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BANANA RESEARCH AT I.C.T.A.

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Introduction

This is a review of botanical researches on bananas carried out at the Imperial College of Tropical Agricultfire from 1922 to 1946, and of the present programme. Various findings have been published from time to time in scientific papers, where they are available to the few botanists who are interested in the intricacies of reproduction and heredity in *Musa*. The object here is not to report any new discoveries, but to give an account of the work as a whole that may be of some interest to a wider circle; and the approach is therefore as untechnical as it can be made, having regard to the highly technical nature of the subject. If apology is needed for repetition of some facts about the earlier work that have already been published more than once, it must be pleaded that the last comprehensive review appeared in 1934, and many readers are likely to find it more convenient to have the historical background redrawn than to be obliged to refer back to earlier publications.

As the paper is essentially a progress report of the Department of Botany, and not a review of banana breeding in general, there is little reference herein to the extensive work that has been carried out concurrently by the Jamaica Department of Agriculture. The omission in no sense implies neglect. On the contrary, the two programmes in Jamaica and Trinidad have been carried on co-operatively, have influenced each other in many ways, and have produced broadly complementary results. To a lesser extent, but still materially, the genetical programme has been influenced by other lines of banana research, especially the investigations into Banana Wilt and into fruit storage and transport pursued by other departments of the College, but those also fall outside the scope of this summary.

The Development of The Programme

The first systematic attempts ever made at breeding new varieties of bananas were begun by the College at its inception in 1922. Their immediate aim, was to produce a new export banana resistant to Banana Wilt (Panama Disease), which was causing grave concern by its ravages on the established Gros Michel variety in Jamaica and elsewhere. The inspiration of the work was largely drawn from the success that had attended the raising of new sugar canes from seed in the thirty years preceding. The amount of useful information available was very slender, and it can now be said without the slightest disrespect that nobody concerned had any conception of the magnitude of the task undertaken. Not only was specific information lacking about the genetics of bananas, but knowledge of a more general kind about genetic systems in plants, and particularly about the cytogenetics of sterility, was rudimentary by comparison with what it is today. In these circumstances the programme opened with investigation of the possibilities of producing seeds in the few edible banana varieties available, whilst efforts were made to get together a collection of varieties for more extensive survey. Evidence was soon found that no good results were likely to be had from crosses between edible banana varieties alone; but there happened to be two species of *Musa* in the botanical gardens in Port-of-Spain with inedible fully seeded fruits, and from pollinations by one of these (later identified as a form of *M. acuminata* Colla) seeds were obtained in Gros Michel fruit at a rate of about one per bunch. A few of these seeds germinated, and the first artificially produced hybrid banana flowered in March 1925.

This first hybrid (I.C. 1) showed a closer resemblance to a commercial banana than might have been expected, considering the characters of its male parent. It was, in fact, an edible banana as good in all its characters as several that are in cultivation, but showed certain defects that unfitted it for the export trade. Compared with the standard Gros Michel it had a rather less symmetrical bunch, a slightly lower number of "hands" and a shorter fruit, and it also showed a tendency to produce occasional seeds. All these shortcomings were quantitatively small, and when I.C. 1 proved to be highly resistant to Panama disease, it gave rise to

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hopes that the whole problem might be fairly easily solved. The next step was to repeat the cross on a large scale in the hope that among a large enough number of seedlings the desired type might occur. At the same time I.C. 1 after bulking up could (as it produced fairly abundant pollen) be self-fertilized, back-crossed with its parents, and used as a male parent on other edible varieties.

Such then was the programme in its second phase, but hopes were not realized. Repetition of the cross gave a series of Fl hybrids which vai ie,1 little from the first example. Some were susceptible to Wilt, and some were in other ways inferior to I.C. 1. One plant (I.C. 2) seemed a little nearer the desired type, especially in being less liable to produce seeds on selfing, and this was released for commercial trials in 1932.

By that time it had become apparent that attainment of the ideal was going to be a long task, and that an interim solution of the problem might be better than none, but I.C. 2 was not regarded as more than that.

Attempts to carry the breeding into later generations gave even less favourable results. Seeds were not readily obtained by selfing or intercrossing Fl plants, and the few F2 seedlings raised all proved inferior to their parents. Backcrossing the Fl to Gros Michel, which was expected to give the best results, was a failure; and backcrossing to the male parent gave, as was expected, plants much inferior to the F1.

These results were partially explained by cytological studies, which were added to the programme as soon as I.C. 1 flowered. It had been realized from the start that in a crop as sterile as the banana there must be irregularity in the reproductive mechanism, and that cytological information would be useful. Examination revealed differences in chromosome number between the parents and the hybrids showing that polyploidy was involved.

The original cross had been between a triploid (Gros Michel) and a diploid (*M. acuminata*) and had produced a tetraploid (I.C. 1). Much later, after examination of a wide range of material, it was found possible to generalize the situation as follows :

1. The basic chromosome number in the section of *Musa* to which the edible bananas belong is x = 11.
2. The fertile species (*M. acuminata*) used in the initial experiments and all others of the same section that have been acquired since are diploids (2n = 22).
3. Most edible bananas are, like Gros Michel, triploid; though a few are diploid
4. All the best of the Fl hybrids obtained from triploid x diploid crosses are, like I.C. 1. tetraploid (2n = 44). Diploids. triploids and aneuploids are also obtained, but none of these approaches as closely as the tetraploids to the characters of a commercial banana.
5. Crossing tetraploids together produces more tetraploids, but these are always inferior to their parents.
6. Crossing triploids with tetraploids (as in the cross Gros Michel x I.C. 1) gives pentaploids and higher polyploids, all of which are commercially worthless.

These generalizations were only arrived at after a great deal of empirical work in what may be regarded as the third phase of the researches. The variety collection was growing steadily, and as the available material increased, a comprehensive programme of cross-pollinations developed. Between 1927 and 1941 the number of inflorescences pollinated was nearly 6,000 and hundreds of seedlings were grown and observed. The policy in this phase was to leave no possible line of attack untried, and even when negative results were obtained, to repeat the cross until the accumulation of failures demonstrated conclusively that it was useless.

In this way the problem was slowly defined and narrowed down by a series of eliminations. The edible varieties were classified into those that give no progeny at all (a class containing some members that would otherwise appear to be very useful material), those that give predominantly diploid or aneuploid progeny of no apparent value for further breeding, and those that give predominantly tetraploid progeny.

From the last class a series of tetraploids was raised by crossing with various fertile diploids, and the teraploids were then crossed together or back-crossed to triploids.

From all this work nothing of direct economic value was obtained, but the effort was not wasted. The workers engaged in it learned thoroughly, as it could be learned in no other way, the behaviour of the diverse material in all types of crosses — diploid with diploid, diploid with triploid, diploid with tetraploid, triploid with tetraploid and tetraploid with tetraploid. They were able to establish beyond doubt that intermediate expression of characters is the rule in *Musa* crosses. The interfertility of the species of *Musa* was found to be surprisingly wide, and even edible bananas sometimes give progeny with species not very closely related to them. But it is rare for characters not present in either parent to appear in the offspring, and when extra-parental characters do appear they are usually unimportant ones or deficiencies. Consequently it was found possible to predict within fairly narrow limits what the offspring of any given cross would look like, with respect to such important characters as angle of bunch, number and size of fruits, and so on. Previously there had always been at least the theoretical chance that a good banana might result from a cross between "unlikely" parents, but accumulated experience showed the chance was so small as to be negligible. Henceforth parents could be chosen on the sum of their phenotypic characters, just as in most simpler plant breeding programmes, subject only to allowance being made for polyploidy, which often causes the characters of one plant to be more pronounced in the offspring than those of the other parent.

The establishment of this fact and of the cytogenetical generalizations already mentioned may be regarded as marking the end of the empirical phase of the researches, though there was no abrupt change of plan at any point but rather a gradual modification as information accumulated. With increasing knowledge of genetic behaviour came an increasing conviction that failure to reach the desired goal was largely, if not entirely, due to lack of the right breeding material. Emphasis had always been laid on the necessity for a large variety collection from which suitable material could be chosen; it came to rest more and more on the necessity for that collection to contain a wider range of fertile diploid forms, only obtainable by collection in the countries where they are indigenous.

The genetical and cytological data obtained indicate that the good qualities of tetraploid hybrids of the I.C. 1 type depend on the fact that they contain the complete gene-complex of their triploid female parents, whilst their defects derive from the added (haploid) gene-complex of their diploid male parents. The constitution of the parental triploids has been evolved through the accumulation of structural changes during hundreds of years of vegetative propagation, and can only reach its full expression as long as it works as an undisturbed unit. The defects of the tetraploids therefore cannot be removed in later generations, because in sexual reproduction of the tetraploid the unit is inevitably broken up, and the chances of recombining it are too remote to afford a basis for practical breeding. This theoretical appraisal of the situation by K. S. Dodds is supported by the actual results of tetraploid x tetraploid crosses, and forms the foundation of further attempts to produce a commercial tetraploid.

For the triploid or female side of the cross that is to give a useful export banana, everything points to the Gros Michel variety as the best available parent. Apart from its susceptibility to certain diseases, that variety has so many of the qualities required in the export trade that somebody has said it might have been specially created for the fruit industry. Many years' study of other established varieties by the fruit trade, as well as our own observations in Trinidad, have failed to find a satisfactory substitute for it, and to start with any other parent is to add unnecessary handicaps in a problem sufficiently difficult without them. At one time attention was given to the possibility of starting with an established variety immune to Wilt and trying to improve its commercial fruit characters, but there are several reasons why this is no longer considered feasible. The chief is that the most promising varieties for such a programme are completely sterile, which is one of the pieces of useful information accruing from negative results in the empirical investigations. Apart from that is the fundamental consideration that introduction of disease resistance by itself has proved the simplest part of the whole problem, whilst it is the commercial fruit characters that give all the trouble. Disease resistance is the rule rather than the exception amongst the fertile diploids. Thus in practice any male parent which would improve the fruit characters of an inferior variety would almost certainly give even better results on Gros Michel and solve the whole problem outright.

Virtually then, the problem narrows down to getting the right male-fertile diploid for crossing with Gros Michel. Such a plant may exist in a wild state in countries where *Musa* is indigenous, or it may have to be built up from a number of forms each good in some characters but deficient in others. If it could be found ready-made much time would be saved, as the synthesis from such material as is now available would at the best be a tedious undertaking. Strong representations to that effect having been made, plans were approved in 1939 for an expedition to the Far East to explore the variation of the nearest banana relatives in the wild state and to collect material of promising forms.

For reasons explained more fully in a later section of this paper, the region chosen for the first exploration was approximately that where Burma, Siam and Indo-China meet. It would be impossible to explore the whole of the vast area over which *Musa* is indigenous, and even the section of the genus that appears to be of the greatest interest covers an enormous area, but the centre of distribution seems from available evidence to be in the region specified.

Plans were suspended on the outbreak of war, and the political condition of the countries named does not at the time of writing afford much hope of their early resuscitation. The policy since 1940 has therefore been to concentrate on genetical researches, collecting data likely to hasten progress when new material becomes available, and at the same time to try how far a suitable diploid can be built up from the existing stocks.

Present Aims

The immediate or "short-range" aim of banana research is still to produce a new export variety resistant to Banana Wilt, otherwise known as Panama Disease, caused by the soil inhabiting fungus *Fusarium oxysporum cubense*. But without neglecting this object it is now possible to state aims in rather broader terms. Since the work started, additional urgency has been lent to it by the rapid spread in the Western Tropics of the Leaf-spot Disease caused by *Cercospora muscle* Zimm. Though the latter disease, unlike Wilt, has proved to be controllable by other means, a resistant variety would afford cheaper control than the present method of spraying. In the background there is always present the threat to the export trade of Bunchy Top, a virus disease that already causes serious losses in the East; and beyond that there is the possibility that at any time a new or hitherto unimportant disease may become prominent and create a need for further breeding. The problems of the banana as a local food crop have hitherto scarcely existed, partly because diseases are less serious when the plants are grown as scattered individuals among other species and partly because so many varieties are available that suitable ones can usually be found for any set of local conditions within banana-growing districts. This happy state of affairs may not always exist, and already the difficulty experienced in growing plantains in some districts points to wider uses for banana breeding.

There are good reasons, therefore, why banana research should be regarded as having a "long-range" aim quite consistent with its more immediate object. In other words, without for a moment losing sight of the urgent need for a "wilt-resistant Gros Michel" we may remind ourselves that the production of that plant is not likely to end banana-breeding. The long-range aim must be to obtain such a complete knowledge of genetic systems in *Musa* that new bananas can be bred as they may be required to meet any new problems that may arise in banana production.

Analysis of Problem

Disease resistance, though it is the primary desideratum, may fairly be said to present only a secondary problem. Resistance, both to Wilt and to Leaf-spot, occurs in many members of the banana complex, wild and cultivated, and is known to be transmissible. The primary problem is how to breed any commercial banana, in face of the fact that the essential character of a banana (its "edibility") is inseparably coupled with sterility.

The existing commercial bananas are undoubtedly the products of centuries of evolution. We do not know how long Man has been cultivating them, and selecting and preserving chance variations giving fruit more to his liking than that of wild plants, but it must be a long-time. It happens that all the best of the varieties so produced are triploid plants, and there is probably a reason for that fact which still has to be found, and which is likely to prove important.

So far, the only practicable method that has been found for utilizing these products of long evolution in breeding is to add to them a gene complex that will not detract from their good qualities and so to produce from them primary tetraploids. That is at present the main hope-of solution of the short-range problem, and it looks a very fair one if the right material can be found. The breeding of primary tetraploids, however, is no answer to the long-range question, which is, in essence, whether it is possible to imitate in a few controlled generations the process of centuries that has built up the primary triploids. Only when that can be done shall we be in a relatively safe position to meet the problems of the future in banana production.

The information required to that end covers a wide field of research, which may be appreciated by dividing it for discussion into five parts, although each line of work is dependent on the others.

We need:

1. Studies of a wide range of cultivated bananas, which must include attempts to discover their constitution by genetical methods.
2. Studies of wild species of *Musa*, primarily to determine which of them have been involved in the ancestry of the cultivated forms.
3. Studies of the incidence of polyploidy and the general breeding behaviour of diploids, triploids and tetraploids.
4. Studies of the incidence and inheritance of parthenocarpy, with attempts to discover the physiological mechanism through which it is expressed.
5. Analysis of the several causes of sterility in various forms of *Musa*.

Each of these lines has in fact already received attention, since the. observations incidental to the empirical attempts at banana breeding have provided a mass of relevant data and also material for further research. Each of them, however, still provides unsolved problems and must still be followed up. The position reached along each line will be briefly indicated.

Survey of Cultivated Forms

Nobody knows how many established varieties of bananas and plantains there are in cultivation. Most of the literature about the group emphasizes its diversity, but varietal studies tend to suggest that the diversity has been somewhat exaggerated. The question is not unimportant to the geneticist, for it affects fundamentally the picture that he must try to draw of the origins of the group.

In seeking the answer, we have first to define the term "variety". If we interpret it in its narrowest sense and apply it to every recognizable form, the total number may well be several hundreds. Some of these "varieties", however, will then differ from others only in single characters, such as colour of fruit or amount of wax on the epidermis. In such cases it is a justifiable assumption that two or more forms are descended from the same original seedling and that the variation has arisen through somatic mutation. There is plenty of evidence that somatic mutation (or "bud sporting") has played a part in the evolution of banana varieties: for example, in Jamaica Larter (Journ. Jamaica Agr. Soc. August 1934) has described no less than six bud mutants of the Gros Michel variety found in commercial plantations.

The important question to the geneticist is how many original zygotes are represented, or in other words from how many distinct individual seedlings the present population has been derived by vegetative propagation. It is not likely that an exact answer will ever be obtained, nor is a very close estimate necessary, but it should at least be possible to determine whether the number is to be measured in dozens or hundreds. At present, all we can say is that edible bananas have certainly been derived in more than one way from a number of different wild forms. The usefulness of knowing approximately the kinds of wild plants that were originally involved, and the steps by which their constitutions have been modified, should need no stress.

There are therefore ample reasons for the maintenance and continued study of a wide collection of edible bananas, in spite of the decision that for immediate breeding purposes the Gros Michel is the only one likely to prove useful. Every new variety that comes into the collection adds something to the sum of knowledge about the group; and a variety quite useless as breeding material may, by closing a gap in the research worker's information, contribute greatly to final success.

Studies to date on the existing collection have led to the hypothesis that all Indo-Malayau bananas and plantains can be classified into three main groups, derived from two natural species and hybrids between the two. This hypothesis provides a great simplification of the origins of the group, but the danger is that it may prove to be an over-simplification, based on an insufficient range of evidence. Observations in the future must therefore be directed to checking the hypothesis and if necessary amending it.

Survey of Wild Forms

The wild forms of *Musa* are of most immediate interest because it is among them that we hope to find the right male parent to solve the problem of the "wilt-resistant Gros Michel". They have still more importance in the long range problem of determining the origins and relationships of bananas in general.

The literature in 1922 contained well over a hundred specific names published under *Musa*, with good or fair descriptions of about forty species, classified into three subgenera and distributed over practically the whole of the Old World tropics. The relationship of the cultivated forms to the wild was little understood and theories about it conflicted. The first problem was therefore to find out how many species were probably concerned in the ancestry of the bananas or sufficiently closely related to be potential breeding material, in order that. effort could be concentrated on the collection and study of those instead of being dissipated over an unnecessarily wide field.

This kind of problem has to be tackled by the collation of information from several sources. Much can be obtained from literature, though it is widely scattered and often in publications. difficult to obtain. Some can be got from dried fragments in herbaria. More is forthcoming from correspondence and most from the material that comes into the collection by the good offices of co-operative correspondents in many countries.

By such methods it has been possible to arrange the available knowledge of *Musa* and step by step to eliminate large sections of the genus as not sufficiently closely related to the bananas to be potential breeding material. Recent publications have suggested the removal of a number of ‘species to the genus *Ensete* Horan., and the classification of those remaining into four sections. Of the four sections only one (*Eumusa*) is judged to be involved in the banana complex, and it consists of no more than half a dozen described species. Of these, as noted above, only two seem to be directly involved in the ancestry of the bananas, but these two are widely distributed and variable, one of them extremely variable.

Our knowledge of these particularly important species is still fragmentary, but enough to show that they are by no means simple. Even in wild forms there are certain irregularities in the reproductive mechanism which must certainly be understood before we can hope to analyse the much more complex systems of the cultivated plants. Again it is only by survey of a sufficiently wide range of material that gaps in knowledge can be filled in.

Polyploidy

Gros Michel and the majority of edible bananas are triploid (2n = 33) . All known wild species are diploid (2n = 22). The economic significance of the triploid condition is still obscure. The occurrence of perfectly edible (parthenocarpic and seedless) diploids among the established varieties shows that polyploidy is not an essential character of an edible banana. On the other hand, all the edible diploids known to us are slenderer plants than the average triploid and produce smaller fruits. There may well be some connection between polyploidy and fruit size, but it would not appear to be a simple or direct one. Tetraploids and higher polyploids are only known among artificially produced hybrids and nothing higher than a pentaploid has ever been raised to flowering : even pentaploids are not very vigorous. Interest therefore centres mainly on the triploids and tetraploids.

As triploidy introduces further complications into a genetic system which is already complicated in the parthenocarpic diploids, little has been done towards the direct cytogenetical analysis of the triploid clones. The principle has been to work from the simpler to the more complex, and this means that most work to date has been done on the diploids.

Polyploidy has, however, been studied further in species hybrids where it is not associated with parthenocarpy; and one of the most interesting results is the finding that in *Musa* polyploidy frequently occurs as a result .of wide species crossing. Several species hybrids, when selfed or backcrossed with their parents give either triploid or pentaploid progeny, or a mixture of both.

How far this information may ultimately help to explain the origin of polyploidy in the edible bananas cannot be stated. But it is evidently a useful addition to our knowledge of genetical behaviour in the genus.

Parthenocarpy

Parthenocarpy is essential in an “edible” banana, and therefore of the greatest importance. One difficulty in studying it is that it seems to be inseparable from some degree offemale sterility. A parthenocarpic form may however, be fully fertile on the male side, and studies of inheritance are therefore possible. Detailed results of such studies by Dodds and Siminonds are at present * in the Press. They show *inter alia* that parthenocarpy can be transmitted through the pollen of parthenocarpic forms, and that it depends on a single dominant gene, though its expression is affected by modifiers.

* i.e. in July 1948.

Parthenocarpy has so far been reported in *Musa* in only three species, two of which are the putative parents of the Indo-Malayan bananas. Even those species have numerous non-parthenocarpic forms, and parthenocarpy has not so far been induced in any form where it does not occur naturally. Knowledge of its behaviour has, however, already been turned to account in the synthesis of one banana variety.

A cross between a parthenocarpic, male-fertile, diploid form of M. acuminata Colla and a non-parthenocarpic diploid form of *M. Balbisiana* Colla gave a plant closely similar to an established variety carried in the collection as Type-20. The result not only helps to prove the hybrid nature of Type 20, but may be regarded as probably only the first step towards further success in the synthesis of genotypes imitating established varieties with great consequent gains in our knowledge of the constitutions of those varieties.

Sterility

Sterility in the bananas is of practical importance whether regarded as an essential feature of any commercial genotype or as the greatest obstacle to breeding operations. From either point of view the analysis of its causes is necessary.

Research to date indicates that some female sterility is probably inseparable from parthenocarpy, representing another expression of the same factors. Some sterility of both sexes in triploids must be ascribable directly to the triploid state. In addition to these causes, structural sterility, which can be demonstrated in certain non-parthenocarpic diploids, must complicate the situation in the parthenocarpic polyploidy. In certain clones, though not in all, there is good evidence of species hybridity as a possible fourth factor inducing sterility.

The investigation of sterility thus provides a connecting link between botanical survey, studies of polyploidy, and studies of parthenocarpy. Direct analysis of the complicated forms must be written off for some time to come as quite impossible. But by proceeding from the simpler forms to others a little more complex, and working simultaneously along the several lines that have been discussed, progress is being made.

Summary

An account has been given of botanical researches on bananas at the Imperial College of Tropical Agriculture since 1922.

The immediate object of the researches is the production of a commercial banana .combining resistance to certain diseases with suitability for the export trade.

The long-range object pursued simultaneously is to obtain such knowledge of the origins, relationships, and genetic systems of the group as will facilitate banana breeding in general in case new needs for it arise.

Many years were spent in attempts to produce the desired type by methods that are largely empirical ; but the information so obtained finally permitted analysis of the problem and formulation of a more scientific programme.

An attempt has been made to show how botanical studies of wild and cultivated forms, and studies of polyploidy, parthenocarpy and sterility have to be integrated to the desired end.

Publications

The following is a chronological list of papers on the botany and breeding of bananas (excluding pathology and fruit storage research) that have been published from the Imperial College of Tropical Agriculture:-

1925 Dash, J. S. - Bananas from seed. Proc. 9th *W.I. Agric. Conf., Jamaica,* 1924, pp. 53-56.

1928 Harland, S. C. - Bananas and Citrus. *Trop. Agriculture (Trin.)* 5 : 23-24, 54-56, 90-91.

1931 Cheesman, E. E. - Banana breeding at the Imperial College of Tropical Agriculture. *Empire Marketing Board Publ.* 47, H.M.S.O., London.

Cheesman, E. E., A note on *Musa ornata*. Kew Bull. 1931 ; 297-99.

1932 Cheesman, E. E. - Genetic and cytological studies of *Musa* L. I. Certain hybrids of the Gros Michel banana. *J. Genet.* 26 : 291-312.

Cheesman, E. E. - Genetic and cytological studies of *Musa* L. II. Hybrids of the Mysore banana. *J. Genet*. 26 : 313-16.

Cheesman, E. E. - Gros Michel and Pisang Embun. *Trop. Agriculture (Trin.)* 9: 87 and 166.

1933 Cheesman, E. E. - Mutant types of the Dwarf banana. *Trop. Agriculture (Trin.)* 10: 4-5. Cheesman, E. E., Wardlaw, C. W. and Spencer, G. E. L. - The Cavendish group of banana varieties, with special reference to Lacatan. *Trop. Agriculture (Trin.)* 10: 218-221.

1934 Cheesman, E. E. - Principles of banana breeding. Trop. Agriculture (Trin.) 11 : 132-37 ; 176-81 ; 203-208. (Reprinted with change of pagination as *Memoirs of the Imperial College of Tropical Agriculture, Botanical Secries* No. 3, 1934).

1935 Cheesman, E. E. and Larter, L. N. H. - Genetical and cytological studies of *Musa* L. III. Chromosome numbers in the *Musaceae*. *J. Genet.* 30: 31-52.

1937 Cheesman, E. E. and Wardlaw, C. W. – Specific and varietal susceptibility of bananas to Cercospora leaf spot. *Trop. Agriculture (Trin.)* 14 : 335-36.

1942 Cheesman, E. E. and Dodds, K. S. – Genetical and cytological studies of *Musa* L. IV. Certain triploid clones. *J. Genet.* 43 : 337-57.

1943 Dodds, K. S. - Genetical and cytological studies of *Musa* L. V. Certain edible diploids. *J. Genet.* 45 : 113-138.

Dodds, K. S. - The genetic system of banana varieties in relation to banana breeding. *Empire. Expt. Agric.* 11 : 89-98.

1945 Dodds, K. S. - Genetical and cytological studies of *Musa* L. VI. The development of the female cells of certain edible diploids. *J. Genet*. 46 : 161-179.

1946 Dodds, K. S. and Pittendrigh, C. S. - Genetical and cytological studies of *Musa* L. VII. Certain aspects of polyploidy. *J. Genet.* 47: 162-177.

Dodds, K. S. and Simmonds, N. W. - Genetical and cytological studies of *Musa* L. VIII. The formation of polyploid spores. *J. Genet.* 47 : 223-241.

Dodds, K. S. - *Musa* Fehi. *Nature* 157 : 729-730.

1947 Cheesman, E. E. - The genus Ensete Horan. *Kew Bull.* 1947 : 97-106.

Cheesman, E. E. - A new classification of the genus *Musa* L. *Kew Bull.* 1947: 106-117.

1948 Cheesman, E. E. - Notes on species of *Musa* L. *Kew Bull.* 1948.

Dodds. K. S. and Simmonds. N. W.-Genetical and cytological studies of *Musa* L. IX. The origin of an edible diploid and the significance of interspecific hybridisation in the banana complex. *J. Genet.* 48 : 285-296.

Dodds, K. S. and Simmonds, N. W. - Sterility and parthenocarpy in diploid hybrids of *Musa*. *Heredity* 2 : 101-117.

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