the sum total of evidence indicating the allopolyploid nature of the New World cottons. Further confirmation of this hypothesis is given below by the demonstration that the duplicate anthocyanin loci are carried on duplicated chromosome segments.

DUPLICATE LINKAGE GROUPS

It has been known for some time that R_1 and a gene for cluster habit are linked; estimates of the cross-over value range from 13.9 to 19.6%:

Source	No. of plants involved	Cross-over percentage	Authority
Coupling, backcross	540	13.9	Harland (1934)
Coupling, backcross	140	17.1	Neely (1942)
Coupling, F_2	1004	18.5	Neely (1942)
Repulsion, backcross, female	1370	14.1	Own data
Repulsion, backcross, male	245	19.6	Own data

Linkage data involving R_2 and *short branch*, a habit character similar to *cluster*, have recently been collected, in a coupling backcross of (Red Sea Island normal \times Pima green *short branch*) \varnothing to Pima green *short branch*, which gave:

Normal		Short branch		Total
Red	Green	Red	Green	
41	7	3	45	96

Crossing-over = 10.4%.

* The Blandy Experimental Farm, University of Virginia.

† In our revised scheme of gene nomenclature in cotton (Hutchinson & Silow, 1939), the cultivated Old World diploid cottons are taken as a basis, and genes which occur in them, or at loci in the New World tetraploids proven homologous, printed in italics. Genes in the tetraploid species, apart from members at loci homologous with those in the Asiatic diploids, are printed in Clarendon type.

Though further data are required before a reliable estimate of the cross-over value can be given, there can be little doubt that the linkage is of much the same intensity as that between R_1 and cluster.

The homology of the anthocyanin loci has been adequately indicated by the demonstration of their respective homologies in the heterologous species, and the similarity of the two habit phenotypes, together with the parallelism in linkage relations, is sufficient to put the homologies of the chromosome segments beyond doubt. This being established, some idea of the degree of gene differentiation in the two genomes may be obtained from a study of the alleles occurring at the homologous loci.

THE TWO ANTHOCYANIN LOCI

Many distinctive patterns of anthocyanin distribution on the plant exist in cotton, and each of them behaves as a unit complex in inheritance. Most of those which occur in the New World tetraploid cottons have been studied, and can be referred to alleles at one or other of the two loci to which reference has already been made. At the R_1 locus only two alleles are known, red-leaf spotless and green-leaf spotless (Harland, 1932). At the R_2 locus several alleles occur (Harland, 1929, 1937; Hutchinson & Silow, 1939)—one red-leaf type, and four or five green-leaf types differing in size of accompanying red petal spot, vegetative red and petal spot being pleiotropic effects of the alleles. No allele is common to both series, except possibly a basal gene for green leaf and petal spot weak or absent. Even the two red-leaf types may be distinguished by differences in the finer details of anthocyanin pattern, such as the intensity of red on vegetative parts, distribution of anthocyanin in the calyx, and the fact that only one of them has a red corolla. Duplicates, in the more commonly accepted usage implying identity of expression, do not therefore exist. Even when the additional alleles which have been described at the homologous loci in the presumptive parental diploid groups are also taken into account—three alleles at R_1 in the wild American diploid species (Silow, 1940; Harland & Atteck, 1941*a*) and fourteen at R_2 in the cultivated Old World species (Silow & Yu, 1942)—there are still no identical duplicates. Nevertheless, exactly the same type of variation exists in the two series—differences in both distribution and intensity of anthocyanin in stem, leaf, petiole, bracts, calyx, corolla, and androecium.

It has been demonstrated that the evolution of species in this genus has been accomplished primarily by allele substitution (Harland, 1936; Silow, 1944). The occurrence of so many different anthocyanin genes affords an opportunity, unparalleled elsewhere, for determining whether there has been any evolutionary divergence between the R_1 and R_2 loci over the long period of time which has elapsed since they were first separated into the New and Old World. So far as the two major groups of diploid species corresponding to this geographic separation are concerned, there is a somewhat greater range of variation in the Old World, but this is undoubtedly the result of a comparison between a group of well-known and widely cultivated forms with a collection of lesser-known species with extremely limited populations. There are certainly no indications of any fundamental divergence between the loci concerned, for various pattern associations in the possible range of combinations of pleiotropic effects appear to be distributed quite at random between them. This applies equally to the same two loci in the amphidiploids, though here there are very slight indications of the beginnings of a functional divergence between the loci at the speciation level. In *G. barbadense* it is the R_2 locus almost entirely

which is concerned in anthocyanin pigmentation, the commonest phenotype being determined by the various green-leaf red petal spot alleles of this series, and the very occasional red-leaf forms by a higher member of this same series. Only in the very restricted var. *darwinii** is the occasional red plant body determined by a gene at R_1 . In *G. hirsutum* as a whole, green-leaf spotless is undoubtedly the most common form. In the Upland section (typical *G. hirsutum*) a red-leaf form, although rather infrequent, is by no means uncommon in certain crop populations, and the allele responsible is invariably located at R_1 ; on the other hand, a single green-leaf, large red petal spot type has much the same low frequency of occurrence, and this gene is at R_2 . The infrequency of lower spot alleles at this locus in the Uplands appears to be determined primarily by mutation pressure of the genotype (Harland, 1937). In the other two varieties of the species (vars. *punctatum* and *marie-galante*) such lower spot alleles at this locus do occur, though less frequently than spotless, and a red leaf, in this case also at R_2 , is occasionally found.

THE TWO HABIT CHARACTERS

Short branch is a modification of the fruiting branch system which occurs occasionally in *G. barbadense*. It has been described, illustrated and investigated by Kearney (1930) in American-Egyptian Pima cotton. The following description is largely based on that of Kearney, and refers to his strain known as 'Reddin short branch'. The fruiting sympodia, which on a normal plant bear from three to six or more nodes, are here reduced to a single developed internode, at the apex of which are borne from one to three flowers. Where only one flower is borne, the appearance is that of a greatly elongated pedicel growing directly from a node of the main stem, but the occasional occurrence of a small bractlet below the flower shows that the structure cannot be regarded as a simple pedicel. Where additional flowers are borne, they develop from accessory buds at the apex of the reduced sympodium. Occasionally there is some fasciation, the pedicels of two or three flowers being fused together. Frequently two or three of these reduced sympodia arise from the same node of the main stem, the additional ones presumably by development from an axillary bud and/or accessory buds, in addition to the one which develops from the single extra-axillary bud from which the fruiting branch at each node of the main stem normally develops.

Several **cluster** or semi-cluster varieties of Upland cotton, *G. hirsutum*, are or have been in cultivation in the United States. The designation **cluster** also refers to the fruiting habit. Exactly the same verbal description as for *short branch* is applicable (illustration in Neely, 1942), though in general the reduction of the sympodium is more extreme in the case of **cluster**. Thus the fruiting branch itself is often extremely short, and the peduncles of the two to four flowers which are borne at its apex often so much reduced that the flowers may occur as a compact cluster within a single set of bracteoles (instead of being each invested by a set of three bracteoles), or even within a single calyx ring.

Published references to the inheritance of *short branch* and of **cluster** refer only to crosses with normal within the respective species in which each abnormality occurs. In crosses with Pima normal, *short branch* shows monofactorial segregation, with an intermediate heterozygote with the number of internodes on flowering branches reduced to two or three (Kearney, 1930). **Cluster** has been reported to behave as a simple recessive

* Classification following Hutchinson (in press).

in some varietal crosses within *hirsutum* (Thadani, 1923; Texas workers, 1928; Neely, 1942), but in others modifier differences lead to blending inheritance between **cluster** and normal in F_2 (Harland, 1939).

To obtain information on the interrelationship of the two mutants, *short branch* and **cluster** were intercrossed, and the F_1 , which was phenotypically very nearly normal, was selfed. On the basis of general interspecific genetic studies in the genus (Harland, 1936; Silow, 1944), extensive minor gene segregation was to be expected in such a cross. Accordingly, the F_2 showed complete intergradation from typical short branch or cluster types to a few fully normal plants. Of 145 plants grown, 139 were short branch, cluster, or combined features of both types, or were obviously heterozygous for one or other mutant; some of these approached normal fairly closely, the majority of their sympodia having four to six internodes, but showing tendencies to short branch or cluster in the possession of occasional sympodia with clusters of two or more flowers at the apex, or showing fasciation. Only the six remaining plants were fully normal. Such a segregation suggested that the genes for *short branch* and **cluster** were independent, in which case, with incomplete dominance of normal, a ratio of 15 affected : 1 normal was expected, or 136 : 9 in a population of 145 plants. To confirm that the non-affected plants were not pseudo-normal by accumulation of modifiers, which would have implied allelomorphism of the main genes concerned, they and six of the least affected plants were tested by crossing each to both a normal *hirsutum* strain and a normal *barbadense* strain, in order partially to re-establish the respective species backgrounds, and thus permit fuller expression of the mutant genes if present. In each of the twenty-four outcross progenies, three plants were selfed, and twenty plants in each of the seventy-two families grown. This material showed that all six of the slightly affected segregates, and two of the six apparent normals in the original F_2 carried a *short branch* or **cluster** gene, but it left no room for doubt that the remaining four plants tested were fully normal, since absolutely no sign of reduced fruiting branch habit was seen in their progeny. The occurrence of such homozygous normals confirms that *short branch* in *barbadense* and **cluster** in *hirsutum* are definitely not allelomorphic, and that normal alleles are carried at the **cluster** locus in the short branch strain, and at the *short branch* locus in the cluster strain. There is no conclusive evidence that the abnormalities are due to identical mutant genes at the two loci concerned, but the differences exhibited by them in the respective species in which they occur are just the type which experience with transference of other characters from one species of cotton to another would lead one to expect if they were so. This likelihood is supported by the fact that in an F_2 of Egyptian *short branch* \times Upland normal, some of the non-normal segregates were of very definite Upland cluster phenotype.

Reduced fruiting branches have not been recorded at all in the Asiatic diploid species, though they characterize some of the American wild diploids—*aridum*, *armourianum*, and *harknessii*, and, to a lesser extent, *vaimondii*. However, neither the **cluster** nor the *short branch* mechanism appears to be concerned in them, since the following hybrids all showed normal fruiting branches (unpublished data of J. B. Hutchinson):

<i>aridum</i>	×	} the cluster strain
(<i>harknessii</i> \times <i>armourianum</i>) F_1	×	
<i>vaimondii</i>	×	
<i>aridum</i>	×	} the <i>short branch</i> strain
<i>vaimondii</i>	×	

It therefore appears probable that the present-day occurrence of **cluster** and *short branch* in the New World cultivated species must be attributed to mutation since the initiation of amphidiploidy.

DISCUSSION

The two anthocyanin loci and the two fruiting-habit loci are so clearly examples of duplication that the two independent but similar linkages involving these characters may justifiably be regarded as genetic evidence of homologous chromosome segments. Their recognition as such affords an opportunity for discussion of the genetic mechanisms concerned in the origin and evolution of amphidiploidy. It is a general implication in the literature that the factorial polymery determined by polyploidy leads to 'masking', a normal allele at any particular locus being able to 'cover' a recessive, not only at the same locus, but also at the duplicated (homologous) locus. Preponderantly recessive deleterious mutants are thereby sheltered from natural selection, resulting in a 'progressive deterioration of the germ-plasm' (Dobzhansky, 1941), so that polyploidy is 'a barrier to true progress' (Manton, 1932). This, as a general description of the consequences of polyploidy, is certainly not applicable to *Gossypium*, nor to most other crop plants. It is based on a conception of complete dominance, which is by no means universal, since many genes are to some extent haplo-insufficient; whilst it ignores the changes in balance which are to be expected as a result of the combination of two completely distinct specific genomes.

It is true that in allopolyploids many characters give duplicate or triplicate factor segregation, as in the case of chlorophyll deficiency in the New World cottons (Stroman & Mahoney, 1925), or grain colour in the cereals, which indicates the existence of mutual masking between loci; and Stadler's (1929) demonstration of an inverse relationship between degree of ploidy and frequency of X-ray-induced mutations also appears to support the masking theory. On the other hand, very many single-factor recessives have been demonstrated in plants known to be allopolyploid, which must therefore be presumed originally to have had a replicated genetic mechanism for all characters. In the amphidiploid *Nicotiana tabacum*, Clausen (1941), by an ingenious analysis, has actually verified this experimentally for a particular simple recessive character, mammoth. Near relatives of both of the presumptive diploid parents of *tabacum* have been found to carry factors dominant to mammoth. Ancestral *tabacum* must therefore have carried duplicate factors for normal growth, although the present-day species has apparently lost one of them. Clausen also cites certain simple-factor lethals, for which it must be assumed that both of the parental species carried normal alleles. He concludes that one of the features of derivation of an established amphidiploid from its raw ancestor must be the elimination or inactivation of many of its normalizing duplications, presumably by gene mutation. In the case of *short branch* and **cluster** in the amphidiploid cottons, this type of analysis has been carried a stage farther. Here the same mutation has been identified in both duplicated loci, instead of in only one of them as in *tabacum*. Each of the reduced fruiting branch mutations is uncommon in the species in which it occurs; strains carrying either of the mutants have been demonstrated to carry normal at the non-affected duplicate locus. The general situation must therefore be that both species carry normal at both of the duplicated loci; yet they definitely do not exhibit mutual masking of recessives. Had only one of the simply inherited reduced fruiting branch characters been identified in

cotton, as is the situation in tobacco, it might likewise have been inferred, in this case wrongly, that the normal at its duplicate locus had become inactivated.

It is by no means necessary to conclude that the divergence between normals, by reason of which they are no longer mutually replaceable, has always occurred since the initiation of amphidiploidy. It is important to recognize that this situation may equally well develop during the period when the parental diploid species are differentiating from one another. In the diploid species of cotton it has been shown (Silow, 1944) that purely genetic changes may be sufficient to account almost entirely for the development of full species distinctions. By the time that degree of chromosomal non-homology has been attained which is in the main requisite for the establishment of amphidiploidy, extensive allele substitution has therefore also taken place. There is, however, little experimental information on the nature of the allele differences to be expected in the component genomes of an amphidiploid. The *Gossypium* anthocyanin series has probably been investigated more fully than any other at this time. Comparison of the R_1 series in the American diploids with the R_2 series in the Old World diploids has given no evidence of any marked evolutionary divergence between the two groups; apparently there is a purely random assortment of different alleles into the species genotypes. Harland & Atteck (1941b) have given some indication of hitherto unexpected differences in physiological effectiveness by their demonstration of the existence, even within the American diploid group of species, of two normal alleles of the crinkled dwarf mutation which differ in their dominance potency over the latter. Stern & Schaeffer (1943) have recently recognized the same phenomenon of multiple allelomorphism amongst normal wild-type alleles in *Drosophila*. These examples give some idea of the kind of subvisible differences possible within the realm of 'normality'. Such straightforward differences in dominance as Harland observed in *Gossypium* are not sufficient in themselves to account for mutual failure of masking between duplicates. The directional differences which exist between various of the anthocyanin alleles in cotton, and the directional differences in physiological activity which Stern & Schaeffer demonstrated between normal alleles at a particular locus in *Drosophila* do, however, provide an adequate basis for the evolution of divergent functions between duplicated loci. Whether this actually is a mechanism by which failure of masking develops remains yet to be proven.

It has been suggested elsewhere (Silow, 1941) that some cases of complementary factors may be indicative of locus duplication. Attention was drawn to this possibility on account of the similarity in mutative steps involved in certain replicated multiple allelomorph series. The examples cited were not drawn from the polyploid New World cottons, but from the diploid Asiatic species. The same problem is involved in them, for it is likely that the so-called diploid species in *Gossypium* are themselves secondary polyploids (Skovsted, 1937; Stephens, 1942). The complementary factor 9 : 7 F_2 ratio occurs where there is full dominance, but no mutual masking between loci. No doubt *short branch* and *cluster* would behave in this way if both occurred in a single species and on the same genotypic background. In the case of the interspecific F_2 between them, where there was complete breakdown of dominance, this ratio became 1 normal : 15 affected. Thus, whether the genes at two loci behave as complementaries or 'duplicates' is determined by the dominance situation which happens to exist in the particular cross studied. This is determined partly, as has been indicated, by the nature of the main alleles themselves, but it is also dependent upon the entire genotype.

Turning, therefore, from consideration of the individual loci to the genotype as a whole, it is evident that the inception of polyploidy will be accompanied by considerable changes in gross genotypic balance. Mere doubling of a single genotype (autopolyploidy) is sufficient to give appreciable changes, such as have been observed in flowering curves or growth curves, or in the different end-point phenotypes reached in fruit shape or leaf shape. Much more spectacular effects accompany allopolyploidy, which combines two totally differently constituted genotypes. The most familiar of these is heterosis, but there are other possibilities in the way of intermediacy, or prepotency of one or other genotype, which may account for the striking changes in dominance relations between main alleles which are so frequent in interspecific hybrids. An interesting example of differences in expression of a particular gene in a derived polyploid and its parental forms is afforded by bract-toothing in *Gossypium*. In the American diploid *G. thurberi* the bracts are simple, and in the Old World *G. arboreum* only slightly toothed, but in their hybrid the bracts are highly dissected as in the New World natural tetraploids (Stephens, unpublished data). Stephens (1944*b*) has shown that bract dissection in the tetraploid species is an expression of the leaf-shape alleles, but the latter are without effect on bract toothing in the diploids. In the masking theory insufficient account is taken of the fact that, because of the new genotypic balance, the range of mutants which can gain expression is likely to be different in diploids and polyploids. The presumed invariable similarity in expression of single-dose mutants in diploids and double-dose mutants in tetraploids also fails to take into account the possibility of a considerable range in quantitative variation in the gene. Ultimate analysis is likely to show that the simple case of restriction to two alternative allelomorphs at a locus is the exception rather than the rule, though it is only by particularly refined methods that near alleles can be distinguished. It must also be remembered that mutation is not confined to the production of fully recessive alleles. In the anthocyanin series in cotton many of the alleles attain expression in single dosage in the diploids, and in the tetraploids all four of the different anthocyanin genes which could be present might gain expression at one or other of the various affected locations of the plant body.

SUMMARY

A newly identified linkage involving anthocyanin (R_2) and a habit character (*short branch*) in the New World tetraploid cottons shows about 10% crossing-over. This linkage group is a duplicate of one previously reported by other workers, and its recognition as such gives further genetic support to the hypothesis of the amphidiploid origin of the New World cultivated cottons.

It is frequently maintained that in a polyploid variability is buffered by extensive masking between duplicates, so that the evolutionary potentialities of the organism are much reduced. The fact that the amphidiploid cottons are at least as variable as the diploid species has led to an examination of the theoretical concepts underlying this situation. Although certain characters in known allopolyploids do give duplicate or triplicate factor segregation, with respect to many other characters such organisms behave as diploids. It is pointed out that identical gene duplication in the component subgenomes of an amphidiploid is likely to be the exception rather than the rule, as much on account of specific divergence which precedes hybridization as on account of evolutionary changes which follow the induction of amphidiploidy. Some examples are

drawn from cotton. Anthocyanin is controlled by genes at duplicate loci of known homologous origin. The various genes affect many different aspects of the anthocyanin pattern, but although the two loci concerned exhibit extreme multiple allelomorphism, identical duplication of genes at them does not occur. Since each gene may gain expression at one or other of the many affected locations of the plant body, complete masking is therefore not an essential concomitant of duplication in this case. Nevertheless there are no indications of any fundamental divergence between the loci concerned, either in the respective presumptive parental diploid groups of species, or in the amphidiploid, but there are some indications of its early stages at the speciation level. In the case of the habit character, reduced fruiting branch, genes in the recessive phase at either of the two duplicated loci concerned can gain expression even when, as in nature, normal genes exist at the other locus. Here masking is completely absent. In cotton subsidiary considerations make it possible to recognize the two habit characters as duplicates, even though diploidization has been carried almost to completion in this case. Had divergence progressed so far that none of the alleles at the duplicate loci were any longer recognizably homologous, the demonstration of their original duplicate nature would have been impossible by ordinary means. Examples are discussed of the type of functional divergence between alleles which, when translated from the diploid to the tetraploid condition, might lead to functional divergence between the genes at duplicated loci, so that masking would not occur. Other considerations, such as the new genotypic balance accompanying polyploidy, are also discussed, and it may be concluded that there is no reason to believe that amphidiploidy adversely affects the evolutionary prospects of an organism.

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