EXPERIMENTS ON THE POLLINATION OF SEEDED DIPLOID BANANAS

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I. Introduction

The assumption is often made that yields of seed on crossing different species or strains of plant reflect the relationship of the plants that are crossed, a high yield indicating a close relationship, and vice versa. This assumption evidently holds good, in a broad sense, in bananas, and has proved a useful source of hypothesis for cytogenetic test. However, seed-setting in bananas, as in all other plants, is subject to the vagaries of season; and a pollination repeated at different times shows wide variation in the results that are obtained. A means of eliminating, or at least of estimating, the effects of variation in the environment would clearly lead to much more accurate characterization of seed yields and hence of relationships. Such a means was devised by Dr K. S. Dodds, and he and the writer carried out one experiment. The method was then used by Mr J. R. Spence in a study made in this department and submitted as a thesis for the Associateship of the Imperial College of Tropical Agriculture. And, finally, another series of experiments was carried out by the present writer.

II. Materials and methods

(a) *Plant material*

The table on p. 33 shows a list of plant material; all were diploid with $2n=22$, except *Musa violascens* with $2n=20$.

(b) *Methods*

The proximal part of a bunch of bananas consists of nodal clusters (hands) of female flowers (fingers), the flowers (in the forms used as female parents, at least) being biseriately arranged. Each hand was treated as a block, individual fingers or pairs of adjacent fingers as plots. Different pollens were applied to the plots at random, the whole forming a randomized block experiment. At maturity the bunch was harvested and records made of 'good' and 'bad' seeds, i.e. seeds that sank and floated in water respectively, experience having shown that the former normally contained an embryo and endosperm while the latter were variously deficient in these structures. Results for 'good' seed alone are treated here. Pollen was applied to the stigmas in paper-lined plasticine cups which could easily be pinched on to the stigma; in the first experiment carried out (No. 6) gelatin capsules were used but found to be difficult to handle and liable to fall off the stigma. It has been shown that the presence of the plasticine cup does not interfere with normal fertilization (Table 1).

The numbers of seeds per plot ranged from 0 to 623. With so great a range of values, a correlation of means and variances might be expected, especially for the smaller seed numbers. Some experiments, indeed, showed clear evidence of such a correlation, and this makes direct application of the analysis of variance undesirable. The device adopted was to

Plant material

Section	Species	Clone	Introduction no.	Notes
Eumusa	*M. Balbisiana* Colla	Ceylon	100	(1)
		Assam	242	(1)
		Calcutta 5	126	—
		Brachycarpa	83	—
		Mauritius	103	—
	M. acuminata Colla	A (Selangor)	53	(1)
		Pisang Lilan	143	(2)
		D	84	(1)
		E	85	(1)
		G	55	(1)
		L	109	(1)
		Buitenzorg	205	(1)
		Annam	144	(1)
		Calcutta 4	124	(1)
		Tavoy	187 A	(1)
		Long Tavoy	187 B	(1)
		Mariani	209	(1)
		Assam A	241	(1)
		Assam B	242 F	(1)
		Langet	269 A, B	(3)
		Borneo	291	(3)
		Pahang	296	(3)
		Wete	310	(3)
		Kedah	180	(3)
	M. Banksii F.v.M.	Bloomfield	139	(1)
	M. errans (Blanco) Teodoro		181	(4)
	M. Basjoo Sieb.		78 A	(1)
	M. itinerans Cheesm.		185	(1)
		Kermode	188 A	(1)
Rhodochlamys	*M. ornata* Roxb.	A	1	(1)
	M. velutina Wendl. & Drude		212	(1)
	M. sanguinea Hook. f.		207	(1)
Callimusa	*M. violascens* Ridl.		108	(1)

Hybrids	Parentage	Notes
S.H. 9	*M. acuminata* A × Calcutta 4	(5)
S.H. 11	*M. Banksii* New Guinea × *M. acuminata* A	(5)
S.H. 13	Calcutta 4 × *M. Banksii* Samoa	(5)
S.H. 19	Calcutta 6 × *M. acuminata* A	(5)
S.H. 20	Calcutta 6 × Calcutta 4	(5)
S.H. 25	Calcutta 4 × *M. Banksii* New Guinea	(5)
S.H. 33	Calcutta 6 × *M. Banksii* New Guinea	(5)
426 A	Long Tavoy × Pisang Lilan	(6)
265	Calcutta 4 × Pisang Lilan	(6)
206	*M. acuminata* A × Pisang Lilan	(6)

Notes. (1) Meiosis and origins have been described by Simmonds & Dodds (1949). It was essentially regular in all but two clones, namely: *M. acuminata* E (85), which was partially asynaptic; and Kermode (188 A), which is probably a natural interspecific hybrid between *M. Balbisiana* and *M. Nagensium* Prain., and which is virtually male sterile (Cheesman, 1948). (2) An edible diploid closely allied cytogenetically to *M. acuminata* A (Dodds, 1943; Dodds & Simmonds, 1948). Heterozygous for interchange. (3) These five clones are recent accessions which are yet incompletely classified. Langet A and B are siblings of Malayan origin, one the yellow-bracted form referred to *M. flava* Ridl., the other typical Malayan *acuminata* with red bracts; Pahang and Kedah are also Malayan in origin; Borneo came from south-east Borneo and is apparently the small-fruited form referred to *M. microcarpa* Becc. Wete came from Pemba, and the presence of *M. acuminata* in Africa is something of a mystery (Baker & Simmonds, 1949); it is phenotypically like some Malayan forms. (4) Phenotypically very like Calcutta 4 and probably only a form of *M. acuminata* (Cheesman, 1948). Our clone was received as seed from Jamaica, and may not be true to label, however. (5) Calcutta 6 and clones of *M. Banksii* were weakly and have been lost in Trinidad. The former, however, was very close to Calcutta 4; and the latter also probably falls within *M. acuminata* (Cheesman, 1948). Most of these hybrids are heterozygous for interchange (cf. Dodds & Simmonds, 1948). (6) Families of hybrids of which more members than one have been used in the pollination experiments. All were heterozygous for interchange and segregated for parthenocarpy (Dodds & Simmonds, 1948).

reject from the statistical analysis all pollen treatments for which the mean per plot was less than 40; this eliminated obvious signs of correlation between means and standard errors and kept the remaining treatments within a reasonable range (Cochran, 1938). As an alternative, the transformation $\sqrt{(X+0\cdot5)}$ was tried in a few experiments and gave essentially the same results on analysis. A logarithmic transformation ($\log_{10}(X+1)$) was also tried but proved to be too 'powerful', in the sense that high means now had the smaller standard errors. The rejection of treatments with low means therefore seemed to be a satisfactory and simple expedient, and the arbitrary level of rejection adopted is believed to have eliminated personal bias.

Table 1. *Calcutta 4: mean seeds per fruit pollinated by Calcutta 4 and Ceylon*

Pollen was applied in plasticine cups and to the unprotected stigmas. Each entry is the mean of eight plots in a randomized experiment.

	Pollen			
	Calcutta 4		Ceylon	
	Plasticine cup	Unprotected stigma	Plasticine cup	Unprotected stigma
Good seed	75·50	77·25	4·75	4·25
Bad seed	28·50	27·50	63·50	64·38

III. Results

(1) *General*

The structures and analyses of the fifteen experiments are set forth in Table 2. It will be seen that Hands (Blocks) are significant in seven of them, and this is doubtless to be attributed to day-to-day changes in weather, successive hands commonly being exposed on successive days. Pollens are significant in twelve experiments, and variance due to this cause is generally far in excess of that attributable to Hands. Coefficients of variation suggest that the experiments are of rather unequal value, since three are low (under 10%), seven medium (10–20%) and five high (over 20%). At best, such an experiment can evidently achieve a remarkably sensitive discrimination of pollen effects (Exp. 9, with a least significant difference of about four seeds per fruit).

The high coefficients of variation and the overall difference in fertility of the two experiments (Table 4) on *M. acuminata* A are noteworthy. This clone shows a genotypically controlled failure of fertilization of a proportion of embryo-sacs which leads to an observed average seed yield of about 50 as against an expected 90 (Dodds, 1945; Dodds & Simmonds, 1948). Evidently, however, genotypic control sometimes breaks down, and uncertainty of degree of fertilization is added as a source of variation in seed fertility to the normal vagaries of seed development. Thus the clone may well be an inherently unfavourable subject for experiment; in which it is to be contrasted with, for example, Calcutta 4 and Long Tavoy (Tables 5 and 6).

(2) *Pollination of* Musa Balbisiana

Table 3 records the results of Exp. 1. All clones of *M. Balbisiana* gave comparable though significantly variable yields of seed on Ceylon. Two other species of Eumusa and the hybrid, Kermode, gave very low yields. It is noteworthy that pollination by Assam significantly exceeded self-pollination by Ceylon; it will be shown below that similar behaviours are common in *M. acuminata*.

Table 2. *Structures and analyses of experiments on the pollination of seeded bananas*

No.	Clone	Hands (Blocks)	Pollens†	Ovaries per plot	Mean squares* Hands	Pollens	Error	c.v. (%)
1	*Balbisiana* (Ceylon)	7	5 (8)	2	28,771**	81,781**	3,064	14·3
2	*Acuminata* A	3	9 (16)	1	2,392**	175	135	20·1
3	*Acuminata* A	4	11 (12)	1	177	1,016	650	36·6
4	*Acuminata* (Calcutta 4)	6	14 (19)	1	677**	2,329**	168	15·0
5	*Acuminata* (Calcutta 4)	5	8 (10)	2	763	1,636	699	27·6
6	*Acuminata* (Calcutta 4)	2	6 (10)	2	833	4,342*	437	22·1
7	*Acuminata* (Calcutta 4)	5	3 (12)	1	50	1,201**	44	11·6
8	*Acuminata* (Long Tavoy)	4	9 (9)	2	112	2,481**	210	13·5
9	*Acuminata* (Long Tavoy)	3	6 (9)	2	571**	219**	17	4·2
10	*Acuminata* (Annam)	4	9 (12)	1	1,042*	436**	36	9·9
11	*Acuminata* (Buitenzorg)	6	12 (12)	1	1,542**	1,509**	206	10·4
12	Mariani	3	7 (7)	2	319	9,631**	148	11·2
13	Mariani	6	11 (14)	1	216	2,627**	148	18·8
14	Assam A	3	6 (7)	2	1,949**	19,478**	226	6·9
15	Assam B	2	7 (7)	2	5,884	7,987*	1,451	23·9

* One asterisk (*) indicates significance at the 5% level, two (**) at the 1% level.
† Number of pollens for which the analysis was made; in brackets, total number of pollens used.

Table 3. *Exp.* 1: *pollination of* Musa Balbisiana *clone Ceylon*
Pollen parents and mean numbers of seeds per fruit arranged in descending order of size

A vertical line indicates level of rejection for analysis, an oblique line a significant difference. Self-pollination in bold-face type.

Assam, 261·8/; **Ceylon, 225·0**; Calcutta 5, 201·2/; *brachycarpa*, 158·3/; Mauritius, 124·7|; *M. itinerans*, 7·1; Kermode, 0·8; *M. Basjoo*, 0·6.
Least significant difference (5%), 30·5.

Table 4. *Exps.* 2 *and* 3: *pollination of* Musa acuminata *clone A*
Pollen parents and mean numbers of seeds per fruit arranged in descending order of size

A vertical line indicates level of rejection for analysis. Self-pollination in bold-face type.

Exp. 2: *Acuminata* L, 67·3; **Acuminata A, 65·3**; Calcutta 4, 61·7; Annam, 61·0; *M. errans*, 59·3; Tavoy, 58·0; *Acuminata* G, 57·0; *Acuminata* D, 47·3; S.H. 9, 44·3|; Long Tavoy, 30·0; Buitenzorg, 23·0; S.H. 25, 2·7; Mariani, 2·3; Assam A, 1·3; *Acuminata* E, 0·7; Pisang Lilan, 0·7.

Exp. 3: Pahang, 85·8; **Acuminata A, 84·8**; Langet A, 84·0; Buitenzorg, 81·5; *Acuminata* L, 80·3; Long Tavoy, 78·5; Annam, 63·0; Calcutta 4, 61·0; Wete, 58·0; *Acuminata* D, 49·8; Borneo, 40·3|; Mariani, 3·5.

Table 5. *Exps.* 4–7: *pollination of* Musa acuminata *clone Calcutta* 4
Pollen parents and mean numbers of seeds per fruit arranged in descending order of size

A vertical line indicates level of rejection for analysis, an oblique line a significant difference. Self-pollination in bold-face type.

Exp. 4: *M. errans*, 100·3; Long Tavoy, 97·8/; **Calcutta 4, 78·0**; Tavoy, 77·5; S.H. 20, 76·5; S.H. 9, 75·8/; Annam, 52·2; S.H. 25, 51·8; *Acuminata* L, 49·3; S.H. 13, 48·8; *Acuminata* A, 47·2; Buitenzorg, 45·5; S.H. 19, 44·0|; *Acuminata* G, 35·2; *Acuminata* D, 32·5; S.H. 33, 31·7; Pisang Lilan 27·7; Assam A, 20·5.
Least significant difference (5%), 15·0.

Exp. 5: **Calcutta 4, 65·3**; S.H. 9, 56·5; 265 (17), 49·0; *Acuminata* A, 46·7; 265 (6), 45·9; 206 (10), 41·6; Bloomfield, 41·0; Pisang Lilan, 37·8|; 426A (3), 7·7; 426A (1), 4·3.

Exp. 6: Long Tavoy, 85·0; **Calcutta 4, 61·0**; *Acuminata* A, 51·8; *M. ornata*, 32·5; Mariani, 29·0; Pisang Lilan, 24·3|; *M. violascens*, 7·8; Ceylon, 0·8; *M. itinerans*, 0·5; *M. Basjoo*, 0·5.
Least significant difference (5%), 26·9.

Exp. 7: Long Tavoy, 72·2/; **Calcutta 4, 57·0/**; *Acuminata* A, 41·2|; *Acuminata* L, 38·0; Pahang, 37·6; Wete, 37·4; Annam, 36·6; Buitenzorg, 34·8; Langet A, 34·6; *Acuminata* D, 33·6; Borneo, 33·0; Assam A, 8·0.
Least significant difference (5%), 9·6.

Table 6. *Exps.* 8 *and* 9: *pollination of* Musa acuminata *clone Long Tavoy*
Pollen parents and mean numbers of seeds in descending order of size

A vertical line indicates level of rejection for analysis, an oblique line a significant difference. Self-pollination in bold-face type.

Exp. 8: Calcutta 4, 62·0; *M. errans*, 61·8; Tavoy, 61·3; Annam, 59·0; **Long Tavoy, 57·4**; *Acuminata* G, 55·9; Buitenzorg 53·5; *Acuminata* L 49·0 |; *Acuminata* E, 23·5.
Least significant difference (5 %), 10·6.

Exp. 9: *M. errans*, 51·3; Calcutta 4, 49·5; Tavoy, 49·0 /; Buitenzorg, 44·0; **Long Tavoy, 41·7**; Annam, 41·7 |; *M. ornata*, 0·0; *M. sanguinea*, 0·0; *M. velutina*, 0·0.
Least significant difference (5 %), 3·8.

Table 7. *Exps.* 10 *and* 11: *pollination of* Musa acuminata *clones Annam and Buitenzorg*
Pollen parents and mean numbers of seeds per fruit arranged in descending order of size

A vertical line indicates level of rejection for analysis, an oblique line a significant difference. Self-pollination in bold-face type.

Exp. 10, Annam: Calcutta 4, 70·5; Long Tavoy, 67·8; Langet 67·0; **Annam, 67·0**; Pahang, 65·8; *Acuminata* A, 64·5; *Acuminata* L, 57·0 /; Borneo, 44·3; Buitenzorg, 42·8 |; *Acuminata* D, 32·3; Wete, 22·0; Assam A, 19·5.
Least significant difference (5 %), 8·8.

Exp. 11, Buitenzorg: *Acuminata* A, 159·0; Wete, 152·8; **Buitenzorg, 152·2**; Pahang, 150·7; Borneo, 148·5; Langet B, 146·0; *Acuminata* L, 137·7; *Acuminata* D, 134·0; Long Tavoy, 128·8; Annam, 119·2; Calcutta 4, 117·7; Assam A, 111·5.
Least significant difference (5 %), 16·6.

Table 8. *Exps.* 12–15: *pollination of Mariani, Assam A and Assam B*
Pollen parents and mean numbers of seeds per fruit arranged in descending order of size

A vertical line indicates level of rejection for analysis, an oblique line a significant difference. Self-pollination in bold-face type.

Exp. 12, Mariani: **Mariani, 99·8**; Assam A, 91·3 /; Annam, 43·0; Long Tavoy, 40·3; *Acuminata* A, 36·2; Buitenzorg, 35·5; Calcutta 4, 35·2.
Least significant difference (5 %), 10·8.

Exp. 13, Mariani: Assam B, 109·2 /; **Mariani, 90·5**; Borneo, 84·5 /; Annam, 63·7; *Acuminata* D, 61·3; Pahang, 57·2; Langet, 53·2; Buitenzorg, 51·2; *Acuminata* A, 51·0; Kedah, 45·2; Wete, 45·0 |; Long Tavoy, 32·8; *Acuminata* L, 32·7; Calcutta 4, 29·5.
Least significant difference (5 %), 14·1.

Exp. 14, Assam A: Mariani, 158·2; Assam B, 149·7 /; **Assam A, 126·7** /; *Acuminata* L, 81·7; Annam, 81·3 /; *Acuminata* A, 61·8 |; *Acuminata* E, 13·0.
Least significant difference (5 %), 13·7.

Exp. 15, Assam B: Mariani, 121·5; Assam A, 110·8; Calcutta 4, 90·0; Annam, 84·5; Buitenzorg, 69·5; Long Tavoy, 46·0; *Acuminata* A, 36·0.
Least significant difference (5 %), 46·6.

(3) *Pollination of* Musa acuminata

The remaining fourteen experiments (2–15) were all made on clones of *M. acuminata* and results are recorded in Tables 4–8. Points to note are that:

(1) Pollination by a related clone (as in Exp. 1) sometimes gave more seed than self-pollination (Exps. 2, 3, **4**, 6, **7**, 8, **9**, 10, 11, **13**, **14**—significant differences in bold face type).

(2) Pollination by widely different species (Tables 5 and 6, Exps. 6 and 9) gave low yields of seed, with the exception of *M. ornata* on Calcutta 4 (Exp. 6). In this case, it is known that the F_1 hybrid seedlings are inviable. *M. violascens* in the same experiment, it may be noted, has $2n = 20$, an illustration of the ease of crossing of some widely different species of *Musa*.

(3) If attention is now confined to pollinations within *M. acuminata*, it will be seen that the following grouping (after Cheesman, 1948) is indicated:

Selangor form	Tavoy form	Annam form	Buitenzorg form	Mariani form
Acuminata A	Calcutta 4	Annam	Buitenzorg	Mariani
Acuminata L	Long Tavoy		Borneo (?)	Assam A
Pahang	*M. errans*			Assam B
Langet	Tavoy			

Table 9 summarizes information on 'crossability' of the five forms, and it is at once apparent that there is a considerable range of differentiation. The Mariani form is markedly separated from all the others. The Selangor-Tavoy distinction is fairly clear—it is, incidentally, accompanied by interchange (Dodds & Simmonds, 1948). The Annam and Buitenzorg forms show affinities with both Selangor and Tavoy but are not close to each other. These conclusions are in very fair agreement with the taxonomy of Cheesman (1948) and lead perhaps to the expectation that the Mariani form may ultimately have to be regarded as a distinct species, while further study of the other forms may reveal simply

Table 9. *Intraspecific differentiation in* Musa acuminata
Seed-setting as percentage of self-pollination

Bold-face type, self-pollination; italics, values based on experiments having coefficients of variation of 20 % or more; roman, values based on experiments having coefficients of variation of less than 20 %.

	Male							
Female	*Acuminata* A	*Acuminata* L	Buitenzorg	Annam	Calcutta 4	Long Tavoy	Mariani	Assam A
Acuminata A	**100**	*99*	*66*	*84*	*83*	*70*	*4*	*2*
Buitenzorg	105	91	**100**	78	77	85	—	73
Annam	96	85	64	**100**	105	101	—	29
Calcutta 4	73	65	60	66	**100**	131	*48*	20
Long Tavoy	—	85	100	102	114	**100**	—	—
Mariani	46	36	47	57	34	38	**100**	91
Assam A	49	65	—	64	—	—	125	**100**

Simplified summary by taxonomic forms, neglecting direction of cross

	Mariani	Tavoy	Buitenzorg	Annam	Selangor
Selangor	32	74	82	87	99
Annam	52	90	71	100	—
Buitenzorg	57	80	100	—	—
Tavoy	33	117	—	—	—
Mariani	106	—	—	—	—

some cytological differentiation within a mass of intergrading phenotypes rather than the existence of distinct taxonomic entities.

The following are not certainly to be placed on the evidence available: *M. acuminata* G, *M. acuminata* D, Bloomfield, Wete and Kedah. The poor setting by pollen of *M. acuminata* E is to be attributed to its partial asynapsis and consequent pollen sterility (p. 33, note (1)).

(4) Two experiments (4 and 5, Table 5) on Calcutta 4 give information on the use of various hybrids as male parents (Table 10). It will be seen that agreement of observed and expected values is, in three cases, good, but that (1) there is considerable variation in the observed values in the second line (Tavoy × Selangor), and (2) Tavoy × Pisang Lilan shows an outstanding disagreement for which no explanation can be advanced at present. Results for Tavoy × *M. Banksii* are in accord with general expectation, since it is known

(unpublished) that *M. Banksii* is cytologically rather close to the Selangor form of *M. acuminata*.

The calculation of expectations needs some justification. They have been computed here as means of percentage seed-setting of the clones parental to the hybrids when used themselves as pollen parents. Two examples will suffice to indicate the theoretical background. Suppose that parents are homozygous for genes which, in hybrid combinations, are responsible for inviability of young zygotes and that such combinations are characterized, not by an all-or-nothing reaction, but rather by a proportion of inviability which varies with genetical and local physiological circumstance. We may then consider two simple theoretical models, namely: (1) dominant interaction and (2) inviability of heterozygotes.

(1) Suppose **AAbb** and **aaBB** are parents, giving 100% viable progeny on selfing; they will give an F_1 **AaBb**, of which a proportion, p, is supposed viable in the young zygotic stage. Backcross genotypes and their contributions to total viable zygotes will be

$$\mathbf{AAbb}\ (0{\cdot}25)+\mathbf{AABb}\ (0{\cdot}25p)+\mathbf{AaBb}\ (0{\cdot}25p)+\mathbf{Aabb}\ (0{\cdot}25).$$

Summing contributions to viability, we have $0{\cdot}50\ (p+1)$, that is, the mean of selfing the recurrent parent and of the F_1 seed yield, as used above.

Table 10. *Hybrids of* Musa acuminata *and Pisang Lilan as male parents on Calcutta* 4 (*Exps.* 4 *and* 5). *Observed and expected seed-setting as percentage of setting on self-pollination*

Origins of male parents	Type of cross	Seed-setting on Calcutta 4 (%) Observed*	Expected†
Calcutta 6 × Calcutta 4	Tavoy × Tavoy	98	100
Calcutta 4 or 6 × *M. acuminata* A	Tavoy × Selangor	97, 87, 41 (75)	83
Calcutta 4 or 6 × *M. Banksii*	Tavoy × *M. Banksii*	67, 63, 56 (62)	?
Calcutta 4 × Pisang Lilan	Tavoy × Pisang Lilan	70, 81 (76)	76
M. acuminata A × Pisang Lilan	Selangor × Pisang Lilan	64	57
Long Tavoy × Pisang Lilan	Tavoy × Pisang Lilan	7, 12 (10)	74

* Means in brackets.

† Means of percentages set by parents on Calcutta 4. Calcutta 6 closely related and assumed equivalent to Calcutta 4.

(2) Suppose the parents are **AA** and **aa** giving 100% viable progeny on selfing. The F_1 is **Aa**, which is supposed p viable in the young zygotic stage. Viability in the backcross is then $0{\cdot}5\ (p+1)$, as before.

If two or more loci operate the results are more complicated. Thus with parents **AABB** and **aabb** and an F_1, **AaBb** which is p viable, we have in the backcross:

$$\mathbf{AaBb}\ (0{\cdot}25p)+\mathbf{Aabb}\ (0{\cdot}25r)+\mathbf{aaBb}\ (0{\cdot}25s)+\mathbf{aabb}\ (0{\cdot}25).$$

The total of viable zygotes is $0{\cdot}25\ (p+r+s+1)$. If we take $r=s=1$ (single heterozygotes fully viable) this becomes $0{\cdot}25\ (p+3)$, which exceeds $0{\cdot}50\ (p+1)$ for all values of p, except $p=1$. If we suppose that **Aa** and **Bb** act independently $p=rs$, and the expression becomes $0{\cdot}25\ (r+1)\ (s+1)$. If, here, $r=s=t$, say, we have $0{\cdot}25\ (t+1)^2$, which is always less than $0{\cdot}50\ (p+1)$, except, again, where $t=1$.

These models are, of course, crude and unlikely to accord exactly with genetical events, but they do provide some sort of conceptual background to Table 10 and help to justify the calculation of expectations.

IV. Discussion

(1) *General*

The experiments described above are, in general, of little value where distantly related clones are used. The finding, for example, that pollens of three species of Rhodochlamys yielded no seed on Long Tavoy (Exp. 9, Table 6) gives no information that is not immediately evident to ordinary taxonomic inspection. Furthermore, it obviously cannot be concluded that because several different pollens give comparably low yields on a certain clone that the clones producing those pollens are related; they merely agree roughly in the distance of relationship to the clone used as female. Thus, in Exp. 6 (Table 5), there is reason to think that *M. itinerans* and *M. Basjoo* are related but that they are far distant from *M. Balbisiana* and *M. violascens*. And, of course, low numerical values are not suitable for statistical analysis.

By contrast, when the pollens used give high yields of seed, the method permits of a fine discrimination between closely related pollens and is thus a powerful adjunct to ordinary cytogenetic and taxonomic study at the intraspecific level. Indeed, it gives some results which could hardly be established by any other means—for example, the finding that yields on self-pollination may be exceeded by those from a close cross-pollination.

(2) *Yields from close cross-pollination*

In both *M. Balbisiana* and *M. acuminata* it was found that pollination by closely related clones sometimes gave seed yields significantly larger than those resulting from self-pollination (Exps. 1, 4, 7, 9, 13, 14). The actual magnitude of the difference is rather variable; mean increases of seed set by cross- over self-pollination as percentages of self-pollination were: Exp. 1, 16%; Exp. 4, 26%; Exp. 7, 27%; Exp. 9, 18, 19 and 23%; Exp. 13, 21%; Exp. 14, 18 and 25%. This implies that there is normally some loss of potential female fertility on self-pollination caused by the elimination in development of certain inviable zygotes, probably homozygous for deleterious recessive genes or structural changes.

V. Summary

1. A method is described for comparing the yields of seed given by different pollens on seeded diploid bananas by adapting the form of the bunch to a randomized block experiment.

2. The results of fifteen experiments are recorded and show that a remarkably accurate discrimination of pollen effects can sometimes, though not always, be achieved.

3. The method has considerable value for the study of relationships at the intraspecific level. Thus *Musa Balbisiana* and *M. acuminata* are shown to be considerably differentiated and, in the latter species, the results accord very well with established cytogenetic and taxonomic knowledge.

4. In both *M. Balbisiana* and *M. acuminata* it was found that pollination by a closely related clone gave higher yields of seed than self-pollination; this was taken to indicate that the clones used were heterozygous for deleterious recessives, homozygous zygotes produced by selfing suffering elimination in development.

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REFERENCES

BAKER, R. E. D. & SIMMONDS, N. W. S. (1949). Report on a visit to British East Africa to study the cultivated and wild bananas. I.C.T.A., unpublished.

CHEESMAN, E. E. (1948). Classification of the bananas. III. Critical notes on species. *Kew Bull.* pp. 11–28.

COCHRAN, W. G. (1938). Some difficulties in the statistical analysis of replicated experiments. *Emp. J. Exp. Agric.* **6**, 157–75.

DODDS, K. S. (1943). Genetical and cytological studies of *Musa*. V. Certain edible diploids. *J. Genet.* **45**, 113–38.

DODDS, K. S. (1945). Genetical and cytological studies of *Musa*. VI. The development of the female cells of certain edible diploids. *J. Genet.* **46**, 161–79.

DODDS, K. S. & SIMMONDS, N. W. (1948). Sterility and parthenocarpy in certain diploid hybrids of *Musa*. *Heredity*, **2**, 101–17.

SIMMONDS, N. W. & DODDS, K. S. (1949). Meiosis in seeded diploids of *Musa*. *J. Genet.* **49**, 221–5.