exudate which always contain a high concentration of diffusible antigens.

It is intended to use this method in investigating the antigenic composition of the organism of bovine pleuropneumonia, and its relationship to that of caprine pleuropneumonia and possibly other pleuropneumonia-like organisms.

G. WHITE

East African Veterinary
Research Organization,
Muguga, Kenya.
Oct. 10.

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² Mansi, W., *J. Comp. Path.*, **67**, 297 (1957).

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⁴ Newing, C. R., and MacLeod, A. K., *Nature*, **177**, 939 (1956).

Incompatibility in *Theobroma cacao*

Knight and Rogers¹ postulated the existence of five incompatibility alleles, at a single locus, in the three self-incompatible but cross-compatible cacao genotypes studied by them. The five alleles differed in dominance, but two were equal; the same dominance sequence, $S_1 > S_2 = S_3 > S_4 > S_5$, was exhibited in both male and female parts of the flower. Their criterion of compatibility and incompatibility was the retention or fall, respectively, of hand-pollinated flowers guarded from insect visits.

I have used a different approach to the problem. Microtomed sections of pollinated ovaries have been microscopically examined. In all cases of self- and cross-incompatibility, a proportion of fertilized ovules shows non-fusion between the egg nucleus and first male gamete and between the polar nuclei and second male gamete; the remaining ovules show normal fusion. Three main types of self-incompatible tree are now recognized wherein the proportion of 'non-fusion' ovules is: (1) 25 per cent; (2) 50 per cent; (3) close to or actually 100 per cent. Compatible pollinations, on the other hand, give all normal ovules. *Theobroma cacao* L. provides, for the first time, an example of an incompatibility mechanism in the flowering plants which has non-fusion of gametes as its fundamental manifestation, the ratios of ovules wherein non-fusion and fusion of gametes take place bearing simple genetic ratios one to the other (1:3, 1:1, 1:0).

On a visit to the West African Cacao Research Institute in 1956, I was privileged to use some of the trees investigated by Knight and Rogers. Pollinated ovaries from guarded flowers were fixed, sectioned and examined.

All genotypes representing a combination of an allele and another recessive to it (for example, $S_{1,2}$, $S_{2,5}$, $S_{3,4}$) gave, on self-pollination, counts wherein the proportion of non-fusion ovules was 25 per cent. The $S_{2,3}$ genotype, a combination of alleles of equal dominance, gave 50 per cent non-fusion ovules on self-pollination. The $S_{4,5}$ genotype did not, however, give on selfing the expected 100 per cent non-fusion content; instead, it gave good 25 per cent counts, suggesting that, in fact, it is not homozygous, but is a combination of S_5 with a second allele recessive to it (say, S_6). The consequences of this assumption do not in any way invalidate the findings of Knight

Table 1. PERCENTAGE RATIOS OF 'NON-FUSION' TO NORMAL OVULES IN CACAO SELFINGS AND CROSSES. INCOMPATIBLE COMBINATIONS IN BOLD-FACE TYPE

Female	$S_{1,2}$	$S_{2,3}$	Male $S_{4,5}$	$S_{2,4}$	$S_{3,5}$
$S_{1,2}$	25	0	0	0	0
$S_{2,3}$	0	50	25	25	0
$S_{2,5}$	0	25	25	0	0
$S_{3,4}$	0	25	0	25	0
$S_{3,5}$	0	0	0	0	25

Cross-pollinations between genotypes carrying the same dominant allele (for example, $S_{2,3} \times S_{2,4}$) also gave 25 per cent non-fusion ovules in the ovary. The cross, $S_{2,3} \times S_{3,4}$, found by Knight and Rogers to be incompatible, likewise gave 25 per cent non-fusion ovules.

All combinations that do not involve the same dominant allele (for example, $S_{1,2} \times S_{2,5}$, $S_{1,2} \times S_{3,4}$) and those that do not involve a duplication of alleles of equal dominance in the presence of the other (for example, $S_{2,3} \times S_{3,4}$) were found to give only normal ovules in the pollinated ovaries. Knight and Rogers found these combinations to be compatible.

The results are summarized in Table 1, which shows the percentage proportion of non-fusion ovules counted. The principal conclusions to be drawn from the results are: (1) that gametes carrying the same dominant allele are those that do not fuse in the embryo-sac; (2) that the fusion or non-fusion behaviour of gametes is determined by the S allele they carry interacting with the diploid tissues (for example, S_2 gametes fuse in $S_{1,2}$ tissues, but not in $S_{2,5}$ tissues), so that incompatibility or compatibility is ultimately determined by the diploid genotype and hence is sporophytically controlled; (3) the similarity of reciprocal pollinations.

From my observations on the incidence of compatibility and incompatibility in progenies arising from crosses between self-compatible and self-incompatible parents, the hypothesis put forward by Knight and Rogers, based on the operation of an allelic series at a single locus, appears inadequate. It seems necessary to postulate the existence of two independent loci, one (P, p) concerned with the production of an 'incompatibility precursor', and another (S), which imparts specificity to the precursor. The P, p locus shows simple dominance and recessivity, and acts before meiosis; the S locus shows allelomorphism and acts after meiosis. If either locus is inactive (pp and $S_{f,f}$, where the f indicates the presence of an amorph), full self-compatibility results. There will therefore be three main types of self-compatible tree: (1) $pp S_{a,b}$ (self-compatible by virtue of the non-production of the precursor); (2) $PP S_{f,f}$ (self-compatible by virtue of amorphism at the S locus); (3) $pp S_{f,f}$ (both loci inoperative). A cross between the first, believed to be representative of the Central-American self-compatible tree, and the second, thought to represent the Trinidad self-compatible, will produce offspring with both loci active, and hence all will be self-incompatible. This result has been obtained.

F. W. COPE

Regional Research Centre,
Imperial College of
Tropical Agriculture,
Trinidad.