NOTES AND COMMENTS

AFFINITY IN COTTON

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WALLACE (1960) explained certain abnormal segregation ratios in cotton in terms of the theory of affinity. More recently, Phillips (1964) brought forward genetical and cytological data from interspecific *Gossypium* hybrids which purported to show the absence of affinity in this genus. There are, however, a number of serious criticisms of Phillips' interpretation of his own data which invalidate his claim.

Phillips' genetical data were taken from a test-cross of the hybrid *G. thurberi* × *G. armourianum*, which segregated for four simply inherited unlinked characters, leaf shape (L), anthocyanin pigmentation (R), corolla colour (Y) and pollen colour (P). The data as presented by Phillips do not, as he claims, provide evidence against affinity in the hybrid. There are two main reasons.

The first point refers to his method of presenting and analysing the four-point segregation data. The breakdown of classes in such a four-point test-cross in terms of recombinants (p) and non-recombinants (q) with (a) full phenotypic classification, and (b) Phillips' condensed classification, are presented in tables 1 and 2 respectively. A sensitive test for quasi-linkage or linkage is possible only with full phenotypic classification, since it is only then that a direct comparison of recombinants : non-recombinants can be made. Analyses of this type have been used by Michie (1955) and Wallace (1958, 1961). It will be seen from table 1 that in Phillips' condensed classification (table 2), the expectation, for any two-point linkage, of the classes $3^{ARM} 1^{THU}$ and $1^{ARM} 3^{THU}$, each add to $\frac{1}{8}(2p+2q) = \frac{1}{4}$, or together = $\frac{1}{2}$, whatever the value of p and q so that they do not contribute anything to a test for linkage. In fact the only test for linkage is that which tests the deviation of the classes ($4^{ARM} 0^{THU} + 0^{ARM} 4^{THU}$) and ($2^{ARM} 2^{THU}$) from the expected ratio 2:6. On Phillips' data this gives $\chi^2 = 0.043$, i.e. very low. The test is, however, relatively insensitive since it does not test $p:q$ directly and can use only half the data. The extent of insensitivity may be realised when one tests his observations (71:207) against the ratio expected when $p = 40$ per cent. This ratio is calculated by substituting $p = 0.4$, $q = 0.6$ in the expectation $\frac{1}{4}q:\frac{1}{4}(2p+q)$, i.e. 3:7. χ^2 testing the fit of 71:207 to 3:7 is 2.6, probability > 0.1 . Thus his data tolerate easily a quasilinkage of about the value so far observed in this and other species.

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It may be the case that Phillips' test is sensitive to the situation where all four loci are expected to be quasilinked and the recombination values are all expected to be of the same order of magnitude, but it is not the most

TABLE 1

*Expected class frequencies in Phillips' (1964) four-point test-cross of the hybrid G. thurberi
× G. armourianum with full phenotypic classification*

Pairs of complementary phenotypes	Allelic composition		Expected frequencies of the complementary phenotypes for each pair of loci					
	ARM	THU	L and R	L and Y	L and P	R and Y	R and P	Y and P
IRYP Lryp	4 0	0 4	q	q	q	q	q	q
LrYP IRyp	2 2	2 2	q	p	p	p	p	q
LRyP lrYp	2 2	2 2	p	q	p	p	q	p
LRYp lryP	2 2	2 2	p	p	q	q	p	p
lrYP LRyp	3 1	1 3	p	q	q	p	p	q
IRyP LrYp	3 1	1 3	q	p	q	p	q	p
IRYp LryP	3 1	1 3	q	q	p	q	p	p
LRYP lryp	3 1	1 3	p	p	p	q	q	q
Each p and q to be divided by 4 so that each column adds to 1								

TABLE 2

*Expected class frequencies in Phillips' (1964) four-point test-cross of the hybrid G. thurberi
× G. armourianum, with Phillips' condensed classification*

Allelic composition		Expected class frequencies for any one two-point segregation	Expected frequencies without linkage	Phillips' observed frequencies
ARM	THU			
4	0	$\frac{1}{8}q$	1	39
3	1	$\frac{1}{8}(2q+2p)$	4	130
2	2	$\frac{1}{4}(q+2p)$	6	207
1	3	$\frac{1}{8}(2q+2p)$	4	149
0	4	$\frac{1}{8}q$	1	32
Totals:		1	16	557

sensitive test. This brings us to the second point. Not only has he made no case for expecting such a situation, but he has given no evidence that *any* of the markers is sufficiently near its centromere to show quasilinear linkage. Markers far from their centromeres will segregate independently regardless of the presence of affinity or of its strength (Michie, 1953; Wallace, 1958). In the absence of cytological evidence, the case for a marker being near its centromere must rest on its previous involvement in one or more quasilinear linkages, and these must show features not conforming to the expected pattern of linkage behaviour—such features as reversal and non-linearity (Wallace, 1958, 1960). In the absence of evidence of this kind, there is no *a priori* reason for expecting independence, one quasilinear linkage, two, three or even six quasilinear linkages; putative affinity data should therefore be tested for all of these possibilities, and if in fact the data show independence there can be no case either for or against affinity.

Next consider Phillips' cytological data (see his tables 2 and 3). These are arranged in a similar manner to the genetical data, *i.e.* the classification of C and D chromosomes is condensed to an enumeration, for the bivalents of each cell, of the number of Cs orientated to one pole and of Ds to the other. The intergenomic C×D hybrids were *G. sturtii*×*G. aridum* and *G. sturtii*×*G. lobatum*. The tests purport to show that there are no signs of affinity. However, these tests have meaning only if the assumption is made that all C chromosomes are centrotypically differentiated from all D chromosomes. If only some of the chromosomes are differentiated, then the inability to distinguish between chromosomes of the same genome introduces two sources of error of considerable magnitude. Firstly, the non-distinction, in his two tables, between chromosomes of the same genome introduces the same confounding effects as did the non-distinction between phenotypes in his genetical data. For the case of cells with four bivalents the confounding effects are the same as those shown in table 2 above. Since most of the cells analysed showed more than four bivalents and the total cell population in both C×D hybrids is small (166 and 203), these confounding effects are of even greater importance than those in the genetical data. The inability to distinguish between chromosomes within genomes, and the occurrence of incomplete pairing give rise to a second problem. Phillips' data on the hybrid *G. sturtii*×*G. lobatum* show that it is possible for all chromosomes to form bivalents since one cell had thirteen bivalents. But most of the cells showed incomplete pairing. Where this is so, we cannot assume that for a given level of bivalent formation the same chromosomes always form pairs or remain as univalents. For example, five cells in the above hybrid had four bivalents. In one cell the bivalents might have involved chromosomes I, II, III and IV, in another cell chromosomes II, IV, V and X, and so on. If only certain chromosomes are differentiated centrotypically, then the interpretation of the segregation behaviour of chromosomes in cells with incomplete pairing will depend upon which chromosomes form bivalents. Phillips' data do not take this into account, and since nearly all the cells in both hybrids show incomplete pairing this factor is of considerable importance.

It is clear, therefore, that Phillips' cytological data provide little useful evidence either for or against affinity. Indeed cytological data are of use in studying affinity only where individual chromosomes are distinguishable one from another. Since the chromosomes of *Gossypium* species are small and

rather uniform morphologically, cytological observations on species hybrids are of little value in studying affinity in this genus.

In his concluding remarks Phillips expresses the opinion that data from wide crosses are more meaningful than those from close crosses, in evaluating the role of affinity in the evolution of *Gossypium*. This concept requires further elaboration. The theory that has been advanced states that the accumulation of centromere differences giving rise to affinity is of use in maintaining species integrity, and therefore at a selectional advantage only where those species are at least partially sympatric, hybridise naturally and in which recombinant types are deleterious (cf. Michie, 1955; Wallace, 1960). The species groups *herbaceum-arboreum* and *hirsutum-barbadense* from which Wallace obtained evidence for affinity do fulfil these conditions (Hutchinson, 1959). On the other hand, the species of the C and D genomes are completely allopatric and do not hybridise naturally. Thus these genomes are probably those least likely to yield affinity data.

Phillips further remarks that affinity cannot account for the occurrence of depauperate types in interspecific F_2 s and F_3 s, since these must result from post-meiotic events. No such claim was made by Wallace (1960). Affinity relates to the rapid reversion to parental type in interspecific hybrids and not to the production of depauperate types, the explanation of which probably lies with Harland's (1933) theory of genetic balance or Stephens' (1950) concept of cryptic structural differentiation. As Wallace has pointed out, these mechanisms are complementary rather than mutually exclusive.

Neither Wallace's nor Phillips' data provide definitive evidence either for or against affinity in cotton. In view of the nature of the material itself this is likely to be obtained only from the study of quasilinkage data from hybrids of species or races fulfilling the above quoted conditions. The junior author is at present engaged in just such a study with crosses between races of *G. arboreum*.

1. SUMMARY

Phillips' cytogenetic data, purporting to show that affinity is of little or no consequence in cotton, are shown to give no evidence either for or against affinity.

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