

SEGREGATIONS IN SOME DIPLOID BANANAS

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(With One Text-figure)

1. INTRODUCTION

The only formal genetics of bananas yet published concerns the inheritance of parthenocarpy in families of the type seeded diploid \times edible diploid. In one such family parthenocarpy appeared to be due to a single dominant gene (**P**), the expression of which, however, was affected by modifiers, but in another case the genetical situation was more complex and was, for the time being, left unanalysed (Dodds & Simmonds, 1948*a*). In this paper the genetical analysis of parthenocarpy is advanced by means of data from several other families, and it is shown that a series of dominants are necessary for the expression of the character. Data are also presented bearing on the segregations from an interracial and from an interspecific cross, the conclusions to be drawn having some evolutionary and taxonomic interest.

2. MATERIALS AND METHODS

The plants used fall into four categories convenient for the present purpose:

(1) *Musa acuminata* Colla. Wild seeded forms of the species and hybrids between them.

Selangor (I.R. 53): a slender, waxy, pigmented plant, typical of the Selangor (Malayan) form of the species (Cheesman, 1948).

Calcutta 4 (I.R. 124): a shorter, non-waxy, little-pigmented plant typical of the Tavoy (Burmese) form of the species (Cheesman, 1948).

Long Tavoy (I.R. 187B): closely allied to Calcutta 4 (Simmonds, 1952) but having a neater bunch and longer fruits, thus having value as breeding material.

Samoa (I.R. 123): one of the forms of *M. Banksii* F.v. M. (Cheesman, 1948). The clone died some years ago and figures here only as a parent of S.H. 13, q.v.

S.H. 9—Selangor \times Calcutta 4: Heterozygous for two interchanges (Dodds & Simmonds, 1948*a*). Used here for the analysis of racial difference.

S.H. 13—Calcutta 4 \times Samoa: has a shapely bunch and rather long fruits and so is of breeding value in some of its parthenocarpic derivatives.

(2) *M. acuminata*. Edible diploids.

Pisang Lilan (I.R. 143): from Malaya. Very closely allied to Selangor from which it differs principally in parthenocarpy and in interchange (Dodds, 1943; Dodds & Simmonds, 1948*a*). Female-sterile but about 50 % male-fertile and much used in breeding and cytogenetic study.

Palembang (I.R. 56): phenotypically like Selangor but the plant is shorter and more densely stooling and the bunch has fewer and fatter fruits. It is heterozygous for interchange (Dodds, 1943) and virtually completely female- and male-sterile; only two seedlings have ever been raised from it, namely, I.C. 52 and I.C. 54, below.

(3) *M. acuminata*. Derivatives of the edible diploids.

I.C. 52: Palembang \times Selangor; a non-parthenocarpic plant heterozygous for one interchange.

I.C. 54: Palembang \times Calcutta 4: a parthenocarpic plant heterozygous for one or two interchanges.

265(16)—Calcutta 4 \times Pisang Lilan: a selection from the family described by Dodds & Simmonds (1948*a*); it has a neat vertical bunch of fully parthenocarpic fruits.

426 A(5)—Long Tavoy \times Pisang Lilan: a selection having rather large parthenocarpic fruits.

(4) Miscellaneous species and hybrids.

M. ornata Roxb. Clone A (I.R. 1): section Rhodochlamys.

M. velutina Wendl. & Drude (I.R. 212): section Rhodochlamys.

M. Balbisiana Colla Clone Ceylon (I.R. 100): section Eumusa.

S.H. 69—*M. ornata* \times *M. velutina*: a rather fertile F_1 within Rhodochlamys.

Tests for parthenocarpy were carried out by protecting bunches against insect pollination and scoring for development of edible pulp at or near maturity. Data so obtained were supplemented by examination of unprotected bunches, a method which tends to underestimate the frequency of parthenocarpy since facultatively seeded types (which, however, are not common) may be scored as seeded rather than parthenocarpic. As many bunches as possible of a plant were examined since there is known to be some variation in the incidence of parthenocarpy—a weakly parthenocarpic plant sometimes shoots non-parthenocarpic bunches.

The banana is a large plant and, to be grown to maturity, requires greenhouse space for 3–6 months and a minimum of 70 sq.ft. of land for 18 months or 2 years; this is about seventy times as many land-time units as a maize plant requires under Trinidad conditions. It follows that the numerous crosses and large families customarily used in the investigation of technically more favourable organisms simply are not practicable here. Furthermore, pressure of space and time demands that priority be given to crosses likely to yield breeding material. Genetical inference is therefore both less detailed and less securely established in detail than one would wish, though doubtless the broad lines of the analysis are correct.

3. RESULTS

(a) *The genetics of parthenocarpy*

Results are summarized in Table 1, of which the first eleven entries are concerned with derivatives of Pisang Lilan. There is evidence of segregation of at least three complementary dominants for parthenocarpy. In Table 2 one of several possible schemes of inference is set forth with regard to constitution of parents and so forth; it is the simplest and most plausible though not necessarily correct in all detail—a reflexion of the limitations of *Musa* as genetical material. It does, however, illustrate what seems to be certain, namely, that complementary dominants are responsible for parthenocarpy. Three loci are distinguished, P_1 – p_1 being the one detected in segregation by Dodds & Simmonds (1948*a*). This locus apparently bears a dominant allele only in Pisang Lilan; in the seeded diploids tested it is homozygously recessive, although one or both of the other two loci, P_2 and P_3 , may bear dominants. Evidently some but not all of the genetic materials of

parthenocarpy are available in wild seeded bananas, the 'switch gene' P_1 , only in Pisang Lilan.

Hybrids of Palembang have been studied less than those of Pisang Lilan, principally because Palembang is highly male- and female-sterile and has yielded only two hybrids with seeded diploids. Hence F_1 ratios are unknown. The two hybrids have been back-

Table 1. *Segregation for parthenocarpy in diploid families of Musa*

Family	Parents		Phenotypes*	Nos. of progeny*		Ratio tested	P	Notes	
	Female	Male		P	p				
206	Selangor	× Pisang Lilan	$p \times P$	5	5	1 : 3	0.16	1	
—	Selangor	× 206	$p \times P$	(1)	4	22	1 : 3	0.37	2
				(1)	15	30	3 : 13	0.89	
—	206	× Pisang Lilan	$P \times P$	(2)	6	11	3 : 5	0.68	2
				(1)	26	13	9 : 23	0.34	2
3006	Selangor	× 206	$p \times p$	(4)	0	48	27 : 37	0.75	2
—	206	× Pisang Lilan	$p \times P$	(3)	29	33	9 : 7	0.25	2
—	265	Calcutta 4 × Pisang Lilan	$p \times P$	(1)	19	22	0 : ∞	—	2
265	Calcutta 4	× Pisang Lilan	$p \times P$	(3)	29	33	3 : 5	0.17	2
1071	S.H. 13	× 265 (16)	$p \times P$	(1)	19	22	1 : 1	0.75	1
426 A	Long Tavoy	× Pisang Lilan	$p \times P$	(1)	83	74	1 : 1	0.52	—
3020	S.H. 13	× 426 A (5)	$p \times P$	(1)	3	29	1 : 7	0.84	1
1209	Selangor	× I.C. 52	$p \times p$	(1)	88	71	1 : 1	0.20	3
1156	Calcutta 4	× I.C. 54	$p \times P$	(1)	4	38	—	—	4
				(1)	11	48	—	—	—

* P, parthenocarpic; p, not parthenocarpic.

- Notes: (1) Dodds & Simmonds (1948*a*), in part reinterpreted.
 (2) In brackets after entry under parental phenotypes number of families combined each having different parents in 206.
 (3) Data from two plantings combined (see § 3 (b)); heterogeneity $\chi^2_{(1)} = 0.61$.
 (4) I.C. 52 was reported in error by Dodds & Simmonds (1948*b*) to be parthenocarpic.

Table 2. *The genetics of parthenocarpy in derivatives of Pisang Lilan*

Parents*	Genotypes	F_1 ratio ($P : p$)*	Backcrosses†
Selangor (p) × Pisang Lilan (P)	$P_1 P_1 P_2 P_2 P_3 P_3$ × $P_1 P_1 P_2 P_2 P_3 P_3$	1 : 3 (206)	$\left\{ \begin{array}{l} P \times P \quad 9 : 7, 27 : 37 \S \\ p \times P \quad 1 : 3, 3 : 5, 9 : 23, 3 : 13 \S \\ p \times p \quad 0 : \infty \S \end{array} \right.$
Calcutta 4 (p) × Pisang Lilan (P)	$P_1 P_1 P_2 P_2 P_3 P_3$ × $P_1 P_1 P_2 P_2 P_3 P_3$	1 : 1 (265)	$\left\{ \begin{array}{l} P \times P \quad 3 : 1, 9 : 7, 27 : 37 \\ p \times P \quad 1 : 1, 3 : 5, 9 : 23 \\ p \times p \quad 0 : \infty \end{array} \right.$
Long Tavoy (p) × Pisang Lilan (P)	$P_1 P_1 P_2 P_2 P_3 P_3$ × $P_1 P_1 P_2 P_2 P_3 P_3$	1 : 7 (426 A)	$\left\{ \begin{array}{l} P \times P \quad 27 : 37 \\ p \times P \quad 3 : 13, 9 : 23, 1 : 7 \\ p \times p \quad 0 : \infty \end{array} \right.$
S.H. 13 (p) × 265 (16) (P)	$P_1 P_1 P_2 P_2 P_3 P_3$ × $P_1 P_2 P_2 - P_3 -$	1 : 1 (1071)	—
S.H. 13 (p) × 426 A (5) (P)	$P_1 P_1 P_2 P_2 P_3 P_3$ × $P_1 P_1 P_2 P_2 P_3 P_3$	1 : 1 (3020)	—

- * P, parthenocarpic; p, non-parthenocarpic.
 † Neglecting direction of cross.
 ‡ Selangor could well be heterozygous at P_2 .
 § See Table 1; other backcrosses have not been tested.

crossed to the seeded parents and the results are given in Table 1. Both families segregated a minority of parthenocarpic plants. 1209 is the first case recorded of the production of parthenocarpic progeny by non-parthenocarpic parents. Thus the complementary interaction of several genes is indicated once again. Some of the loci concerned must be different from those responsible for parthenocarpy in Pisang Lilan, but the data are too sparse to make detailed inference worthwhile. But, at least, the general mode of control must be comparable with that inferred for Pisang Lilan.

Parthenocarpy has also segregated in two interspecific hybrids. In *M. Balbisiانا* Ceylon \times Pisang Lilan there were two parthenocarpic and three non-parthenocarpic plants (Dodds & Simmonds, 1948*b*) while in *M. ornata* \times Pisang Lilan the ratio was 3:10. Evidently both these species have genetic backgrounds favourable for the expression of parthenocarpy.

There is an interesting practical corollary to these results. If Selangor or Pisang Lilan is used as male parent on the edible triploid Gros Michel, parthenocarpic tetraploids are produced which suffer from the same phenotypic defects as their male parents, i.e. poorly shaped bunches and, often, small fruits. Long Tavoy has, for a seeded diploid, relatively long fingers and a very shapely bunch, characters which at once indicate its use as a male parent. Only one seedling of parentage Gros Michel \times Long Tavoy has yet been raised to maturity; it usually has a well-shaped bunch of long but non-parthenocarpic fruits. Sometimes, however, it bears a parthenocarpic bunch of excellent size and form. Evidently, Long Tavoy's deficiency in the dominants necessary for parthenocarpy is responsible here for the production of a tetraploid having a marginal dose of the genes necessary for the penetrance of the character. This may prove to be a frequent or even invariable behaviour among the progeny of this cross—the point is under test. Meanwhile, parthenocarpic derivatives of Long Tavoy are being bred (e.g. 3020 and backcrosses to Long Tavoy) with the expectation that not only will their tetraploid descendants be consistently parthenocarpic but that they will also avoid the tendency (which is shown by some tetraploids having a seeded male parent) to set occasional seeds.

(*b*) *The genetics of bract and flower persistence*

There are cultivated varieties of banana which show varying degrees of persistence of the bracts and flowers of the male axis. The character ranges from one in which the axis is completely concealed by the withered relics to one in which it retains only a few clusters of flowers or scattered bracts; often the abortive ovaries of the male flowers swell a little and persist even after the rest of the flower has dropped. Among wild seeded bananas a comparable persistence of bracts is common in *M. Balbisiانا* but is not known in *M. acuminata*; thus in the latter the character is apparently confined to the cultivated, parthenocarpic forms of the species.

Recently, segregation for this persistence has been observed in families of *M. acuminata* derived from crossing seeded diploids by edible diploids, that is, in families used also for the analysis of parthenocarpy. Plants were scored as: non-persistent (Grade 1); slightly persistent (Grade 2, scattered floral relics with or without a few bracts persistent); very persistent (Grade 3, male axis concealed or nearly so by bracts and flowers). Intermediate grades were also distinguished. The character was somewhat inconstant from bunch to bunch of one plant, but in the end plants could fairly confidently all be classified as deciduous (Grade 1) or persistent (Grades 2 and 3), though the latter category covered a considerable range of behaviours.

The three families reported upon here are:

(1) 3006, a backcross of the parthenocarpic 206 (1) by Pisang Lilan (Table 1). Neither the parents (Selangor and Pisang Lilan), nor a selfed family of Selangor, nor the F_1 (206, ten plants) showed any signs of persistence.

(2) 1071, a cross of the parthenocarpic 265(16) to S.H. 13. Of the parents, Calcutta 4 and S.H. 13 and their selfed progenies were non-persistent. One parent of S.H. 13 (i.e.

Samoa) no longer survives and no record of its phenotype exists; but it was most probably deciduous. The family 265 segregated for the character but detailed records are not available; of three survivors, two are deciduous and one (265(16)) persistent (Grade 2).

(3) 3020, which is analogous to 1071 in having S.H. 13 as female parent and a hybrid of Pisang Lilan as male parent. The male parent, 426 A (5), is non-persistent; there is no record of its siblings except that two survivors are also non-persistent. The family has been grown in two places, namely, at the Imperial College of Tropical Agriculture, Trinidad, and at the Banana Breeding Station, Bodles, Jamaica. The segregations for parthenocarpy agreed as between the two plantings, but those for bract persistence did not, as shown below. For this reason the two plantings will be treated as separate families.

Results are given in Table 3. The first three families agree in containing about 40–50 % of persistent plants ($\chi^2_{(2)}=0.72$); the fourth family, however, the Jamaican planting of 3020, contains twice as many and is significantly discrepant ($\chi^2_{(3)}=44.23$). This is evidently an effect of environment, because clones grown and scored in both places show consistently different degrees of persistence; for example, 1071(10) is Grade 1 deciduous in Trinidad but Grade 2 persistent in Jamaica; 265(16) is Grade 2 persistent in Trinidad, Grade 3 in Jamaica. The two places do indeed provide very different environments for bananas.

Table 3. *Joint segregation for parthenocarpy and persistence of bracts and flowers*

Family*	Parthenocarpic		Non-parthenocarpic		Persistent (%)	$\chi^2_{(1)}\dagger$	Q‡
	Deciduous	Persistent	Deciduous	Persistent			
3006	10	16	12	1	44	8.15	0.901 ± 0.105
1071	36	47	59	15	40	23.90	0.674 ± 0.0994
3020(1)	13	20	22	9	45	5.22	0.580 ± 0.177
3020(2)	4	51	14	26	81	9.86	0.746 ± 0.137

* 3020(1) was grown at the I.C.T.A., Trinidad; 3020(2) at the Banana Breeding Station, Bodles, Jamaica. See text.

† All significant at 5 % or higher level of significance.

‡ Yule's coefficient of association; with standard errors. Differences all non-significant.

Those in Trinidad are grown under shade with a fairly high natural rainfall and poor soil; those at Bodles are unshaded and grown in a fertile irrigated land in a dry area. Obviously, detailed analysis of such a variable character is impossible, but nevertheless some interesting conclusions may be drawn from the data. Persistent phenotypes are known only in cultivated *M. acuminata* or in bananas having a recent ancestry of parthenocarpy. In the families under discussion they have been produced from crosses of non-persistent phenotypes in two cases (3006 and 3020), from non-persistent × semi-persistent in one (1071). Complementary gene control is indicated, conditional in action upon the presence of the genetical background of parthenocarpy.

The contingency χ^2_c given in Table 3 show that parthenocarpy and persistence are associated in inheritance. This might be due to linkage or to pleiotropy. The latter is a tempting assumption, for it has been suggested above that the genetical background of parthenocarpy is necessary for the expression of persistence, and the present suggestion is but a slight extension of the same idea. It is a tempting assumption for another reason too, namely, that there is a possible physiological relation between the two characters. Thus, a slight degree of parthenocarpy has recently been induced in unpollinated seeded diploid banana fruits by the application of naphthalene acetic acid, suggesting that parthenocarpic fruit development is due to natural hormone production, as previously proposed by Dodds (1943). A well-known effect of plant hormones is to prevent the

operation of abscission mechanisms, and in bananas naphthalene acetic acid has been shown to prevent or delay the abscission of styles. It is suggested therefore that genetical control of both parthenocarpy and persistence operates through the control of native growth substances and that pleiotropy is responsible for the association between the two characters.

The last column of Table 3 gives Yule's measure of contingency, Q . Differences between families appear to be considerable but are, in fact, non-significant.

It should be added that numerous genetical models have been compared with these data on bract persistence but that no satisfactory fit has been found. Presumably pleiotropy and environmental variation complicate the results beyond the possibility of formal interpretation.

(c) *Segregation from an interracial cross*

Cheesman (1948) has discussed the taxonomy of intraspecific differentiation in the variable *M. acuminata* and has recognized five forms. Dodds & Simmonds (1948*a*) have shown that such intraspecific differentiation is sometimes accompanied by cytological differentiation, the hybrid Selangor \times Calcutta 4 (a cross between the Selangor and Tavoy forms) being heterozygous for two interchanges, though its parents are homozygous. It is this hybrid, S.H. 9, upon which are based the results presented below.

An F_2 and two backcrosses of F_2 plants were raised and the seedlings were scored for three vegetative characters: *Blackness* ranged from (I), a few pale brown markings on the upper parts of the sheaths and lower parts of the petioles to (III), a full dense black which almost completely obscured those parts of the plant; *Redness* ranged from (I), none, to (III), a strong pink flush on the petioles and midribs which was always more prominent on young suckers than on older pseudostems; *Waxiness* ranged from (I), none, to (III), a dense white deposit upon sheaths, petioles and undersides of laminas. Variation in segregating families was continuous; plants were scored on the scale I–III for each character, and intermediate classes I–II and II–III were distinguished, but have been combined with grades II and III respectively in the summary presented below. Families were also scored for certain characters of the inflorescence, namely, the habit of the fruit bunch (vertical-oblique-horizontal), the habit of the male axis (vertical-horizontal), and the disposition of the bracts of the male bud (imbricate or convolute at the tips). The habit of the fruit bunch varies with the vigour of the plant; the degree of imbrication of the bracts of the male bud decreases markedly with increasing age of the bud. Detailed plant-by-plant scorings of inflorescence characters were therefore not attempted.

Results are set out in Table 4. The parents, it will be seen, were virtually true-breeding, though there was, perhaps, slight variation in the degree of blackness in Calcutta 4 \times Calcutta 4. In the F_1 redness and lack of wax are dominant; blackness, however, exceeds that of the darker parent. In the F_2 , variation in plant characters was continuous and, though the vegetative phenotype of Calcutta 4 was approximated in seven plants (14 %), no plant resembling Selangor occurred at all—in particular, no fully waxy plants were recovered. There was no decisive evidence of linkage though $\chi^2_{(1)}$ for Redness-Waxiness and Redness-Blackness were respectively 3.76 and 2.19 with deviations in favour of parental phenotypes. In inflorescence characters the F_2 varied remarkably little; no bunch seen resembled that of either of the parents, and probably few could have been distinguished from that of the hybrid.

Data on fertility of twenty-three F_2 plants are given in Table 5. They were obtained by backcrossing one to three bunches of each by pollen of Calcutta 4 and Selangor. There was no evidence of any difference between the pollens, and so fertilities have been summarized as means of the two pollens. Plants were classified for vegetative phenotype (Blackness, Redness and Waxiness) as in Table 4. In all three cases the median class has

Table 4. *Segregation from an interracial hybrid of Musa acuminata*

Clones and families	Plant characters								
	Blackness			Redness			Waxiness		
	I	II	III	I	II	III	I	II	III
Calcutta 4	×	—	—	×	—	—	×	—	—
Selangor	—	×	—	—	—	×	—	—	×
S.H. 9 (Cal. 4 × Selangor)	—	—	×	—	—	×	×	—	—
1062 (6) (S.H. 9 × S.H. 9)	—	—	×	—	—	×	×	—	—
1062 (55) (S.H. 9 × S.H. 9)	×	—	—	×	—	—	—	×	—
1948 (Cal. 4 × Cal. 4)	30	0	0	30	0	0	30	0	0
1638 A (Sel. × Sel.)	0	10	0	0	0	10	0	0	10
1062 (S.H. 9 × S.H. 9)	17	18	14	30	10	9	24	25	0
1936 A (1062 (6) × Cal. 4)	11	28	13	27	18	6	44	1	7
1936 B (1062 (6) × Sel.)	3	27	15	10	18	17	10	10	25
1973 A (1062 (55) × Cal. 4)	40	12	0	47	5	0	49	3	0
1973 B (1062 (55) × Sel.)	14	33	3	0	22	28	2	18	30

Clone, etc.	Inflorescence characters		
	Habit of fruit bunch	Habit of male axis	Tip of male bud
Calcutta 4	Vertical	Vertical	Imbricate
Selangor	Horizontal	Horizontal	Convolute
S.H. 9	Horizontal	Vertical	Intermediate
1062	Horizontal-oblique	Vertical	Intermediate
1936 A	Horizontal-oblique	Vertical	Imbricate
1936 B	Horizontal	Vertical	Convolute
1973 A	Oblique	Vertical	Imbricate
1973 B	Horizontal	Vertical*	Convolute

* But in occasional plants (c. 10%) it was more or less horizontal.

Table 5. *Fertilities (good seeds per fruit) of twenty-three F_2 plants of Calcutta 4 × Selangor classified by vegetative phenotype; and data on fertilities of parents for comparison*

	Grade*		
	1	2	3
Blackness	8.1 (9)	11.8 (11)	11.4 (3)
Redness	7.6 (14)	19.4 (3)	12.0 (6)
Waxiness	9.2 (11)	11.2 (12)	—

Sums of vegetative grades*†

3	4	5	6	7	8	9
5.0 (3)	7.1 (6)	10.1 (6)	17.2 (6)	7.9 (2)	—	—

For comparison: Selangor × Selangor, 50.0; Calcutta 4 × Calcutta 4, 76.9; Calcutta 4 × Selangor, 30.0; S.H. 9 × S.H. 9, 35.4; S.H. 9 × Selangor, 24.0; S.H. 9 × Calcutta 4, 27.4.

* In brackets: numbers of plants.

† See text.

the highest mean though only in the case of Redness are differences significant (v.r. (2, 20) = 5.3). The data are reclassified in the second part of Table 5 by adding together the three scores; the sums obtained range from 3 (plants resembling Calcutta 4) up to 7 (e.g. S.H. 9), 8 (e.g. Selangor) and 9 (an extreme phenotype which has not been seen). Again, the median class (6) is the most fertile, significantly more so than 4 or 5 and probably 7.

The most fertile single plant (28.4 seeds per fruit) was about as fertile as S.H. 9 (Table 5), but the general average was only 10.3 seeds per fruit. S.H. 9 is heterozygous for two interchanges, and such gametic sterility as occurs can virtually all be attributed to the effects of interchange (Dodds & Simmonds, 1948*a*). 1062 segregated for interchange (as judged by pollen fertility and study of the male cytology of a few plants); certainly some homozygotes were present. Thus if cytological causes alone were responsible for sterility in 1062 we should expect fertility to range from moderate (as in S.H. 9 with two interchanges) to high (in homozygotes). This does not happen; therefore much sterility in 1062 must be due to the segregation of genetically rather than cytologically infertile genotypes.

The backcrosses of F_2 plants showed an equal complexity of segregation for plant characters and variation was again continuous. In inflorescence characters the range of variation was wider than in the F_2 but, even so, the parental limits were not approached (with the possible exception of a few bunches in 1973B).

Formal genetical interpretation of the results is not attempted for it is evident that many genes and complex interactions are involved. Evidently the Selangor and Tavoy forms of *M. acuminata* are highly differentiated, genetically as well as cytologically.

(d) Segregation from an interspecific cross

The two *Rhodochlamys* species *M. velutina* and *M. ornata* are easily crossed; the interspecific hybrid, S.H. 69, is the most fertile yet found in bananas, and this is correlated with a nearly normal male meiosis (10.4 bivalents per nucleus, no interchanges, two inversions). One hundred of its backcross progeny derived from several different pollinations have been tested for ploidy by counting of chromosomes and examination of stomata. All were diploid; hence polyploid spore production, so typical of hybrids of *Musa*, was at least rare in this material; it does, however, occur occasionally in S.H. 69 (see below).

Characters of the parents and F_1 hybrid are:

Character	<i>M. ornata</i>	<i>M. velutina</i>	Hybrid
Plant:			
Suckering	Dense	Sparse	Intermediate
Height	c. 2 m. to bunch	c. 1 m.	c. 2-3 m.
Wax	Waxy	Glabrous	Waxy
Bunch:			
Colour	Green	Magenta	Purple
Fruits	Glabrous, indehiscent	Hairy, dehiscent	Glabrous, indehiscent
Bract:			
Colour	Pale violet without and within	Violet without, magenta within	Violet without and within
Male flowers:			
Anthers	Purple	Yellow	Pink
Stigma	Abortive	Present	Present

The F_2 was for the most part vigorous, though about one-quarter of the plants died before flowering or showed symptoms of unbalance. The chromosomes of four conspicuously weakly plants were examined: two were diploid ($2n=22$) and two pentaploid ($2n=55$). Their more vigorous siblings could all confidently be diagnosed as diploid. Of thirty-six vigorous plants about a half seemed to be at least as fertile as the F_1 , as judged by outpollinated bunches; one plant had abortive male flowers but the rest bore more or less abundant pollen. Thus the vigour and fertility of some of these F_2 plants shows that there is no effective reproductive isolation between the species.

With regard to segregation in the F_2 it is sufficient to note that about a quarter or more of the plants broadly resembled *M. ornata* (but had paler bracts) but none approached

M. velutina with its characteristic colour, hairiness and dehiscence of the fruits. Indeed these three characters did not even occur individually though a small minority of plants showed traces of dehiscence and hairiness of the fruits. Waxiness of the plant (in contrast to its behaviour in Calcutta 4 × Selangor) shows heterozygous expression and segregated in the F_2 17 non-waxy (as in *M. velutina*); 10 faintly waxy; 16 fully waxy (as in *M. ornata* and the F_1).

Two plants have been selected from this family as being of possible use as ornamentals; one has the general appearance of *M. ornata* but has very pale, virtually white bracts (the first known in the genus?) and the other resembles the hybrid but has an intensely purple and very ornamental bunch.

4. DISCUSSION

(a) *The evolution of parthenocarpy and the edible diploids*

The genetic materials of parthenocarpy in Pisang Lilan have been shown to consist of at least three dominant* genes subject in their action to the influence of modifiers that affect the amount and rate of development of edible pulp, seed fertility and so forth (cf. Dodds & Simmonds, 1948*a*). Two out of three of these dominants are found in wild seeded bananas which have no history of parthenocarpy and they may thus be presumed to have some (unknown) function or functions in the wild plant. By contrast with these genes, which we may call 'wild', one other dominant (P_1-p_1) exists which has so far been found only in Pisang Lilan; this may be termed the 'switch gene', and it alone can realize the potentialities for parthenocarpy of a system of wild dominants. Has this switch gene evolved in response to selection for parthenocarpy or could we expect to find it in wild bananas—is there, in fact, no real difference between a wild and a switch gene?

The latter possibility seems unlikely, for it implies that parthenocarpic bananas could be produced simply by crossing suitable wild forms and that this could occur occasionally in nature. Such plants, being more or less sterile, would surely be at a selective disadvantage and we should expect a tendency for the switch gene to be modified towards recessivity by the process described by Fisher (1930, 1931). Selection for parthenocarpy by man, however, would tend to produce dominance (or at least a fairly high degree of heterozygous expression), in direct contrast to the presumed effects of non-human selection. This hypothesis, of course, is analogous to that proposed for certain dominants in poultry by Fisher (1935, 1938).

The switch locus, it is assumed therefore, owes its nature to human selection and a hypothesis as to the evolution of parthenocarpy may be summarized as: (1) the accumulation of a complex of dominants from wild bananas, (2) the evolution of a dominant switch locus and (3) the accumulation of sterility genes and modifiers of parthenocarpy. This process would have given rise to primitive edible diploids whose evolution would then have proceeded by interbreeding and by backcrossing as male parents to the wild bananas of the neighbouring forests. Male sterility would follow in the advanced edible diploids from the effects of interchange and other structural chromosomal hybridity. Only with the imposition of total male and female sterility would the process of genetic exchange with wild populations come to an end. The whole process is summarized in the diagram (Fig. 1).

* The word 'dominant' here means simply 'having heterozygous expression', a conventional and convenient terminology even if rather a loose one.

The time and place of the origins of the edible diploids presents some problems of interest. Some at least are old enough to have lost all male-fertility while others—Pisang Lilan for example—are male-fertile and must have had a shorter clonal history. Thus the oldest may be as old as the crop and the youngest may be very recent or even contemporary in origin. With regard to the place of origin Dodds & Simmonds (1948*a*) pointed out that the phenotypes of some edible diploids were those of the Selangor form of *M. acuminata*; others had characters of both Selangor and Tavoy forms and were thought to be hybrid in origin, conclusions which were supported by the study of interchange cytology. There are no known edible diploids having the phenotypes of the Tavoy

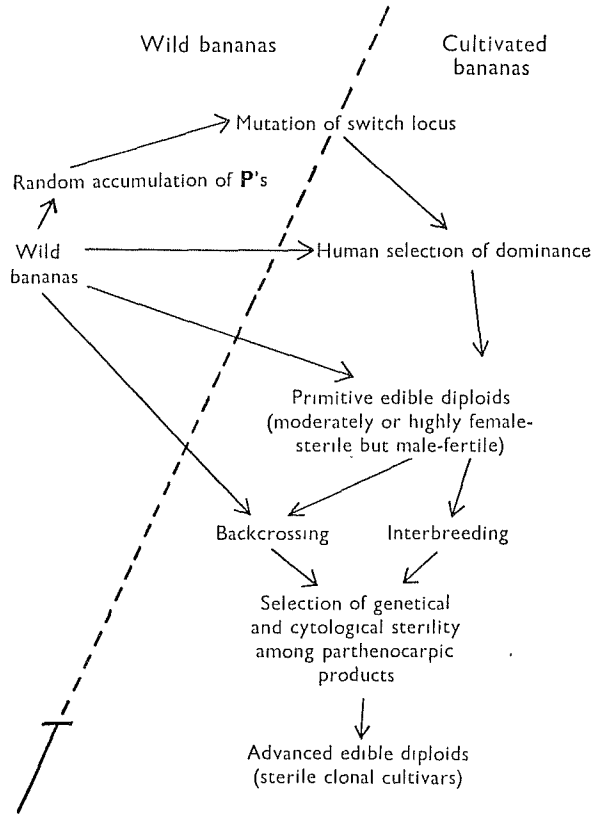


Fig. 1.

form alone*; nor are there any particularly suggestive of other forms of *M. acuminata*. Thus the evidence, so far as it goes (and we only have knowledge of six edible diploids), points to Malaya as the place of origin of parthenocarpy in *Musa acuminata*, rather than to the continent to the north or to the islands south and west of the peninsula. This suggestion is consonant with the results of Dodds & Simmonds (1948*b*) who showed that a certain edible diploid (type 20) probably originated from a cross of seeded *M. Balbisiiana* (which is native to Malaya) by a Malayan *acuminata* edible diploid such as Pisang Lilan.

* But some of the plants recently raised at the I.C.T.A., for breeding purposes closely resemble the Tavoy form; thus some members of 1071 (S.H. 13 × 265 (16), see above) reveal hybrid origins only in their interchange cytology, though they derived genes for parthenocarpy from Pisang Lilan, the Selangor form of the species.

(b) Intra- and interspecific differentiation

The two crosses reported here are characterized by (1) vigorous and fertile F_1 hybrids; (2) continuous rather than discontinuous variation in the F_2 ; (3) failure to recover (in small F_2 families, it is true) parental phenotypes; (4) high vigour and at least moderate fertility of many F_2 plants. The conclusions drawn are that: (1) the parents are not reproductively isolated; (2) the parents are genetically highly differentiated; (3) the degree of differentiation is of roughly the same order in the two crosses.

The significance of the lack of reproductive isolation is hard to assess in the absence of exact knowledge of geographical distribution. In *M. acuminata* hybrids of the races (or perhaps a zone of introgression) might be looked for between northern Malaya and Southern Burma—i.e. in the Isthmus of Kra—for it is there that the forms must meet if they have a geographical boundary in common. It is virtually certain that such crossing has occurred in the history of the edible diploids. The natural distribution of *M. ornata* is apparently unknown, although the species is widely cultivated. It was originally described from Chittagong. *M. velutina* comes from Assam. Here again introgression seems to be a possibility if geography permits.

The high degree of genetical and cytological differentiation of the two forms of *M. acuminata* has an obvious bearing on their status—should they not be regarded as species or at least as varieties? This question can best be settled by reference to *M. acuminata* as a whole, within which several grades of differentiation seem to occur, some greater and some less than that established in this paper (Simmonds, 1952). The information upon which to base a general conclusion is not yet available.

5. SUMMARY

1. Crosses of diploid seeded *Musa acuminata* with edible diploid bananas show that parthenocarpy is due to several dominant genes some of which are found in the wild bananas. At least one of these dominants is so far only known from an edible banana and it is believed to have evolved under human selection.

2. Persistence of bracts and flowers on the male axis of the bunch is probably due to complementary genes which can achieve expression only in the presence of the genetical background of parthenocarpy. Persistence and parthenocarpy are associated in inheritance and it is suggested that this is due to pleiotropy, the two characters having a common physiological cause, namely, growth substances.

3. An interracial cross between the Selangor and Tavoy forms of *M. acuminata* gave evidence of wide genetic difference between the parents. Variation in the F_2 was continuous and segregations were not simply interpretable. Much seed-sterility in the F_2 was attributed to genetical rather than cytological causes. There was an unexplained association between seed fertility and phenotype.

4. An interspecific cross between the *Rhodochlamys* species, *M. ornata* and *M. velutina*, chosen because of the high fertility and meiotic normality of the F_1 , gave many vigorous and fertile types in the F_2 , thus demonstrating the absence of any major reproductive isolation between the two species.

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