⁂The Co-Dominance Theory: Genetic Interpretations of Analyses of Mesocarp Oils from *Elaeis guineensis*, *Elaeis oleifera* and Their Hybrids

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ABSTRACT

Determination of the fatty acid and triglyceride compositions of the F_1 (*Elaeis guineensis* X *E. oleifera*), F_2 and the backcross hybrid mesocarp oils demonstrated that most fatty acid and triglyceride compositions of oils from hybrid palms are intermediate between those of their respective parentals. These data, as well as the acyl group (saturated/palmitate and unsaturated/oleate) distribution of triglycerides of the F_2 mesocarp oils provide genetic proof for co-dominance in the F_2 generation which shows a characteristic segregation into the co-dominance ratio of 1:2:1 (i.e., 1 *E. guineensis*: 2 F_1 hybrid: 1 *E. oleifera*). Similar analyses into the backcross hybrid mesocarp oils on the whole confirmed co-dominance when the backcross ratio of 1:1 was obtained. These results are used to develop the Co-Dominance Theory of *Elaeis* palm hybridization which makes successful predictions for mesocarp oils from the different hybrid palms.

INTRODUCTION

The active altering, through the process of breeding, of palm oil composition to meet the ever-changing requirements of the world market has been attempted between *Elaeis guineensis* (the West African oil palm) and *E. oleifera* (sometimes called *E. melanococca*, *Corozo oleifera* or the South American oil palm) in recent years by many workers.

One of the major breeding objectives of this hybridization is to incorporate within a single palm the advantageous features of the 2 species with particular emphasis on the high yield of *E. guineensis* and the highly unsaturated oil of *E. oleifera*.

Hybridization is possible between the 2 species and fertile progeny has been produced on a plantation basis. Analyses of mesocarp oils from different oil palm hybrids have revealed a mesocarp oil intermediate in unsaturation and of carotene content with respect to those of their respective parentals (1,2).

Backcrosses (between F_1 hybrids with parentals, *E. guineensis* or *E. oleifera*) have been reported by McFarlane et al. (3) in which the F_1 hybrid oil exhibited its intermediate degree of unsaturation, indicative of co-dominance of the genetic information expressing oil composition which is inherited from each parental. While co-dominance was suggested in their report, genetic proof of this was lacking except for the qualitative recognition of the third intermediate type in fatty acid compositions.

The importance of the oil palm is its oil. From the chemical point of view, the problem of palm oil triglycerides has been approached in 2 complementary ways: the biosynthesis of triglyceride molecules and the composition of natural triglycerides with particular emphasis on the common patterns of acyl group distribution.

So far, analyses of mesocarp oils have been done with emphasis on the chemical characteristics only up to the F_1 generation and not further.

Our paper examines this hybridization from biochemical and genetic angles. Analyses of the fatty acid and triglyceride compositions of the F_1, F_2 and backcross hybrid mesocarp oils have been done.

Further studies into the composition of triglycerides with regard to the common patterns of saturated and unsaturated acyl group distribution reveal co-dominance in the F_2 generation which shows a characteristic segregation into the co-dominance ratio of 1:2:1 (i.e., 1 *E. guineensis*: 2 F_1 hybrid: 1 *E. oleifera*). The details of the various crosses performed are further developed into the Co-Dominance Theory of *Elaeis* palm hybridization.

MATERIALS AND METHODS

Sources of Oil Palm Hybrids

The oil palm hybrids were obtained from the following sources: Harrison and Crosfield (Malaysia) Pvt. Ltd., Socfin Pvt. Ltd., Chemara Research Station and United Plantation Pvt. Ltd.

Scheme for Triglyceride Analysis

The scheme for triglyceride analysis of *E. guineensis*, *E. oleifera* and their hybrids is shown in Figure 1.

Separation of Triglycerides from Other Partial Glycerides by TLC

The triglycerides (80-100 mg) were separated on a thin layer (1 mm) of silica by developing with petroleum ether (bp 60-80 C)/diethyl ether/formic acid (60:40:1.6, v/v). The separated glyceride components were detected with a methanolic solution of 2′,7′-dichlorofluorescein (0.1%, w/v). The triglyceride band was then scraped off the plate with a spatula into a tube, and extracted 5 times with hexane (20-cm^3 portions). The extracts were combined, and the solvent removed under a stream of nitrogen. A portion of the triglyceride obtained was reserved for enzymic hydrolysis and the rest was converted to methyl esters (4) for determination of the fatty acid composition of the whole glyceride by gas liquid chromatography (GLC).

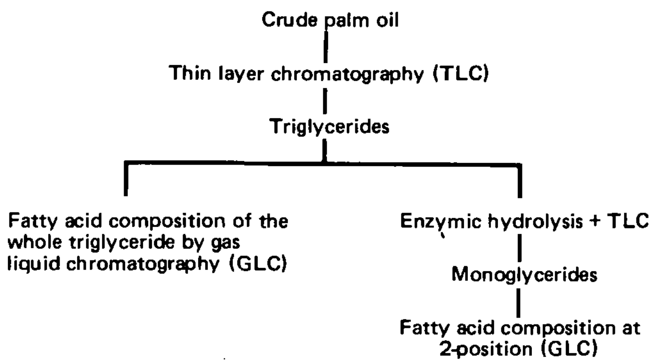

FIG. 1. Scheme for triglyceride analysis of *E. guineensis*, *E. oleifera* and their hybrid mesocarp oils.

Pancreatic Lipase Hydrolysis

The method of Luddy et al. (5) was modified as follows. Tris (hydroxymethyl) methylamine (tris) buffer (1 M; pH 8.0; 1 cm^3), calcium chloride solution (2.2%; 0.1 cm^3) and a solution of bile salts (0.05%; 0.25 cm^3) were added to the triglyceride (up to 5 mg) in a stoppered tube and the mixture was allowed to equilibrate at 40 C in a water bath for 1 min before the pancreatic lipase preparation (1 mg) was added. The mixture was shaken vigorously with a flask shaker at this temperature for 1.5 min. The solution was extracted 3 times with diethyl ether (10-cm^3 portions), and the solvent layer washed twice with distilled water (5-cm^3 portions) and dried over anhydrous sodium sulfate. Upon removal of the solvent, the products were separated by thin layer chromatography (TLC) on Silica Gel G (0.3 mm thick) with petroleum ether (bp 60-80 C)/diethyl ether/ formic acid (60:40:1.6 v/v) as the solvent system. After spraying with 0.1% methanolic 2′,7′-dichlorofluorescein solution, the monoglyceride band was identified and trans-esterified directly on the adsorbent. The monoglyceride band was scraped into a 50-mL round-bottomed flask containing 5 cm^3 of 0.5 M sodium methoxide solution and heated under reflux for 10 min. Two cm^3 of 60% perchloric acid was added and the contents were heated under reflux for 3 min. Then 5.0 cm^3 of heptane was added and heated to reflux for 1.0-2.0 min. The supernatant solvent was pipetted out, and the residue was again heated under reflux twice with 5.0 cm^3 heptane. The extracts (methyl esters) were combined and analyzed by GLC.

Analysis of Methyl Esters by GLC

The methyl esters were analyzed using a Hitachi gas chromatograph Model 183 on a pair of stainless steel columns, 2 m × 4 mm, 10% DEGS, Chromosorb B, A/W, DMCS, 60-80 mesh. The column, injector/detector temperatures were 180 and 200 C, respectively. The carrier gas (N_2) flow rate was 10 cm^3/min.

CALCULATION

List of Symbols

G = *Elaeis guineensis*, unknown variety; D = *E. guineensis*, variety Dura; P = *E. guineensis*, variety Pisifera; T = *E. guineensis*, variety Tenera; M = *E. oleifera*; F_1 = 1st filial generation (*E. guineensis* × *E. oleifera*); F_2 = 2nd filial generation (F_1 × F_1); χ^2 = Chi-Square test; $\chi^2_{0.95}$ = Chi-Square test at 5% level of significance; † = calculated according to Vander Wal's method; †† = calculated according to the Co-Dominance Theory proposed in this paper; t = trace.

Calculation of Expected Values

All the oils of progeny from a cross were pooled and a single analysis was made.

The expected values were calculated as follows:

Hybrids	Expected values
F_1	$0.5(GG + MM)_O$
F_2	$0.25(GG)_O + 0.5(GM)_O + 0.25(MM)_O$
F_1 × GG	$0.5(GM + GG)_O$
F_1 × MM	$0.5(GM + MM)_O$

O = observed values.

Calculation of Triglyceride Composition According to Vander Wal's Theory

Vander Wal (6) proposed the 1,3-random, 2-random distribution hypothesis for the calculation of the triglyceride classes: SSS, SUS, SSU, USU, UUS and UUU from pancreatic lipase data.

He has further (7) described in detail a procedure for calculating percentages of the individual triglycerides, as well as for triglyceride classes. The fatty acid composition of the whole triglyceride was determined by GLC. The percentages of the acyl groups in the 2-position were found by analyzing the 2-monoglycerides after pancreatic lipase procedure. Thus, the percentages of acyl components in the 1-, 2- and 3-positions may be found, assuming the 1- and 3-positions are identical.

RESULTS

Table I compares the observed (O) and expected (E, based on the Co-Dominance Theory proposed in this paper) fatty acid compositions (mol %) of the triglycerides of the various crosses. χ^2 test shows that the observed and expected fatty acid compositions agree at the 5% level of significance.

The various oils obtained for F_1, F_1 × G and F_1 × M show intermediate characteristics in terms of fatty acid composition (including saturation and unsaturation) when compared to the various respective parentals.

From the analyses of individual fatty acids in the F_1 generation, all fatty acids analyzed (except linoleic acid) have compositions intermediate to those of the parentals,

TABLE I

Comparison of Observed (O) and Expected (E)†† Fatty Acid Compositions (mol %) of *Elaeis* Palms

	Elaeis palms									
	G	M	F_1		F_1 × G		F_1 × M		F_1 × F_1(F_2)	
Fatty acids	O	O	O	E	O	E	O	E	O	E
12:0	0.1	t	t	t	t	t	t	t	t	t
14:0	1.3	0.2	0.8	0.75	0.6	1.0	0.5	0.5	0.4	0.8
16:0	47.0	21.0	37.1	34.0	41.4	42.1	36.2	29.1	39.1	35.6
16:1	–	t	t	t	t	t	t	t	t	t
18:0	3.3	0.2	1.5	1.75	0.9	2.4	0.4	0.8	0.7	1.6
18:1	39.7	58.3	52.2	49.0	48.2	46.0	52.8	55.3	53.3	50.6
18:2	8.4	20.0	8.3	14.2	8.9	8.4	9.3	14.3	6.5	11.3
20:0	0.1	–	0.1	0.05	–	0.1	t	t	0.1	0.1
18:3	0.1	0.3	0.2	0.2	0.1	0.1	0.7	0.2	0.1	0.2
Unsaturated	48.2	78.6	60.6	63.4	57.2	54.4	62.8	69.7	59.8	62.0
χ^2	–	–	3.1		1.4		5.7		3.3	
$\chi^2_{0.95}$	–	–	15.5		14.1		12.6		14.1	

TABLE II

Comparison of Observed (O)† and Expected (E)†† Triglyceride Compositions (mol %) of *Elaeis* Palms

Triglyceride with *n*-double bonds	G	M	F_1		$F_1 \times G$		$F_1 \times M$		$F_1 \times F_1(F_2)$	
	O	O	O	E	O	E	O	E	O	E
0	8.3	1.2	3.4	4.75	4.2	5.8	2.6	2.3	3.7	4.1
1	36.7	7.6	24.2	22.25	28.4	30.4	22.2	16.0	26.9	23.2
2	33.3	26.5	39.1	29.9	40.3	36.2	38.2	32.8	38.9	34.5
3	14.9	36.4	24.8	25.65	20.7	19.9	26.7	30.6	24.4	25.2
4	3.4	21.1	7.3	12.25	5.7	5.4	8.9	14.2	5.1	9.8
5	3.3	6.6	1.2	4.95	1.1	2.3	1.3	3.9	1.6	3.1
χ^2	–	–	8.2		1.7		7.5		4.2	
$\chi^2_{0.95}$			11.1		11.1		11.1		11.1	

G and M.

Furthermore, all individual fatty acids in $F_1 \times G$ and $F_1 \times M$ show fatty acid compositions intermediate to that of the particular crosses, whereas all individual fatty acids in the $F_1 \times F_1$ (i.e., the F_2 generation) exhibit fatty acid compositions of F_1.

Table II compares the observed (O) and expected (E, based on the Co-Dominance Theory proposed in this paper) triglyceride compositions (mol %) of the various crosses. χ^2 test shows that the observed and expected triglyceride compositions agree at the 5% level of significance.

The degree of unsaturation in the triglyceride compositions (contributed by 0-5 double bonds) is also intermediate when compared to the parentals G and M. This again is significant at the 5% level when the χ^2 test is performed.

Table III shows the triglyceride compositions (mol %) of the various oils obtained from F_2 generation in terms of saturated (S) and unsaturated (U) fatty acids in the triglyceride molecules. The ratio of SUS:SUU:UUU in the $F_1 \times F_1$ crosses agrees with 1:2:1 (the co-dominance ratio) at the 5% level of significance when the χ^2 test is performed.

Table IV, A and B, details the triglyceride compositions (mol %) of the various oil obtained from backcrosses of F_1 hybrids with parentals in terms of saturated (S) and unsaturated (U) fatty acids in the triglyceride molecules.

Table IVA shows that backcrosses of F_1 hybrids with parental G (*E. guineensis*) result in SUU:SUS = 1:1 at the 5% level of significance. However, SUU:SUS ≠ 1:1 at the 5% level of significance when the backcross of F_1 hybrids with parental M (*E. oleifera*) is done.

Table IVB shows that backcrosses of F_1 hybrids with parental M (*E. oleifera*) result in SUU:UUU ≠ 1:1 at the 5% level of significance. However, SUU:UUU ≠ 1:1 at the 5% level when the backcross of F_1 hybrids with parental G (*E. guineensis*) is performed.

Table V shows the triglyceride compositions (mol %) of the various oils obtained from F_2 generation in terms of saturated palmitate (P) and unsaturated oleate (O) fatty acids in the triglyceride molecules. The ratio of POP:POO:OOO in the $F_1 \times F_1$ crosses agrees with 1:2:1 at the 5% level of significance when the χ^2 test is done.

Table VI, A and B, details the triglyceride compositions (mol %) of the various oils obtained from backcrosses of F_1 hybrids with parentals in terms of saturated palmitate (P) and unsaturated oleate (O) fatty acids in the triglyceride molecules.

Table VIA shows that backcrosses of F_1 hybrids with parental G (*guineensis*) result in POO:POP = 1:1 at the 5% level of significance. However, POO:POP ≠ 1:1 at the 5% level of significance when the backcross of F_1 hybrids with parental M (*oleifera*) is performed.

Table VIB shows that backcrosses of F_1 hybrids with parental M (*oleifera*) result in POO:OOO ≠ 1:1 at the 5% level of significance. However, POO:OOO ≠ 1:1 at the 5% level of significance when the backcross of F_1 hybrids with parental G (*guineensis*) is done.

Table VII compares the observed (O) and expected (E, based on the proposed Co-Dominance Theory) fatty acid compositions (mol %) at the 2-position of the triglycerides of the various crosses. χ^2 test shows that the observed and expected fatty acid compositions agree at the 5% level of significance.

This table shows that 78-91% unsaturated fatty acids occupy the 2-position of the triglyceride molecule. Here again, the various oils obtained for F_1, $F_1 \times G$ and $F_1 \times M$, respectively, show intermediate characteristics in terms of fatty acid composition (including saturation and unsaturation) when compared to the various respective parentals.

From the analyses of individual fatty acids in the F_1 generation, most fatty acids analyzed have fatty acid compositions intermediate to those of the parentals, G and M.

Furthermore, all individual fatty acids in $F_1 \times G$ and $F_1 \times M$ show fatty acid compositions intermediate to that of the particular crosses, whereas all individual fatty acids in the $F_1 \times F_1$ (i.e., the F_2 generation) exhibit fatty acid compositions of F_1.

DISCUSSION

It has been shown that hybrid oil palms obtained from crosses of *E. guineensis* and *E. oleifera* have a high yield of mesocarp oil, having a higher degree of unsaturation which is intermediate between the 2 parentals (1-3).

TABLE III

Triglyceride Compositions (mol %) of Various Oils Obtained from the $F_2(F_1 \times F_1)$ Generation (Co-Dominance Ratio Testing) Saturated (S) and Unsaturated (U)

Triglycerides	F_2^a O†	F_2^a E††	F_2^b O	F_2^b E
SUS**	29.9	22.1	22.9	22.1
SUU	42.9	44.1	44.2	44.3
UUU**	15.5	22.1	21.4	22.1
Total	88.3	88.3	88.5	88.5
χ^2	4.8		0.1	
$\chi^2_{0.95}$	6.8		6.0	

F_2^a, F_2^b = F_2 from 2 different sources.
**Includes both symmetrical and unsymmetrical isomers.

TABLE IV

A: Triglyceride Compositions (mol %) of Various Oils Obtained from the Backcrosses of F_1 Hybrids with *E. guineensis* (and *E. oleifera*) Saturated (S) and Unsaturated (U)

	Hybrids							
	MD × P		F_1 × T		F_1 × G		F_1 × M	
Triglycerides	O†	E††	O	E	O	E	O	E
SUU	41.10	36.95	39.1	30.0	43.3	36.2	43.9	32.85
SUS**	32.80	35.95	20.9	30.0	27.1	35.2	21.8	32.85
Total	73.90	73.5	60.0	60.0	70.4	70.4	65.7	65.7
χ^2	0.9		5.5		3.7		7.4	
$\chi^2_{0.95}$	3.8		3.8		3.8		3.8	

B: Triglyceride Compositions (mol %) of Various Oils Obtained from the Backcrosses of F_1 Hybrids with *E. oleifera* (and *E. guineensis*) Saturated (S) and Unsaturated (U)

	Hybrids							
	F_1 × M		MD × P		F_1 × T		F_1 × G	
Triglycerides	O†	E††	O	E	O	E	O	E
SUU	43.9	32.85	41.0	26.9	39.1	28.6	43.0	30.25
UUU**	21.8	32.85	12.8	26.9	18.1	28.6	17.5	30.25
Total	65.7	65.7	53.8	53.8	57.2	57.2	60.5	60.5
χ^2	7.4		14.8		7.7		10.8	
$\chi^2_{0.95}$	3.8		3.8		3.8		3.8	

**Includes both symmetrical and unsymmetrical isomers.

TABLE V

Triglyceride Compositions (mol %) of Various Oils Obtained from the $F_2(F_1 \times F_1)$ Generation (Co-Dominance Ratio Testing) Palmitate (P) and Oleate (O)

	Hybrids			
	F_2^a		F_2^b	
Triglycerides	O†	E††	O	E
POP	21.1	16.1	18.0	17.4
POO	31.5	32.2	34.8	34.8
OOO	11.8	16.1	16.8	17.4
Total	64.4	64.4	69.6	69.6
χ^2	2.7		0.0	
$\chi^2_{0.95}$	6.0		6.0	

F_2^a, F_2^b = F_2 from 2 different sources.

The results obtained in this paper confirmed this finding. These results can be explained genetically if *Elaeis* palms possess 2 allelomorphic genes G and M. If *E. guineensis* has allelomorphic genes GG and *E. oleifera* has allelomorphic genes MM, the apparent failure of one of these allelomorphic genes to dominate the other in the F_1 generation gives us the opportunity to test co-dominance genetically.

If a cross is effected between these 2 species of *Elaeis* palms, all the progeny of the first filial generation are intermediate in its characteristics called GM (F_1). If these F_1 palms are allowed to breed among themselves (selfing), the second filial generation (F_2) shows a characteristic segregation into GG, GM and MM in the proportions of 1:2:1 (see Fig. 2).

Backcrosses performed between F_1 heterozygous with homozygous parentals will predict a co-dominance in the genotypes:

1 GM : 1 GG and 1 GM : 1 MM

which are reflected phenotypically as:

1 SUU : 1 SUS and 1 SUU : 1 UUU
1 POO : 1 POP and 1 POO : 1 OOO

It can be seen from Figure 2 (proposing the Co-Dominance Theory of *Elaeis* palm hybridization) that a genetic explanation for acyl group distribution in the triglyceride molecule can be obtained if we assume that: (a) *E. guineensis* has a genotype of GG and *E. oleifera* has a genotype of MM; (b) positions 1 and 1′ in the triglyceride molecule are genetically controlled by G and M; (c) position 2 in the triglyceride molecule is genetically controlled by another gene; (d) allele G (genotype) determines the phenotypes saturated (S) and palmitate (P) in the triglyceride molecule; (e) allele M (genotype) determines the phenotypes unsaturated (U) and oleate (O) in the triglyceride molecule; (f) alleles G and M determine placement of positions 1 and 1′ in the triglyceride molecule in equal probabilities, thereby determining S/P and U/O, respectively, in the phenotypes; (g) position 2 in the triglyceride molecule will phenotypically show U/O in the phenotypes.

Assumptions c and g are supported by enzymic hydrolysis results (Table VII) and by Gunstone's work (8; Table I) which reveals that the constituent acids are not distributed completely at random, but that, in vegetable fats, unsaturated C_{18} acids are more likely to be found in the 2-monoglycerides remaining after hydrolysis.

Current theories of acyl group distribution are based on chemical studies which have looked for a general pattern of behavior to correlate the results and, hopefully, to predict triglyceride structure from a knowledge of component acids (8).

Mono-Acid Theory

This theory has been abandoned. It views that natural triglycerides are supposed to be mixtures of simple triglycerides with no mixed triglycerides present, i.e., all the palmitic acids occur as tripalmitin and all oleic acids as triolein.

Random Distribution Theory

This theory is not generally accepted. It proposes that component acids are distributed at random (by chance, statistically) among all hydroxyl groups of all glycerol molecules;

the amount of any triglyceride is then easily calculable from the amounts of the constituent acids. However, 2 important observations militate against its general acceptance: (a) the content of fully saturated triglycerides (SSS) differs from that predicted by random distribution for most proportions of saturated acids; (b) enzymic hydrolysis has shown that the proportions of acids attached to the 2-position of glycerol differ from those in the total fat. In spite of this, Scholfield and Dutton (9,10) have obtained results for highly unsaturated vegetable fats which fit the random distribution pattern.

Restricted Random Distribution Theory

This is a modified theory of the Random Distribution Theory that accommodates the 2 discordant observations while still adhering to an essentially random pattern. Kartha (11) has found it useful to restrict the amount of SSS to that which can remain fluid in vivo and he considers this to be the experimentally observed amount of fully saturated triglyceride wherever this is less than that predicted by random distribution. The remaining acids are distributed in random fashion among the triglyceride types, SSU, SUU and UUU. Vander Wal (6) has introduced a different restriction. He considers the secondary hydroxyl group to be acylated by unsaturated groups shown experimentally to be in that position. This view is essentially that proposed by A.S. Richardson (personal communication to R. Vander Wal, 1957) and resembles Gunstone's theory within this framework.

Even Distribution Theory

First proposed by Collin and Hilditch (12), this theory grew out of the observation that the content of fully saturated triglyceride was very small in all fats except those containing more than about 60-66% of saturated acid and has since been expressed in various ways as the idea has developed (8).

Possible theories of acyl group distribution have been examined by Gunstone (8), all of which are based on the hypothesis, for which there is experimental evidence, that the secondary hydroxyl of glycerol is acylated only by oleic, linoleic, or linolenic acids unless there are not enough

TABLE VI

A: Triglyceride Compositions (mol %) of Various Oils Obtained from the Backcrosses of F_1 Hybrids with *E. guineensis* (and *E. oleifera*) Palmitate (P) and Oleate (O)

	Hybrids							
	MD × P		F_1 × T		F_1 × G		F_1 × M	
Triglycerides	O†	E††	O	E	O	E	O	E
POO	26.9	28.05	27.5	21.85	30.4	24.85	30.0	23.0
POP	25.2	26.05	16.2	21.85	19.3	24.85	16.0	23.0
Total	52.1	52.1	43.7	43.7	49.7	49.7	46.0	46.0
χ^2	0.1		2.9		2.5		4.3	
$\chi^2_{0.95}$	3.8		3.8		3.8		3.8	

B: Triglyceride Compositions (mol %) of Various Oils Obtained from the Backcrosses of F_1 Hybrids with *E. oleifera* (and *E. guineensis*) Palmitate (P) and Oleate (O)

	Hybrids							
	MD × P		F_1 × T		F_1 × G		F_1 × M	
Triglycerides	O†	E††	O	E	O	E	O	E
POO	30.0	22.0	26.9	17.05	27.5	19.6	30.4	21.05
OOO	14.0	22.0	7.2	17.05	11.7	19.6	11.7	21.05
Total	44.0	44.0	34.1	34.1	39.2	39.2	42.1	42.1
χ^2	5.8		11.4		6.4		8.3	
$\chi^2_{0.95}$	3.8		3.8		3.8		3.8	

TABLE VII

Comparison of Observed (O)† and Expected (E)†† Fatty Acid Compositions (mol %) at 2-Position of Palm Oil Triglycerides

	Elaeis palms									
	G	M	F_1		F_1 × G		F_1 × M		F_1 × F_1	
Fatty acids	O	O	O	E	O	E	O	E	O	E
12:0	t	–	t	t	t	t	t	t	–	t
14:0	0.4	t	0.5	0.2	0.2	0.4	0.4	0.2	0.2	0.4
16:0	19.5	8.9	12.8	14.2	14.4	16.2	11.1	10.9	11.1	13.5
16:1	–	t	t	t	t	t	t	t	t	t
18:0	1.8	0.5	0.6	1.1	1.1	1.2	0.4	0.5	0.2	0.8
18:1	61.3	62.5	69.5	61.9	66.6	65.4	67.3	66.0	69.4	65.7
18:2	17.0	28.0	16.7	22.5	17.7	16.8	20.7	22.4	19.1	19.6
20:0	t	–	–	t	t	t	–	–	–	t
18:3	t	0.1	t	t	t	t	–	–	t	t
Unsaturated	78.3	90.6	86.2	84.4	84.3	82.2	88.0	88.4	88.5	85.3
χ^2			3.3		0.4		0.4		1.3	
$\chi^2_{0.95}$			11.1		11.1		11.1		11.1	

of these acids to achieve this.

Three theories have been proposed by Gunstone (8).

Theory 1. The 2-hydroxyl group is preferentially acylated by unsaturated C_{18} acids. The 1- and 1′-hydroxyl groups are acylated subsequently by all remaining acids and by a C_{18}-unsaturated acid not required at the 2-position. Within these limits, the distribution of acyl groups at each position is statistical.

Theory 2. The 2-hydroxyl group is preferentially acylated by unsaturated C_{18} acids. One of the primary hydroxyl groups then reacts preferentially with the remaining acids of this type, and finally the other primary hydroxyl group reacts with the acids that remain. Within these limits, the distribution of acyl groups at each position is statistical.

Theory 3. The 2-hydroxyl group is preferentially acylated by unsaturated C_{18} acids. One of the primary hydroxyl groups then reacts preferentially with acids other than unsaturated C_{18} acids, and finally the other primary hydroxyl group reacts with the acids that remain. Within these limits, the distribution of acyl groups at each position is statistical. (Since there is no known means of distinguishing between 1′- and 1-positions, theories 2 and 3 give the same arithmetical results.)

Of the 3 theories of acyl group distribution which have been proposed and examined by Gunstone (8), theory 1 is preferred because it is considered to provide a satisfactory correlation of most of the available experimental results which can be accepted as reasonably reliable.

According to this theory, the secondary hydroxyl group of glycerol is preferably acylated by unsaturated C_{18} acids such as oleic, linoleic and linolenic; the 2 primary hydroxyl groups are subsequently acylated by the acids that remain and the distribution of acyl groups at each position is statistical. Note that Gunstone's theory 1 requires the 2 primary hydroxyl groups to be acylated by remaining acids and this distribution of acyl groups at each position is statistical, which agrees well with the idea of segregation probabilities required by Mendel's Second Law, the Law of Independent Assortment.

Table I indicates the validity of the Co-Dominance Theory of this paper when these results support the 1:2:1 prediction for all fatty acid compositions (mol %)—except for linoleic acid, where allele G seems to be dominant over allele M—of the F_2 generation. Backcross hybrid fatty acid compositions further support the Co-Dominance Theory's prediction of 1:1. The intermediate fatty acid composition of F_1 generation also lends credence to the Co-Dominance Theory and further confirms the results of previous workers.

Table II, which deals with triglyceride compositions, further strengthens the position of the Co-Dominance Theory among lines similar to those discussed in the preceding paragraph.

The predictions of the Co-Dominance Theory with regard to saturated (S)/palmitate (P) and unsaturated (U)/ oleate (O) acyl group distribution in triglycerides are further confirmed by Tables III and V which deal with $F_1 \times F_1$ crosses (selfing), showing a characteristic segregation in the co-dominance ratio of 1:2:1. Analyses into selfing (F_2 generation) hitherto have not been done on mesocarp oils of *Elaeis*. The chemical characteristics of this F_2 generation reveal 1 *E. guineensis* : 2 F_1 hybrid : 1 *E. oleifera*. From the Co-Dominance Theory, it can be seen that, qualitatively, there are 3 types of mesocarp oils in the F_2 generation, i.e., mesocarp oils characteristic of the *E. guineensis*, the F_1 hybrid and the *E. oleifera*. This accounts for the qualitative recognition of a third intermediate type in, e.g., fatty acid compositions, of previous workers. Our paper predicts quantitatively that these different mesocarp oils are in the ratio of 1:2:1 all in accordance with the Co-Dominance Theory outlined in Figure 2.

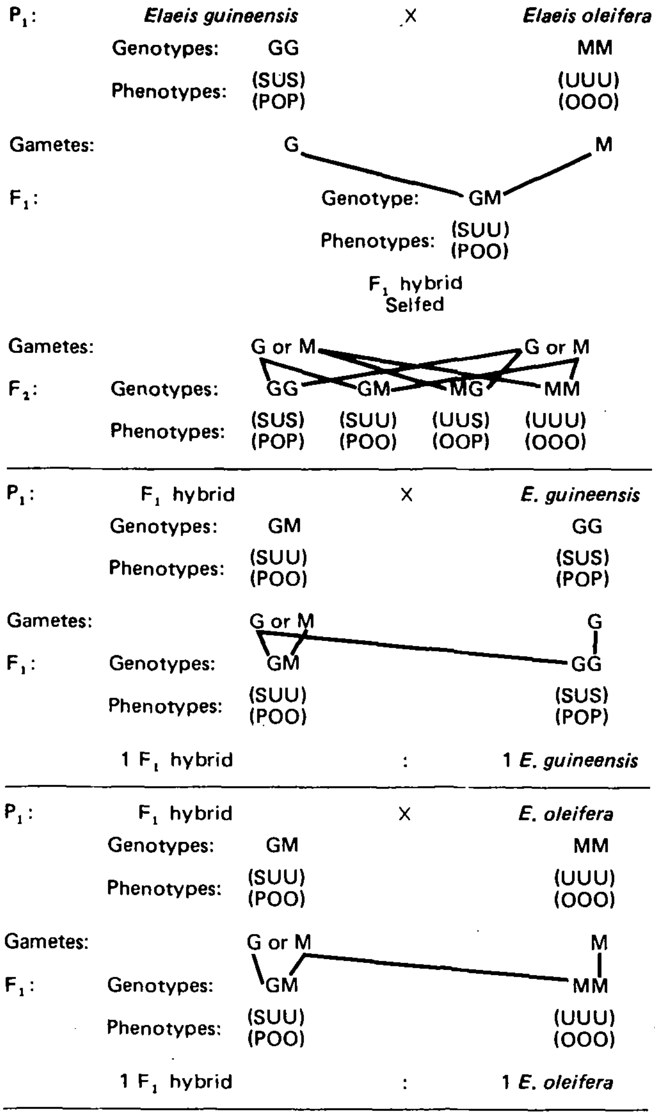

FIG. 2. The Co-Dominance Theory of *Elaeis* palm hybridization—a genetic explanation for acyl group distribution in the triglyceride molecule.

Backcrosses conducted on limited samples support the predictions of the Co-Dominance Theory. It is notable that, while the backcross between $F_1 \times G$ gives a predicted ratio of 1 SUU : 1 SUS (also 1 POO : 1 POP), the backcross between $F_1 \times M$ for SUU:SUS (also POO:POP) does not give a ratio of 1 SUU : 1 SUS (also 1 POO : 1 POP) (Table IV, A and B, respectively), all in accordance with the Co-Dominance Theory.

Tables IVB and VIB show that the backcross between $F_1 \times M$ does not give the predicted ratio of 1 SUU : 1 UUU (also 1 POO : 1 OOO), which it should. As there is only one sample of the cross between $F_1 \times M$ available for testing at this time of writing, further work into this particular backcross will be examined. However, the backcross between $F_1 \times G$ for SUU:UUU (also POO:OOO), does not give a ratio of 1 SUU : 1 UUU (also 1 POO : 1 OOO) (Tables IVB and VIB, respectively), as predicted by and according to the Co-Dominance Theory of this paper.

McFarlane et al. (3) reported that mesocarp oils obtained from $F_1 \times G$ exhibited a typical *E. guineensis* mesocarp oil composition, whereas that obtained from $F_1 \times M$ exhibited a typical F_1 hybrid oil composition. The report claimed that this would appear to account for mesocarp unsaturation in accordance with the laws of Mendelian inheritance. Actually, the crosses performed by McFarlane et al. (3) are backcrosses and the law of Mendelian inheritance is Mendel's Second Law of Independent Assortment. What McFarlane et al. obtained for the backcrosses are at variance with our results and their interpretations contradict with co-dominance, which they had suggested. Our results show that the backcross ratio of 1:1 (F_1:G or F_1:M) as predicted by the Co-Dominance Theory is obtained (Table IV, A and B, and Table VI, A and B, for saturated and unsaturated palmitate and oleate, respectively), and not one which exhibited a typical *E. guineensis* (G) mesocarp oil composition and one which displayed a typical F_1 hybrid oil composition.

It would appear that the Co-Dominance Theory of this paper is the genetic equivalent to Gunstone's theory 1 of the Restricted Random Distribution Theory. The predictions of the Co-Dominance Theory are supported very well by the intermediate nature of fatty acids and triglycerides; the co-dominance ratio prediction is supported in almost all the results, as well as in the backcross ratios between F_1 and the 2 parentals.

This Co-Dominance Theory may be more generally applicable for most vegetable oils and fats (especially *Elaeis* palm kernel oils) in light of its successful predictions for mesocarp oils from *Elaeis* palms.

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Study on Neutral Lipid Composition of Malagasy Zebu Fats: I. Quantitative Analysis of Fatty Acids and Sterols

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ABSTRACT

The fatty acid and sterol compositions of different parts of Malagasy zebu (*Bos indicus*) were evaluated. Investigation by gas liquid chromatography using Carbowax 20 M revealed 35 fatty acids, mainly palmitic (24-27%), stearic (13-24%), and oleic (25-37%) acids. Odd-numbered, iso and anteiso fatty acids were also detected. Small differences in composition were observed between the hump and the kidney fats of *B. indicus*. Comparison between industrial tallow of *B. indicus* and *B. taurus* revealed slight differences in the stearic/oleic acid ratio (0.83 and 0.46, respectively). An OV 17 column was used to separate 9 sterols, mainly cholesterol (89-98%). β-Sitosterol was also found at lower concentrations in all the samples.

INTRODUCTION

With a livestock of more than 10 million animals, meat consumption is rather high in Madagascar, in comparison with some African and Asian countries (1). Madagascar also exports chilled, frozen and canned meat (corned beef). The livestock essentially comprises bovines since there are only 230,000 caprines and 200,000 ovines. The Malagasy zebu (*Bos indicus*) is characterized by its small size (averaging 350 kg weight when being slaughtered). Withers are topped by humps of various volume, depending on sex (bigger for male) and the fattening stage of the animal. The zebu hump tissue is essentially adipose (60-85%).

There has been no previous work on fatty acid and sterol patterns of zebu lipids. We studied the neutral lipid composition of several samples of different parts of malagasy zebu (hump, kidney fat, industrial tallow) and compared the obtained results to those better known of *B. taurus* (2). The first published results cover the quantitative analysis of fatty acids and sterols of those samples.

EXPERIMENTAL PROCEDURES

Four samples of zebu hump tissue and one sample of kidney fat were collected from a local market in Antananarivo. Industrial tallow samples of *B. taurus* (Laboratoire Interrégional de la Repression des Fraudes et du Contrôle de la Qualité, Marseilles, France) and industrial bone tallow samples of *B. indicus* (Prochimad Co., Madagascar) were obtained.

Fat tissues were extracted with hexane in a Soxhlet apparatus for 12 hr and the solvent was removed using a rotary vacuum evaporator. In some cases, melted lipid samples of zebu hump tissues were obtained in a drying

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