INTRODUCTION

The main problem confronting the Botany Department of the Imperial College of Tropical Agriculture is the production of a banana which is both resistant to Panama disease caused by Fusarium cubense E.F.Smith and Cercospora leaf spot, and has all the good commercial qualities of Gros Michel. It is extremely unlikely that such a banana already exists, since it has been found that Gros Michel, with its attractive appearance on ripening, pleasing flavour, good storage qualities, compact bunch rendering transport easy, and long fingers, and very high degree of sterility, was an extraordinarily fortunate introduction to the West Indies. It is therefore necessary to breed the required banana. Since Gros Michel has all the required characters with the one exception of disease resistance it is the natural starting point of the breeding programme, the intention being to add this extra character to its genotype with the minimum disturbance.

Work in the early part of the investigations here has strongly supported the feasibility of this method; I.C. 1 and probably I.C. 2 have been produced by pollen of the seeded diploid Musa acuminata on Gros Michel. Single restitution in the triploid Gros Michel has produced these two plants, among others less useful, with the triploid genotype of the female parent plus a haploid genome from the fertile diploid. This has brought in disease resistance, and Gros Michel has brought its favourable characters, but unfortunately these are affected by the less favourable commercial qualities brought in from the male parent, so that these two clones just fall short of saving the banana industry, although I.C. 2 might be used to carry on until something better is produced. The male parent, M.acuminata, is a fully fertile seeded diploid with rather short fingers and rarely more than five hands, at least at St.Augustine, and a sub-horizontal bunch which gives an asymmetrical mature bunch, difficult to pack owing to the negatively geotropic growth of the developing fingers. This character is of the utmost importance because the vertical symmetrical bunch of Gros Michel is necessary to avoid damage to the bunches standing in ships' holds without any protective packing. Moreover Gros Michel itself has not genotypically a vertical bunch. Small, weak bunches may even be sub-horizontal, and the vertical heavy bunch on an active, healthy stool appears partly a result of its own

weight. M. acuminata is therefore not a particularly suitable male parent, and fortunately in the collection here there is a considerably better one called Long Tavoy. It is similar to acuminata but differs in an almost vertical bunch, longer fingers and more hands to the bunch, and therefore by utilising it there is a good chance of improving upon I.C. 1 and I.C. 2.

The practical side of the breeding programme should therefore consist of pollinating all Gros Michel fingers with pollen from Long Tavoy. However this simple, highly practical outlook is not enough. One objection is the time factor. Owing to the sterility of Gros Michel very few plants can be expected and of these a large proportion will be useless. I.C. 1 was one of 18 seedlings of which only four reached the flowering stage and the other three were not disease resistant. It is purely a matter of luck as to whether this method will be successful in a reasonable time so that work is still required to explore methods of reducing the time. Another objection is that it is not absolutely certain that this method can yield the desired result. Much more work than has been outlined above has been necessary to establish the probability of success by this method, and one important point has not been mentioned. This is sterility. Even a very occasional seed in a banana is a very serious commercial drawback and I.C. 2 is more fertile than Gros Michel. An occasional seed is found in it. Recent work by Dodds is pointing the way to overcome this difficulty. He grew a progeny of fifty plants from M. acuminata pollinated with Pisang Lilan, a sterile parthenocarpic diploid with partial pollen fertility, and has found a graded series from seeded, non-parthenocarpic to sterile parthenocarpic types, but with female sterility and parthenocarpy independent of one another. In addition all show partial male fertility. This suggests that a suitable parthenocarpic diploid might be used as the male parent, when it could bring extra female sterility to offset the naturally greater fertility of the tetraploid, and might make the difference between a commercial banana and a very suitable type spoilt by the occasional production of a seed.

Leaving aside such new ideas which present and future academic work may suggest, there are two lines of attack on the central problem, both being concerned with reducing the time factor. One line is to increase the yield of viable seed from Gros Michel and the other is an attack via the diploid pollen parent. It is necessary to ensure as far as possible that the diploid is really the most suitable and most likely to give a high propor-

tion of desirable seedlings. It might, for example, pay to breed a relatively homozygous diploid, so that at least the male gametes would be somewhat alike, and the variability of the progeny would be reduced. If a desirable type homozygous diploid was selected, this would materially increase the chances of obtaining the required seedling. A single example will show that our present diploid clones are by no means homozygous. In Dodds' progeny out of acuminata by Pisang Lilan one of the plants produced an almost vertical erect bunch, strongly reminiscent of M. ornata, but quite different from either of its parents, both of which have pendulous bunches.

The first line of attack on the female is peculiarly difficult, apart from obvious measures such as germination technique and time of pollination for the best results, and requires a thorough understanding of edible triploid banana sterility, which is affected by several factors including cytological sterility, reduced by the restitution that is necessary for the production of the required progeny; physiological sterility; and the possibility of incompatibility perhaps caused by differential pollen tube growth rates. Of these physiological sterility, which is a phrase covering many very imperfectly understood phenomena, is probably the most important and the most difficult to investigate. It appears to be affected by parthenocarpy and the extra development of succulent tissues conferring edibleness, and two types of evidence point to it. Investigation of embryosac development by both Dodds and Pittendrigh has shown much embryosac degeneration which is very difficult to explain on the cytological behaviour, and when cutting bunches of edible bananas for seeds it is frequently noticed that the seeds are not scattered at random but are found in little groups of two or three close together. This was noticed in Bluggoe and I.C. 44 but the most striking case occurred in one of Dodds' edible diploids, Pisang Lilan pollinated with M. ornata, where no seeds had been found in about 40 bunches and then in one finger 3 good seeds were found close together, suggesting that several viable zygotes can together, but not separately, overcome some physiological barrier to development.

This short account gives some idea of the manifold problems in bananas, many of which approach the physiological sterility in their elusiveness. In addition such a clone as Gros Michel is very difficult to work with owing to its high sterility. It would be well nigh impossible to investigate the conditions for its seed formation, since as many as ten bunches might have to

be studied before a single seed was obtained. It is therefore necessary to work with more favourable material to obtain results and ideas which might be applied successfully to the commercially important but scientifically unsuitable clone of Gros Michel.

A minor problem was to find a suitable investigation for the author from which he could obtain some results of value in the relatively short period of just under one year. Owing to the limited equipment of the Botany Department, he had been forced to wait until his predecessor completed his work, before the one microscope that approached being good enough for the necessary cytological work was available. After some discussion the problem decided upon was one mentioned by Cheesman and Dodds in their paper on the results of pollinating the numerous edible triploids in the collection (1942 pp. 347-8). In some ways it proved to be an unfortunate choice since the work has been hampered all along by lack of material. Most of the required plants proved unexpectedly weak and insufficient bunches were shot.

The edible triploid clone known as Bluggoe, often called Moko locally, is a popular plantain type banana which needs to be cooked before eating owing to its high starch content. On taxonomic grounds it appears to be a triploid derivative of the seeded diploid M. Balbisiana, a very tall and vigorous plant which resembles the strong growing edible triploids in general habit far more than its slender cousin M. acuminata, which is thought to be similar to the diploid ancestor of Gros Michel. Results of previous pollinations of Bluggoe by acuminata have shown that it is relatively fertile, a conclusion confirmed by the occasional occurrence of seeds in unbagged, open pollinated bunches, and its behaviour is closer to that of a typical triploid than is that of many edible bananas, where the only seeds are a result of restitution; there are a number of diploids, a few aneuploids and tetraploids reported in the progeny due to acuminata and the related Calcutta 4. This suggests that Bluggoe may be a useful clone for investigating female behaviour, since it exhibits both the more normal triploid behaviour, and the rather unusual banana restitution, and in addition it is relatively fertile, which allows results to be achieved without excessive labour on many bunches, which could not be expected to produce any seeds.

The problem arises in that these pollination results showed that when Balbisiana, the apparently related seeded diploid, was used as pollen parent the seed yield was much lower (the figures are quoted in Table 2),

and of the few seedlings obtained six were weaklings of which one was found to be tetraploid, the others dying before they could be counted; two were vigorous and one proved to be triploid and the other tetraploid. This difference in behaviour is remarkable since on taxonomic grounds Bluggoe is certainly not more closely related to acuminata than to Balbisiana, and moreover Balbisiana produces what appears to be excellent pollen in great abundance. When actually pollinating Balbisiana pollen appears to be much better than acuminata although of course this macroscopic appearance is not really critical.

In the present work these data had to be verified by careful pollination which would allow no doubt in interpretation, and, if possible, the reason for these puzzling pollination results was to be elucidated. One of the requirements was an accurate description of meiosis in Bluggoe, which is the first full description of male meiosis in a triploid banana. For the rest the work was to consist of an elucidation of the behaviour and relationships of the various progeny of Bluggoe that have been retained in the collection here. These will be dealt with more fully in the next section.

In concluding this introductory discussion it should be emphasized that the problem outlined briefly above was intended merely to provide an objective for what was bound to be a limited investigation and was never considered to be of paramount importance. It was expected that working along lines designed to answer this question, problems of wider application would be raised and perhaps in part answered, especially as Bluggoe is quite a suitable clone for elucidating the complex female behaviour of edible bananas. Finally a warning is required in that we now have evidence to state that results obtained with other plants must be applied to bananas with great caution. Bananas are most unusual in many ways, the regular method of lifting bracts subtending hands of flowers is one of their useful abnormalities, but many of their unusual cytological behaviours are very baffling, and particularly so is their apparent disregard of the rules of the present orthodox cytology. These statements will be supported and amplified in the ensuing work, where it will be found that the normal cytological methods may break down owing to the special conditions; and the importance of physiological interrelationships, about which we know practically nothing, appears to be far greater than in most cytogenetical work.