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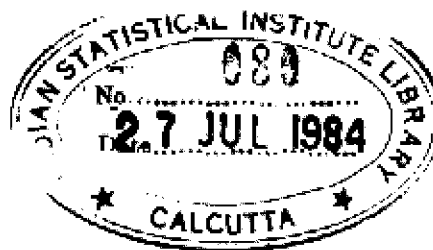
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BIOMETRICS OF BILATERAL SYMMETRY IN PLANTS

Pt (1)

By

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A C K N O W L E D G E M E N T

One day in late 1960, I happened to lay my hands on two hibiscus flowers (Hibiscus rosasinensis). The petals of one uniformly veered in a direction opposite to that of the other. This, as far as I know, was an unrecorded phenomenon. When I showed the flowers to Prof. C.R. Rao, he told me that although I could report on this observation immediately, it would be desirable if I had examined several other hibiscus flowers before writing about them. This was the birth of a new branch of biology - numerical plant morphology. I thank Prof. C.R. Rao, F.R.S., Director, Research & Training School, Indian Statistical Institute for his continued interest and guidance in my work.

I wish to record my appreciation of the diligent and the most cordial manner my colleagues Sarat Kumar De, Artist and Purna Chandra Dutta, Steno-Typist have been working with me during the past ten years. I thank them for their constant help including that I received for the preparation of this treatise.

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## Biometrics of Bilateral Symmetry in Plants

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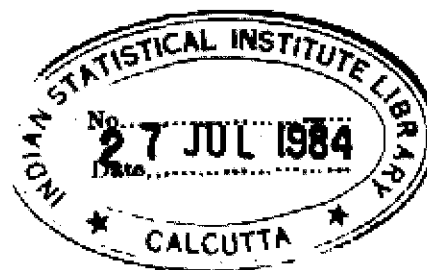
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LIST OF PAPERS APPENDED

1. Aestivation in Malvaceae. Nature, 201 : 515-516 (1964).
2. Floral asymmetry in Malvaceae. J. Bombay Nat. Hist. Soc., 62 : 402-409 (1964).
3. Floral structure and stamens in Bombay ceiba L. J. Genet., 59 : 294-328 (1966).
4. Floral structure and stamens in Ceiba pentandra L. Gaertn. J. Bombay Nat. Hist. Soc., 62 : 394-411 (1965).
5. Variation in the floral organs of Hibiscus rooseae L. J. Indian Bot. Soc., 45 : 30-43 (1965).
6. Stamen number and pollen size in levo- and dextro-rotatory flowers of Bombacaceae. Rev. Palaeobotan. Palynol., 2 : 133-139 (1967).
7. The three kinds of stamens in Bombay ceiba L. (Bombacaceae). Bull. Jardin Bot. de l'Etat., 35 : 185-211 (1965)
8. Aestivation of perianth of Arecu catechu Linn. fruits. J. Bombay Nat. Hist. Soc., 63 : 270-282 (1966).
9. Aestivation of coconut flowers. Ceylon Coconut Quart., 20 : 123-130 (1969).
0. Asymmetry in the aestivation of perianth of palm fruits. Phytomorphology, 21 : (1971) (to appear shortly).
1. Right-handed, left-handed and neutral palms. Principles, J. Palm Soc., 15 : 63-68 (1971).
2. The non-inheritance of asymmetry in Cocos nucifera L. J. Genet., 58 : 42-50 (1962).
3. Asymmetry in palm leaves. J. Bombay Nat. Hist. Soc., 68 : 204-231 (1971).
4. Foliar spiral and ptyxis in Cordyline rubra Gaert. ex Kunth. Prog. Nat. Inst. Sci. of India, 35 : 267-272 (1969).
5. Pre-foliation in Scindapsus officinalis Schott. J. Bombay Nat. Hist. Soc., 67 : 250-258 (1970).
6. Fibonacci Numbers for palm foliar spirals. Acta Bot. Neerl., 19 : 249-256 (1970).

17. Why Fibonacci Sequence for palm leaf spirals ? Fibonacci Quart., 9 : 237-244 (1971).
18. Fibonacci system in aroids. Fibonacci Quart., 9 : 253-263 (1971).
19. The dependence of yield on asymmetry in coconut palms. J. Genet., 58 : 186-215.
20. A  $2^7$  Confounded Design\* for a manurial experiment on coconut. Sankhya, B, 31 : 85-102.

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## BIOMETRY OF BILATERAL SYMMETRY IN PLANTS

### 1. INTRODUCTION

#### Synopsis :

During the past ten decades, observations relating to symmetry, asymmetry, dis-symmetry, radial symmetry, rotational symmetry, bilateral symmetry and ambidexterity in the fields of botany, zoology, geology, chemistry, crystallography, physics, astronomy, engineering, mathematics, music, poetry and art were recorded by various scientists. The present treatise is a summary of an elaborate study on bilateral symmetry or mirror-image symmetry occurring in various plant organs. Unlike most of the earlier reports, the problem here has been tackled unified on a quantitative basis, thereby creating situations where sophisticated techniques of statistics could be effectively employed. As a result, many unexpected facts came to light. The facilities and freedom available at the Indian Statistical Institute for the collection and analysis of data on varied subjects have to a great extent enabled the emergence of a new branch of biology, namely, numerical plant morphology, which has brought forth the following results.

1. It has been made possible to reconstruct successfully the sunflower head (capitulum). This problem intrigued several mathematicians and biologists alike during the last over one hundred years;

2. A strong evidence has been adduced for a possible existence of geo-physical influence on the growth of plants (and animals);

3. Bilateral symmetry in many plants has been found to be non-genetical. But the discovery of its association with an important character like fruit-yield is biologically an intriguing situation. Evidence for this has been reported from the coconut and other crop plants;

4. The expression of asymmetry of leaves and stem as a morphological character can help to assign some doubtful species of plants to their proper positions in phylogeny;

5. The leaves of most species of palms are arranged in the crown in accordance with the Fibonacci angle which accounts for different crowns showing different numbers of spirals that always synchronise the terms in the Fibonacci Sequence. Asy<sup>ym-</sup>metry of palm leaves has been found to help the distribution of leaves on the stem more efficiently;

6. The discovery of the dependence of fruit yield on leaf asymmetry has enabled a better statistical estimation of the effect of manurial treatment on the coconut;

7. A significant change in the fruit/tuber yield has been brought about by changing the direction of growth of stem-twiners.

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## 2. ASYMMETRY IN PLANTS

Life on earth started with spherical symmetry when primitive single-celled plants and animals floated and tumbled about in the water. When living forms settled to the bottom of the sea or clung to the shores, a permanent up-down axis was created giving rise to radial symmetry. The early animals that evolved from primitive life had their axis shifted from the vertical to the horizontal. So a single plane of symmetry remained dividing the animal into right and left sides. Locomotion created a fundamental difference between front and back. Hence, a bilateral symmetry is generally found in the world of animals. Bilateral symmetry of the above type in plants is not very common. The stems of certain cacti such as Opuntia, the flattened phylloclades of Muhlenbeckia and Phyllocladia are some examples. The leaves of Iris and similar plants are bilateral. All plants which are truly distichous, as grasses, may be regarded as bilaterally symmetrical. The flowers of Cruciferae, having two of their stamens directly opposite to each other which are shorter than the remaining four, show bilateral symmetry. Most flowering plants show radial symmetry which centres around an axis of rotation. The vertically elongated axes such as those of the main stem and primary roots and many flowers and fruits in particular show radial symmetry.

The leaf of Begonia is clearly asymmetric since the two halves of the lamina, separated by the midrib, are much dissimilar in area and form. But if we consider two consecutive leaves on the same shoot of Begonia, the asymmetric leaves seem to complement each other. In one leaf the left half is larger, and in the other the right half is larger.



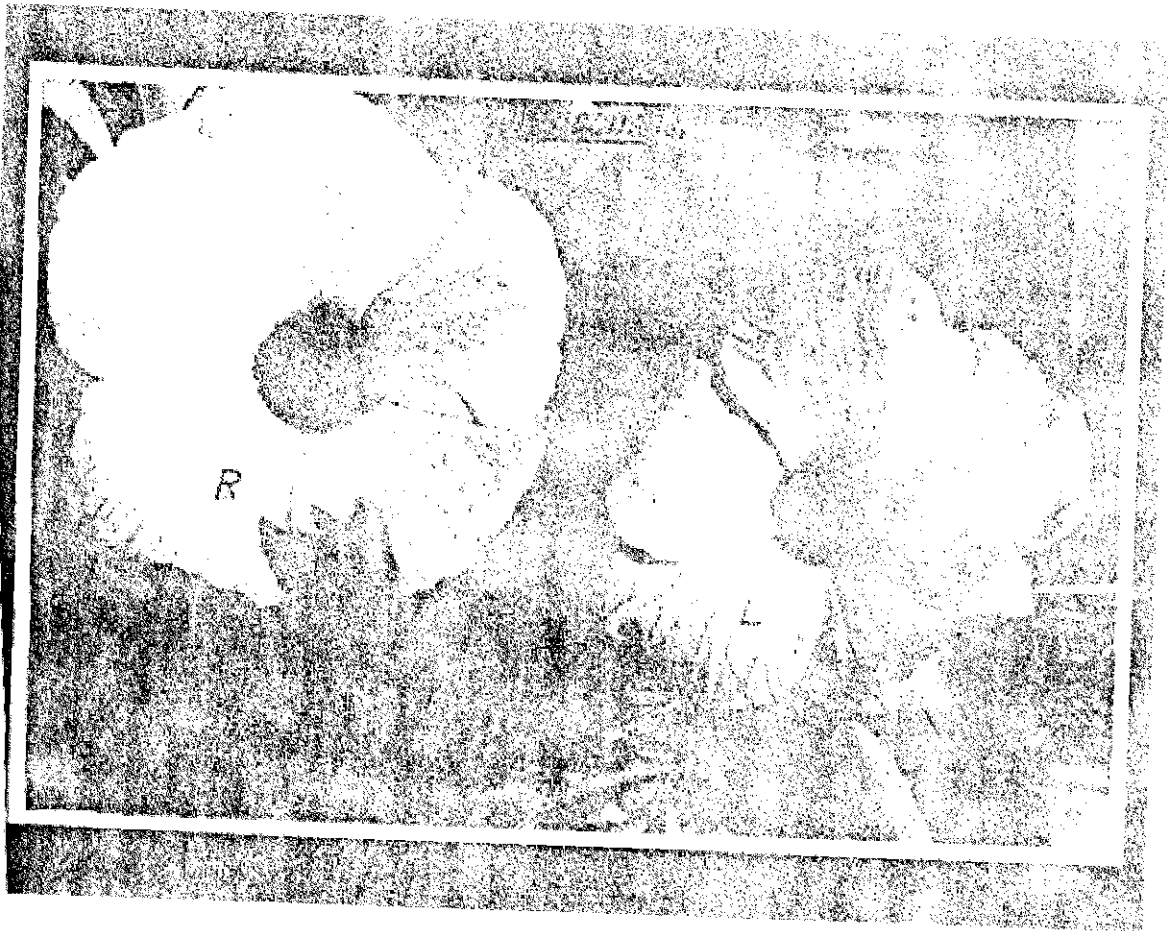
The plant or its shoots may still be considered to have overall symmetry inspite of the asymmetric leaves. In margoosa (Melia azedarach) where the leaf is pinnate, each leaflet is oblique and very much asymmetric (excepting the single terminal leaflet). But the opposite leaflets complement each other. Spiraling stems show typical asymmetry. Here again while in some species the stems coil clockwise, <sup>in</sup> the others they move counter-clockwisely. In exceptional cases, the same species may show right- and left-twining shoots within the same individual plant, as for example, Mikania scandens. The tendrils of many plants show right- and left-handed coiling within a plant. In a large number of flowering plants, the leaves are produced one at a time (alternate phyllotaxis) and are seen distributed on the stem spirally, causing asymmetry. In some plants (or shoots) the spiral is right-handed and in others, left-handed. Since the axils of the leaves showing spiral arrangement give rise to secondary branches, the production of lateral branches (and their subsequent orders of branching) may also be regarded as showing right- and left-handedness. Asymmetry in the aestivation of corolla is clearly displayed in flowers of Malvaceae, Bombacaceae and a few other families. The petals of a flower of these plants regularly twist either clockwise or conversely. The arrangement of the perianth of palm fruits show either contortion or imbrication (rarely valvate). Under these two categories, right-handed and left-handed individuals are noticed. The bilateral symmetry cited above are comparable to the external symmetry of human body where each half is asymmetrical by itself.

I was attracted by to this fascinating branch of study in 1960 when I began collecting quantitative data on its various manifestations. Such observations made on large

and analysing the data statistically have unfolded additional valuable information. A botanist who has no regard for numbers would have failed to notice the several variations that have become obvious when observations on a numerical basis have been given importance.

Bilateral symmetry as found in the twining stems, phyllotaxis, ptyxis of lamina, aestivation of corolla and perianth, distribution of flowers on inflorescences etc. has been reported in the appended papers published during the past decade. The topics that are enumerated or discussed briefly in this treatise are as follows :

- a. Construction of the sunflower head; occurrence of Fibonacci Numbers in plants;
- b. Global data on the foliar asymmetry of the coconut; presenting some coconut data through Fractile Graphs;
- c. Asymmetry of palm leaves and similar data on two other species;
- d. Bilateral symmetry in the aestivation of corolla and palm perianth;
- e. Association of fruit yield with foliar spiral;
- f. Effect of handedness of stem growth on fruit yield in cow pea, and tuber yield in a gram;
- g. Statistical analysis of bilateral symmetry in plant organs;
- h. A  $2^7$  Confounded design for a manurial trial on coconut.



### 3. BILATERAL SYMMETRY IN THE ACTIVATION OF COROLLA AND PERIANTH

#### Introduction :

If one looks at the flowers of cotton or the familiar hibiscus critically, the five free petals will be seen partially overlapping with one another in an order leading to regular twisted condition. All the five petals in one flower twist clockwise (left-handed) and in another counter-clockwise (Fig.1). Within a plant, the two kinds of flowers are distributed more or less equally. This situation is prevalent in almost all the species of Malvaceae (cotton family) and Bombacaceae (silkcotton tree family). Such a peculiarity began to be known from 1964 (PAPER No.1). Voluminous data collected on several species of these two families also showed that the two kinds of flowers in each species are distributed randomly (PAPERS, 2-4). However, Hibiscus rosasinensis on the basis of 32,918 flowers examined showed an excess of lefts, the difference being statistically significant ( $\chi^2_1 = 20.6263$ ). The numbers of stamens per flower as well as the size of dry and water-soaked pollen grains according to the activation of the corolla were also compared (PAPERS, 5-7). Similar bilateral symmetry of flowers is noticed in a few other families, the important of them being Sterculiaceae, Filicesae, Cochlospermaceae, Euphorbiaceae, Caricaceae, Linaceae, Plumbaginaceae, Theaceae, Palmaceae, Tropaeolaceae, Rutaceae, Papaveraceae and Oxalidaceae.

#### Palm perianth :

Palm flowers have each six structures known as perianth segments that are comparable to the sepals and petals of other flowers. The outer whorl of 3 perianths representing

the sepals and the three representing the petals display varied kinds of overlapping. As the female flowers/fruits are more convenient to make accurate observations, the aestivation of perianth of several fruits from 23 species of palms were studied in detail (PARKER, 8-10). The salient findings of the study are given below.

The pistillate (female) flowers, like the males, invariably have imbricate calyx which also show right- and left-handedness. The petals of pistillate flowers in species like Caryota and Arenga are valvate, others like Dictyosperma album, Ptychosperma elegans, P. macarthurii, Ptychoraphis singaporensis, Actinorhynchia callanaria, Rhopalostylis sapida show only imbricate aestivation. But in many others, some fruits have imbricating and the rest contorting corolla. The ratio of fruits with contorting corolla to those with imbricating ones varies with species, the top positions being occupied by Phoenix sp. Clockwise and counter-clockwise rotating petals are clearly discernible among flowers/fruits <sup>beset with</sup> contorting corolla. Here again the numbers of fruits showing the two kinds of rotations are distributed equally. There exists a striking association between the aestivation of calyx and that of corolla in the same fruit. In species like Actinorhynchia callanaria and Rhopalostylis sapida without an exception, all the fruits which show left-handed calyx have right-handed corolla, and vice versa with fruits having right-handed calyx. This association persists appreciably in Archontophoenix sum- inghamia, Chrysalidocarpus luteaceus, Dictyosperma album, Heterospatha alata, Ptychosperma elegans, P. macarthurii and Ptychoraphis singaporensis. In several other species, such an association is not perceivable. In the Caryotid and Ptychospermate palms, flowers are arranged in clusters of three (2 males and a female) or two (males). The males bear

imbricate calyx and valvate corolla. The flower at the left end of a cluster in some species (Aranea pinnata) is left-handed and that at the right end is right-handed. But in Caryota and others, a reversal of the handedness of the males is noticed. The flower clusters are arranged spirally on the spike, and so, right- and left-handed spikes can be distinguished. The aestivation of calyx of the pistillate flowers in the clusters depends considerably on the spirality of the spike.

No association has been found to exist between the kind of foliar spiral of a palm and the aestivation of its fruits. Also there is no association between the aestivation of a fruit and the kind of foliar spirality of the seedling that develops out of it.

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#### 4. ASYMMETRY OF THE LEAF

Introduction : Phyllotaxis may be defined as the arrangement of leaves on the stem in relation to one another. From a node, three or more leaves may develop as in Nerium odoratum or Aleonia scholaris which arrangement is known as whorl phyllotaxis. In plants like Calotropis or Ixora, there are two leaves at each node, one across the other. Such opposite phyllotaxis is of two kinds; opposite and decussate as in Ixora, Parviflora, or opposite and superposed as in Psidium guajava. However, in a great majority of the flowering plants, only one leaf is produced in each node and this arrangement is known as alternate phyllotaxis. In grasses, or more strikingly in Ravabala madagascariensis, the leaves which are alternate are distributed one above another along two opposite vertical rows. Such is the distichous arrangement. But in other species, any two consecutive leaves are placed at an angular deflection of about  $137.5^\circ$ , and this arrangement leads to a spiral mechanism which is clearly asymmetric. The younger of any two leaves on a main stem or on a lateral shoot may be placed nearer to the older leaf by its left side or its right. In the former case, the spiral will move left-handed (clockwise) and in the latter, counter-clockwise (PAPER, 11). Thus, bilateral symmetry can be seen in plants where the phyllotaxis is alternate. By effecting controlled cross-pollination between known coconut palms, the progeny of the four parental combinations (L x L; L x R; R x R; R x L) with regard to the foliar arrangement showed a 1:1 proportion of left-spiralled and right-spiralled ones (PAPER, 12).

Data on several coconut palms from 36 <sup>countries</sup> centres or regions round the tropics were collected. In some regions from where I could not myself collect the data, colleagues were

supplied with adequate explanation and illustrations to distinguish the left-spiralled palms from the right-spiralled ones. The global data are given in Table 1. (Page 11). Out of 45698 palms, 50.8 per cent were left-handed. That is, the lefts and rights are distributed almost equally, the difference not being statistically significant. The data have been split into two groups on the basis of hemispheres. Statistical treatment of the data indicates an important association between foliar asymmetry and hemisphere. That is, the lefts are significantly more in the northern hemisphere, and rights are significantly more in the South, vide Tables 2 and 3 (page 11A). That the unidirectional rotation of the earth causes opposing effects between the hemispheres is well-known. Some plants do demonstrate this effect, especially the twining plants and others with spiral phyllotaxis such as the coconut.

#### Fractile Graphical Analysis :

The technique of Fractile Graphical Analysis developed by P. C. Mahalanobis is being applied more and more in different fields of studies. This technique in the form of bivariate graphs can be used for any set of (not less than four) observations on one or more variates made in the physical world provided the observations are capable of being ranked or arranged in some linear order. Observations on a single variate are also amenable to this type of analysis because each observation has necessarily a time co-ordinate associated with it in the form of the order of observation. The observations are made in the form of two independent interpenetrating sub-samples which are statistically equivalent, or the available data are subdivided into two samples in a suitable random manner. Following



Table 1

Cocos nucifera : Distribution of left- and right-spiralled palms

A. Northern hemisphere

country/ region	Lefts	Rights	L + R	L - R
1. Trust Territory of Pacific Is.	275	245	520	30
2. Philippines	726	774	1500	- 48
3. North Borneo	244	332	576	- 88
4. Sarawak	275	325	600	- 50
5. South Vietnam	1833	1478	3311	355
6. Malaya	583	556	1139	27
7. Southern Thailand	609	536	1145	73
8. Assam	254	252	506	2
9. Andaman Is.	658	505	1163	153
10. East Pakistan <sup>Bangla Desh</sup>	499	586	1085	- 87
11. Bengal, Orissa & Andhra	2258	2084	4342	174
12. Ceylon	1803	1754	3557	49
13. Madras	2042	2018	4060	24
14. Kerala	2875	2722	5597	153
15. Mysore, Gujarat & Maha-	997	875	1872	122
16. Nigeria }ashtra	222	278	500	- 56
17. Dahomey	520	510	1030	10
18. Ghana	568	557	1125	11
19. Ivory Coast	505	554	1059	- 49
20. Sierra Leone	784	749	1533	35
21. Surinam	475	335	810	140
22. British Guiana	416	239	655	177
23. Jamaica	467	443	910	24
<b>Total for N. hemisphere</b>	<b>19888</b>	<b>18707</b>	<b>38595</b>	<b>1181</b>

B. Southern hemisphere

1. Tonga Is.	234	266	500	- 32
2. Western Samoa	96	104	200	- 8
3. American Samoa	516	484	1000	32
4. Fiji	223	277	500	- 54
5. New Hebrides	265	235	500	30
6. New Caledonia	216	334	550	- 118
7. Br. Solomon Is. Protecto- rate	1461	1621	3082	- 160
8. Papua & New Guinea	406	398	804	8
9. Netherlands New Guinea	414	586	1000	- 172
10. Central Java	220	249	469	- 29
11. Mauritius	15	19	34	- 4
12. Seychelles Is.	556	455	1011	101
13. Tanzania	728	725	1453	3
<b>Total for S. hemisphere</b>	<b>5350</b>	<b>5753</b>	<b>11103</b>	<b>- 403</b>

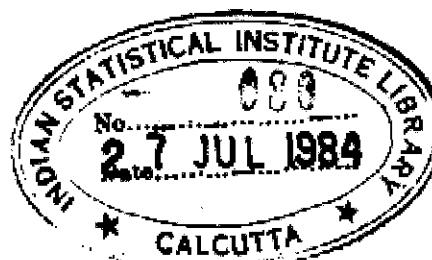


Table 2. Test for homogeneity of population

Particulars		Northern hemisphere	Southern hemisphere
1. Number of countries	N	23	13
2. Lefts & Rights	L+R	38595	11103
3. Lefts	L	19888	5350
4. Proportion of lefts	P*	0.5153	0.4818
5. $X^2_{N-1} = \frac{N}{1} \frac{(L-TP)^2}{TP} + \frac{N}{1} \frac{(R-T(1-P))^2}{T(1-P)}$		157.1742	75.5689
6. Degrees of freedom	N-1	22	12
7. Level of significance	α%	5%	5%
8. Significant value of $X^2$		33.92	21.03
9. Remark		$X^2$ significantly differs	$X^2$ significantly differs.

p\* = overall proportion of lefts based on pooled data in each hemisphere

Table 3. Values of  $X^2$

Particulars		Northern hemisphere	Southern hemisphere
1. Number of countries	N	23	13
2. Lefts & Rights	T	38595	11103
3. Lefts	L	19888	5350
4. Rights	R	18707	5753
5. $X^2 = \frac{(L-T/2)^2}{T/2} + \frac{(R-T/2)^2}{T/2}$		36.1384	14.6274
6. Degrees of freedom		1	1
7. Level of significance	α%	5%	5%
8. Significant $X^2$ value	2.9%	3.84	3.84
9. Remarks		$X^2$ significantly differs.	$X^2$ significantly differs.

laid down in the technique, the data on the distribution of left- and right-spiralled coconut palms are shown in such Fractile Graphs.

With the Chi - test performed on the global data shown in Table 1, we only know that the palms of a particular foliar spirality ~~is~~ are significantly more in one hemisphere and that the other kind is distributed <sup>at a</sup> in higher proportion in the other hemisphere. But we are unable to get a measure of how the various regions within a hemisphere compare with those of the other. The Fractile Graphical Analysis seems to take care of this deficiency.

Coconut <sup>data</sup> from three regions (Jorhat, Assam; Gale, Ceylon; Southern New Guinea) are considered for the F.G.A. There is some difference in the mode of recording observations in these centres. I was moving through different fields and around houses in Jorhat and recorded the kind of spirality of the palm that came to my sight in a time series. The entire data relating to 598 palms (Table 4) are split up into groups/

Table 4 (page 17A)

of 50 continuous observations each. Every odd-numbered group formed sub-sample 1, and every even-numbered group, sub-sample 2. The proportions of left-spiralled palms in each group were calculated and plotted. The graphs for the two sub-samples are shown in Fig.2 (top). The data from Ceylon were from a regularly planted garden. The palms were observed row by row in a regular order. The left- and right-spiralled palms of data from New Guinea are marked on a plan (Fig.3) according how they are distributed within a long strip of land. This plan was divided into equal rectangles and the lefts and rights in each were counted. The proportions of



COCONUT PALMS, DEYICH (16°N. LAT.)

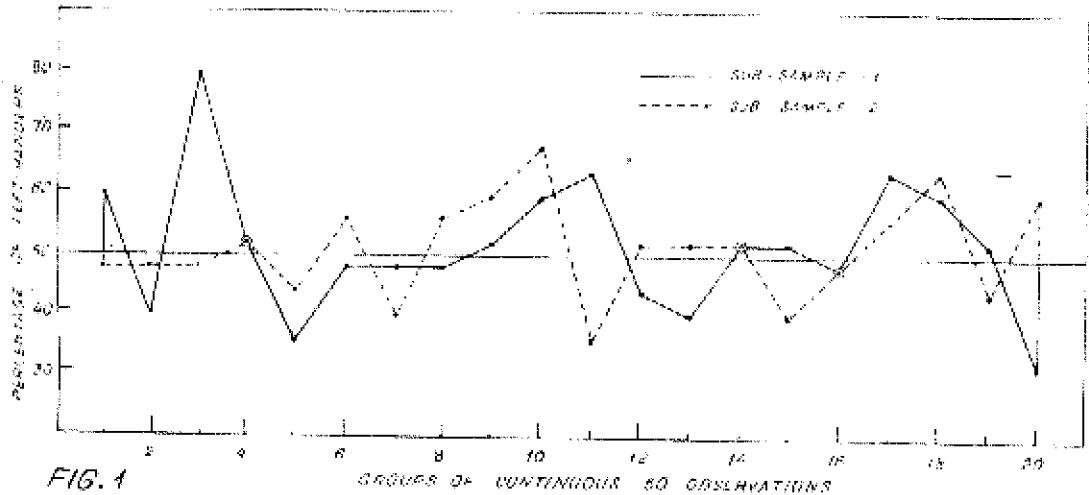


FIG. 1

COCONUT PALMS, JOPHAT (27°N. LAT.)

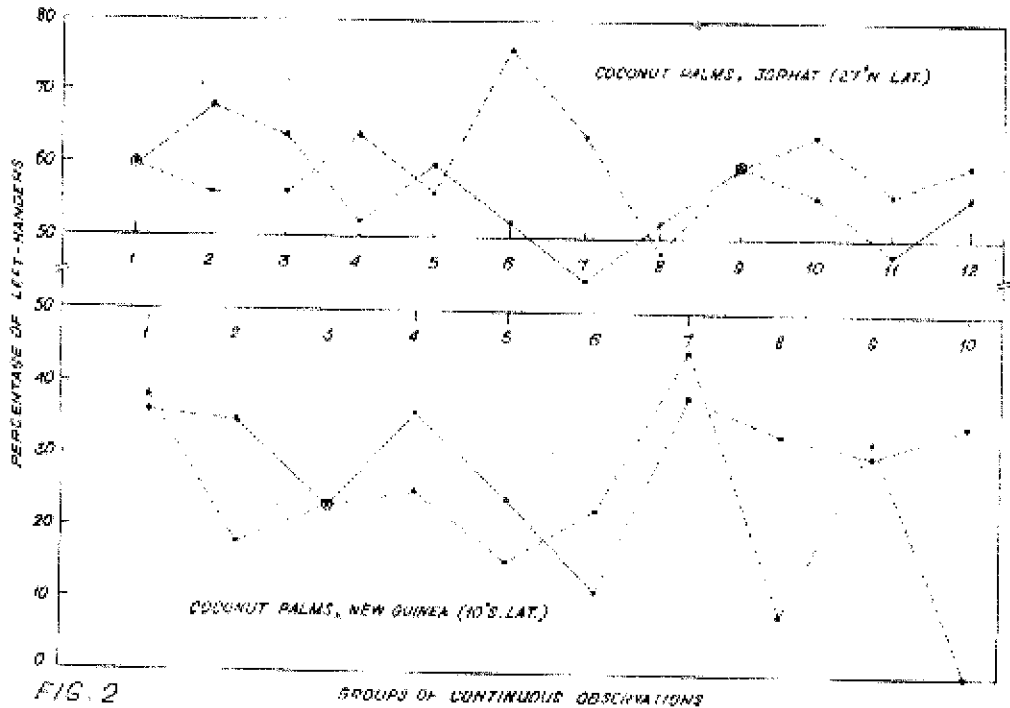


FIG. 2

GROUPS OF CONTINUOUS OBSERVATIONS

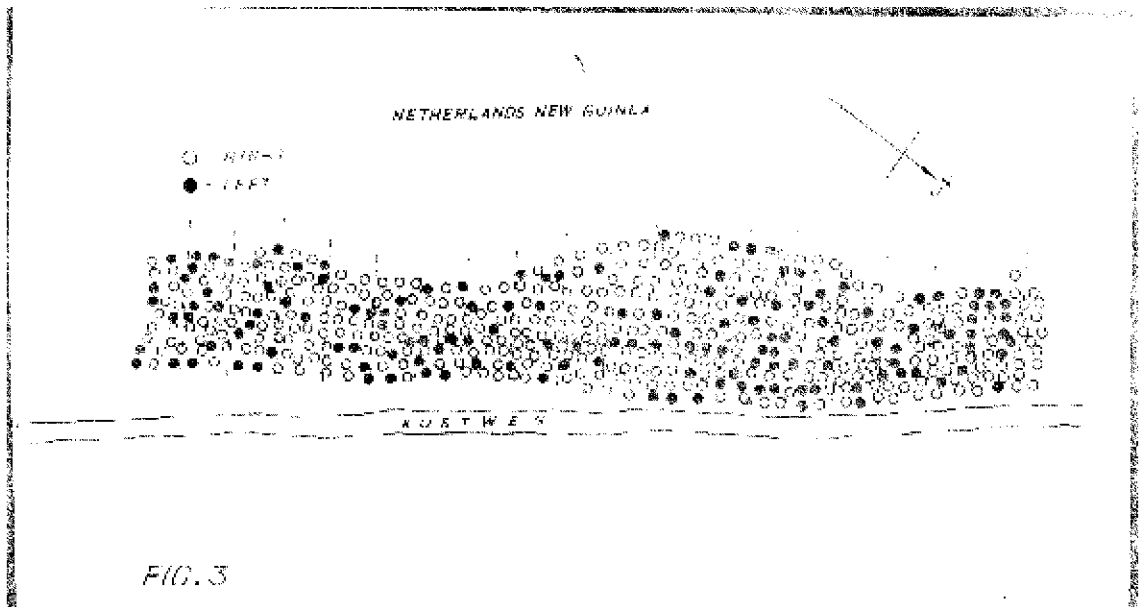
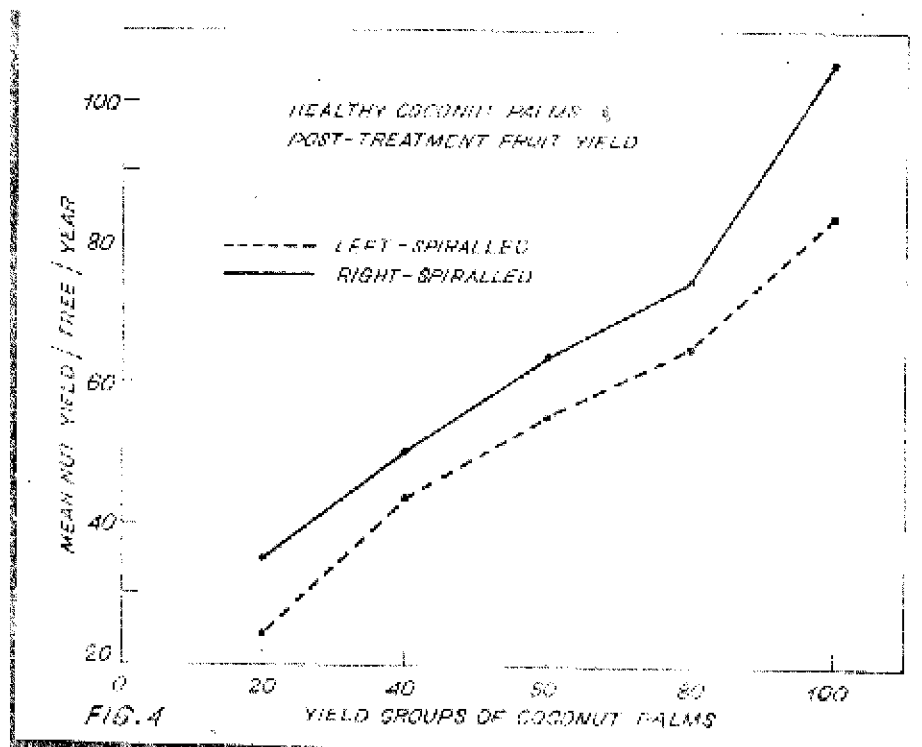


FIG. 3



lefts was calculated for each group.

The three sets of graphs shown in Figs. 1 & 2 relating to the three countries are similar in one respect. The graphs representing the two sub-samples in each group interpenetrate at intervals, thereby suggesting that the two kinds of palms are distributed uniformly throughout the area of observation. Another fact obvious from these graphs is that while the graphs on data from Ceylon move around the 50 per cent line, those of Jorhat and New Guinea remain much above and below the 50 per cent level respectively.

The graphs in Fig.4 show another striking phenomenon. I have reported elsewhere in this treatise (page 23) that  $\mu$  right-spiralled coconut palms/produce on an average more number of fruits than  $\mu$  left-spiralled ones. The  $\chi^2$  test results have shown that the yield difference between the two kinds of palms is statistically significant for the healthy palms, more significantly for the post-treatment period. However, this test could not reveal whether the significance/difference was brought about by the difference in a few palms or the entire population. The graphs in Fig.4 were prepared by arranging the mean fruit yield per palm in an ascending order both for the left-spiralled and right-spiralled palms. These graphs do not cross each other and their separation from each other suggests that the two groups of palms differ greatly between themselves with regard to fruit production. This situation is in marked contrast with the graphs illustrating the distribution of left-handed and right-handed coconuts.

## 5. BILATERAL SYMMETRY OF THE LAMINA

The spiral arrangement of leaves in the stem leads to an asymmetry in the shape of the leaf (PAPER, 13). In palm leaves, the central rachis (akin to the mid-rib) tends to divide the leaf blade into two linear halves, and one half appears to be the mirror image of the other. Even the number of leaflets on one half differs from that of the other, the difference becoming statistically significant in species which bear smaller numbers of green leaves in the crown. In order to measure the degree of this asymmetry, fifteen species of which eight belonging to the pinnate type, five to the palmate type and the last two to a type having bi-pinnate leaves were selected. 54 of the individual palms thus selected were left-spiralled and 53 right-spiralled. The numbers of leaflets from the left and right halves of 453 leaves from left-spiralled palms and 457 leaves from right-spiralled palms were counted and the difference between halves calculated.

The pinnate palms showed a higher degree of asymmetry in the leaves. Here the left half of leaves from left-spiralled palms and the right half of those from right-spiralled palms bore excess leaflets than their counterparts. The two species of Caryota bearing bipinnate leaves bore almost equal numbers of the primary leaflets (rachises) on both the halves, but the ultimate second order leaflets in Caryota mitis showed an appreciable difference between halves. The palmate palms showed the least variation between halves of leaves. Though belonging to the palmate group, young Rhapis excelsa behaves like a pinnate palm by showing the maximum dissimilarity between halves of leaves.



Ptyxis :

The term ptyxis relates to how the leaf blade (lamina) is folded, rolled or packed at the shoot-apex during the bud stage. For example, the lamina of the banana leaf is rolled from margin to margin, and the rolling is always counter-clockwise. But in grasses, while some leaves roll clockwise, others move counter-clockwisely. The lamina of a mango leaf is neither rolled nor folded. The lamina of most palms is folded like a fan. The leaf of water-lily is rolled from its two longer margins towards the mid-rib. If both the margins roll along the upper surface of the leaf, it is known as involute as in Scindapsus officinalis, and if along the lower surface, the ptyxis is known as revolute.

Cordyline rubra :

This ornamental plant bears lateral branches, and each shoot bears a crown of leaves. The leaves are arranged in two clear attractive spirals as in banana. In banana, however, the two spirals always move right-handed in all the varieties of all the species examined. But in Cordyline, while in some shoots the two spirals move clockwise, in others they veer counter-clockwisely. The two kinds of shoots are distributed randomly in any large population. The lamina remains rolled in bud stage and the direction of coiling is either left-handed or right-handed. There is a strong positive association between the directions of the leaf arrangement and rolling of lamina. (PAPER, 14). The kind of data gathered from only six shoots is shown below.

Table 1. Cardyline rubra : Data on foliar spiral & ptyxis

Leaf spiral	Convolution of successive leaves	Total	
		L	R
Right	R L R R R R L L R R R R R R R L L L	5	13
Right	R R R R R R L L R R R R R R R R R R	1	17
Right	R L R R R R R L L R R L L R R R R R R R R	5	15
	Total	<u>11 45</u>	
Left	R L L L L L R R R R R L L L L L L L	11	6
Left	L L L L L L R L L L L L L L L L L L L L L L L	19	1
Left	L L L L L R R L L L L L L L L L	12	2
	Total	<u>42 9</u>	

Scindapsus officinalis :

The lamina of this weak-stemmed climbing ornamental plant rolls in one of three ways, left-handed convolution, right-handed convolution and involution. A right-convolution is usually followed or preceded by a left-convolution and the occurrence of this frequency has been found to be statistically significant. But when a lamina shows involution, there is a high probability that the next one also will show involution (PARKER, 15). Data from five shoots are given in Table 2.

Table 2. Scindapsus officinalis : Ptyxis

Shoot	Ptyxis of successive laminae	Total		
		L	R	I
1	R L R I I L R I I I I I I I I L R I	3	4	11
2	L R L R L I R I I I I I L R I R L	5	9	7
3	L R L R L R L R L R L R	6	6	12
4	R L R L R L R L R L R L I I	6	6	2
5	R L L I L R L R L R L R L R	7	6	1

## 6. HANDEDNESS IN THE STEM

### Stem twining :

Various kinds of stems also display bilateral asymmetry. Weak-stemmed twiners coil around a support either clockwise or conversely. In and around ~~axsupperxwithaxclockwiselyx~~ Calcutta, about 95 percent of the stem twiners have been observed to move counter-clockwise and only the remaining small percentage of species are left-handed. The direction of twining appears to be genetical with most species. However, in Mikania scandens or Senecio confusus, within the same plant some shoots twine clockwise and others counter-clockwise. With Mikania scandens further interesting results were obtained. Charles Darwin in his CLIMBING PLANTS mentions that this species twines clockwise and also says that it is extremely difficult to come across the two kinds of twining within a species. However, as an exception, Darwin mentions that Fritz Muller in South Brazil recorded Mikania twining counter-clockwise. This South <sup>ma</sup>African weed belonging to the sunflower family is a serious menace to Agricultural land in many parts of India, more so in Bengal. Observations were made on this species at Calcutta during different seasons. About 67% of the stems twined clockwise and the rest counter-clockwise. I was able to extend the observations to Jorhat (Assam), Ernakulam (Kerala), Gale (Ceylon) and Jogjakarta (Indonesia) covering a region between 24°N to 10°S. It was found that the percentage of lefts progressively increased from 48 per cent at Jogjakarta (10°S) to 70 per cent at Jorhat (24°N). This is another clear indication that some plants demonstrate the influence of geophysical forces on them more vividly than others.

Under the heading No.8, results of an experiment are reported in which Vigna sinensis, a stem twiner that always moves counter-clockwisely and Dioscorea esculenta that always moves clockwisely were subjected to three conditions of growth. By changing the normal direction of twining, statistically significant difference in the fruit/tuber yield was brought about in these two species.

Twisting stems :

Most palms and many other trees show the scars of shed leaves or bear leaf bases on the stem. Where the phyllotaxy is alternate, spiral patterns can be made out and a stem may appear to twist to the left and another to the right. In some temperate timber trees such as Quercus, Ficus, Taxus, Castanea as well as the tropical Casuarina, the stem actually twists. A survey made in some forests of Czechoslovakia, U.S.S.R., Norway, Sweden and Scotland, it was found that a majority of these species twisted counter-clockwisely. Casuarina equisetifolia in the tropics also invariably twists counter-clockwisely.

Cacti :

In the realm of cacti one comes across beautiful twisting stems. The presence of several clusters of spines at specific positions on the cladodic stems makes the twist more obviously felt which, in addition, add beauty to the plant.

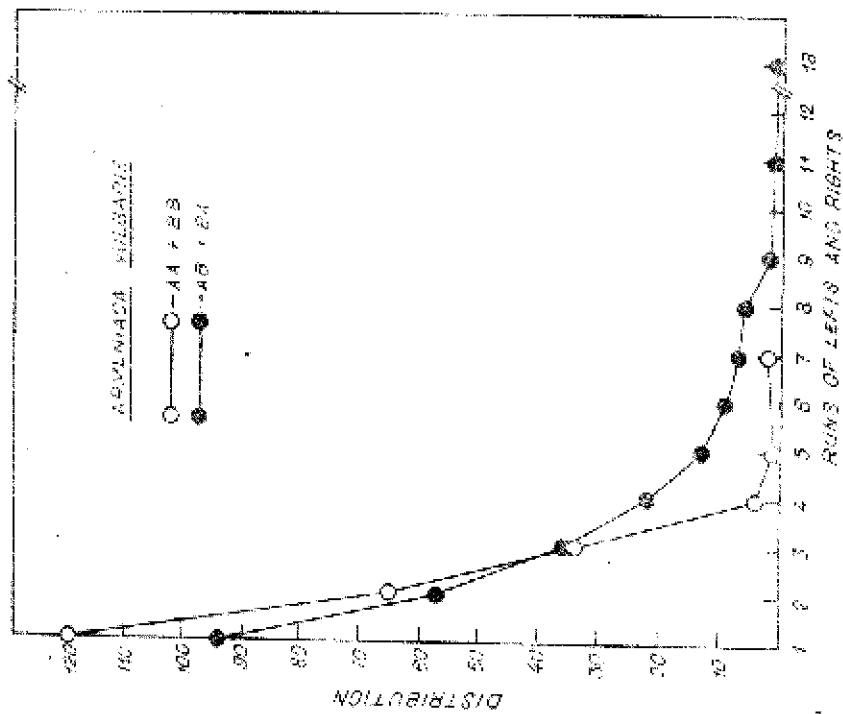
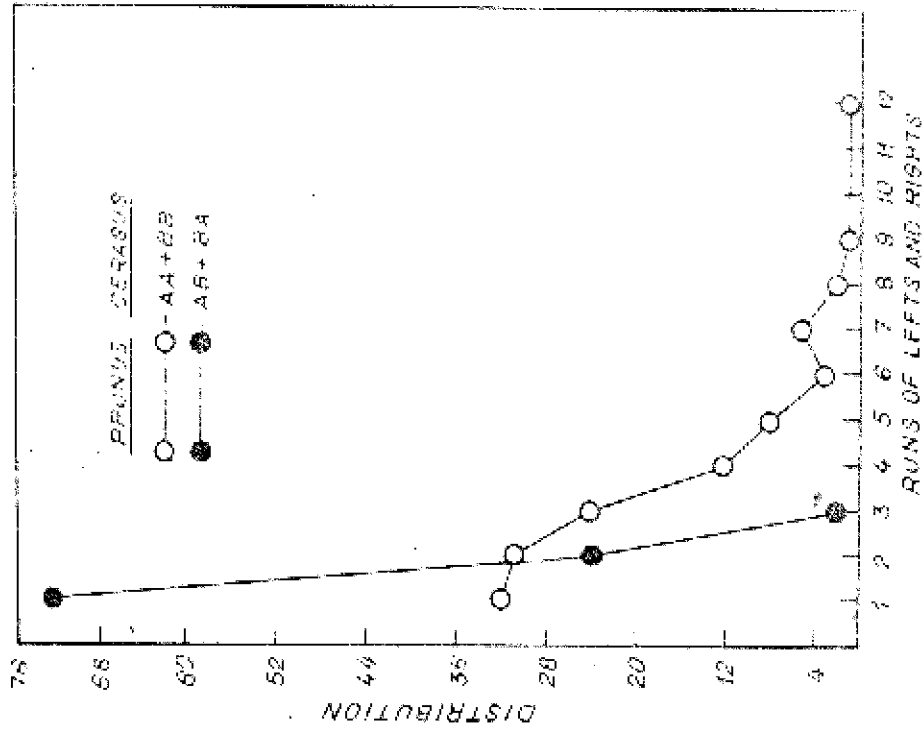
Data were obtained on the direction of stem twist in two species of Euphorbia (E. antiquorum and E. perillifolia). E. antiquorum has three wings on the stem on whose margin pairs of thorns are distributed. The main stem gives rise to lateral shoots at the nodes. The main stem as well as the off-shoots twist clockwisely or counter-clock

found that the main stem continues to show the same kind of twisting however tall it may grow. But all the off-shoots of a ~~same~~ main stem do not show the same kind of twisting. There is a positive association between the twist of the main stem and that of off-shoots. In any plant, about two-thirds of the first order off-shoots twist like that of the main stem and the rest unlike it.

Euphorbia neriifolia has a cylindrical stem with five slanting rows of spines. From each node, upto five off-shoots may develop. Like E. anticyperum, there exists a positive association between the twist of the main stem and that of first order off-shoots.

Kinds of branches in temperate fruit trees :

Some data on the spirality of main stem and that of off-shoots were collected from Bratislava (Czechoslovakia) on four temperate fruit trees such as Armeniaca vulgaris, Prunus cerasus, P. avium and P. domestica. Only young plants were selected which produced lateral branches from every leaf axil. For each species data on about 50 plants were recorded. The spirality of the main stem and that of the off-shoots (commencing regularly from the lowest one) were recorded for each plant. <sup>Data recorded on Armeniaca vulgaris are briefly mentioned below.</sup> The number of off-shoots examined per plant ranged from 11 to 53. All plants bore left- and right-spiralled off-shoots. However, it is clear from the data that the ~~left-spiralled~~ ~~right-spiralled~~ left-spiralled trunks bore more right-spiralled off-shoots, and the right-spiralled ones an excess of left-spiralled branches. Chi square analysis was performed on the condensed data given in Table 1 to test the dependence of the trunk and off-shoots. This value at 1 d.f. turns out



to be 78.126 which means that the trunks and off-shoots are clearly associated for the foliar spirality statistically significantly. However, here the peculiarity is that when the trunk is left-spiralled, majority of the off-shoots are right-spiralled, and vice-versa when the trunk is right-spiralled.

Table 1. Armeniaca vulgaris : Summary of data on foliar spiral

Trunk	Plants	Off-shoots		
		Right	Left	R + L
Right	23	155	325	480
Left	27	342	232	574
R + L	50	497	557	1054

$$\chi^2 = 78.126$$

Having recorded the spirality of the off-shoots in an ascending order, the relationship of any two adjoining off-shoots for the spirality was examined. They are either similar or dissimilar for the handedness. Thus, the like and unlike pairs (LL, RR, LR, RL) were recorded for all the plants in a species. The data for the LL and RR pairs were pooled. Also those of LR and RL were pooled separately. The frequency distribution of like and unlike pairs are plotted, and Figs. 1 and 2 show the results for Armeniaca vulgaris and Prunus cerasus. The graphs show mirror image situations. In the first species, the unlike pairs have a wider distribution than the like pairs. This situation is just reversed for Prunus cerasus. It is further interesting that two species of the same genus (Prunus cerasus and P. alium) behave oppositely. Thus,

he biometrics on the morphology of these fruit trees have revealed another inherent difference between two closely resembling species of the same genus.

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EFFECT OF PHYLLOTAXIS ON FRUIT PRODUCTION  
IN SOME TROPICAL CROP PLANTS

Introduction

Most species of plants with alternate phyllotaxis show left- and right-handedness in the arrangement of their leaves on the individual members. Although this asymmetry is not generally determined (PAPER NO. 12), fruit-yield was found to be associated with foliar arrangement in a few species.

In the most useful tree, Cocca nucifera, those individuals with right-handed foliar spirals produce significantly a greater number of fruits than the left-handed ones. Fruit-yield data on the coconut obtained from Jamaica, Tanzania and the Trust Territory of the Pacific Islands support those collected from India. Also in two more species of palms (Boerhaavia flabellifera and Areca catechu), a significant right-left difference in fruit-yield was noticed. Similar observations were also extended to the bast fibre crop, Hibiscus cannabinus (Neenan hemp).

Statistically designed experiments were conducted with Lima sinensis whose stem normally twines counter-clockwise, to study the effect of artificially changing the direction of their twining. The method of the experiment and results are recorded under the next section.

Foliar spirals in palms

The phyllotaxis of palms is always alternate, and in most species, two consecutive leaves are placed at an angular deflection of  $137.5^\circ$ . This leads to a spiral mechanism in the arrangement of leaves. This angle makes with the remaining angle ( $222.5^\circ$ ) to complete one full revolution, a proportion (0.618) which is spoken of as Golden Proportion. The Fibonacci Sequence

(1,1,2,3,5,8,13,21,34 .... ) also bears this Golden Proportion between two consecutive stages (excepting the few lower ones). Because of such a situation, the number of foliar spirals in a palm species always synchronises a Fibonacci Number (Davis, 1970, 1971a (PAPERS, 16, 17). Thus, there are palms having a single foliar spiral ~~in a palm species always~~ (Areca catechu), two (Arenga saccharifera), three (Borassus flabellifer), five (Cocos nucifera) and eight spirals (Elaeis guineensis). Fibonacci system can be seen also in pine cones, Anthuriums(PAPER, 18), pine-apples, cycas cones etc.

To an observer viewing from the base of any leaf, if the immediately younger leaf is nearer by the observer's left-hand side, this palm is regarded as left-spiralled, and if nearer to the right-hand, the palm is considered right-handed (Davis, 1971b, PAPER, 18).

The foliar spirals are non-genetic in their inheritance as evidenced by the results of artificial breeding followed in Cocos nucifera (Davis, 1962). But surprisingly, an important character like fruit-yield was found to depend on the direction of foliar spirals (Davis, 1963, PAPER NO. 19). Data from Cocos nucifera, Borassus flabellifer and Areca catechu are presented to substantiate the above fact.

#### A. Cocos nucifera Linn.

##### 1. Data from India :

From 1953 to 1960 I was in charge of a micro-nutrient manurial experiment on a 8-hectare coconut plantation at the Central Coconut Research Station, Kayangulam, Kerala (India). 128 of the 384 experimental palms were healthy, another 128 were in the early stage of a contagious disease known as Root (Wilt) and the rest were severely affected by the disease.

the trees were chosen without regard to their spirality. But as no data on nut-yield were available for these palms, I decided to see whether the non-inherited asymmetry had anything to do with the yield. Each palm was subsequently classified for its leaf spiral and I found to my great surprise the large effects. 77 of the 384 palms were right-spiralled (according to single spiral).

The summary data given in table 1 shows the mean fruit yield for the left-spiralled and right-spiralled palms under the three categories according to their condition. The significance of these figures is given in Table 2.

Table 1. Cocos nucifera: Annual yields of fruits (Data from Kerala, India)

Category	Number	12 years (1949-1960)		6 years (1955-1960)		
		Mean	Variance	Mean	Variance	
Healthy	R	58	57.69	437.42	65.60	616.46
	L	70	49.82	366.74	54.28	455.17
Early diseased	R	60	32.95	292.12	36.54	323.24
	L	66	30.55	375.34	33.10	524.72
Late diseased	R	56	22.05	266.56	23.63	314.68
	L	64	20.04	186.59	20.33	239.12

N.B. Spiral determination made on the basis of positions of two consecutive leaves

Table 2. Cocos nucifera : Significance of Right-Left yield differences (Data from Kerala)

Comparison		degrees of freedom	t	P
Healthy	12 years	126	2.22	0.15
"	6 years	126	2.77	0.0041
Early diseased	12 years	124	0.733	0.234
"	6 years	124	0.933	0.18
Late diseased	12 years	118	0.736	0.21
"	6 years	118	1.09	0.14

The values for the t test show that the right-left yield

difference is significant in the case of the healthy palm! The data for the diseased trees are not in themselves significant, but are in the expected direction, and considerably enhance the significance of the data on the healthy trees. In fact, the over-all probability that the <sup>lefts</sup> ~~rights~~ produce as many or more nuts as the <sub>rights</sub> ~~lefts~~ is about .00014. Thus, there is no doubt of the significance of the result, and it is more important to show that rights yield more than lefts in other species and climates. Satyabalan and others (1964) could not, however, observe any significant difference in the yield between the two types of coconut in another population from Kerala.

## 2. Data from Tanzania :

Dr. A.R. Arthur-Worsop, Chief of the Coast Agricultural Station, Government of Tanzania, had kindly sent me data on the fruit-yield in coconut. Those on 481 palms subjected to a Cultivation Experiment for the period from 21.1.60 to 22.12.65 are summarized in Table 3.

Table 3 (page 26)

A right-spiralled palm, on an average, produced 80.32 nuts per year, while a left-spiralled one produced only 64.77 nuts per palm, the difference being 24.01% which is highly significant. This figure is even greater than that (20.9%) I got from the palms in Kerala.

## 3. Data from Jamaica, West Indies :

Dr. R.W. Smith, Agronomist of the Coconut Industry Board Jamaica supplied me with yield data on the Jamaica Tall Variety of coconut. Among the sets of data, the one relating to the field F/2 Boston (St. Ann. clay loam No.78) is the largest and relating to a longer duration (from 1961-1969). The data

Table 3. *Cocos nucifera* : Nut-yield data from Tanzania(1960-65)

Treatment and Replication	Right spiral		Left spiral	
	No. palms	nuts picked	No. palms	nuts picked
8 Treat.No.8 Replic.1	6	818	9	783
" " " 2	7	348	7	477
" " " 3	9	1075	6	323
" " " 4	7	58	9	302
	29	2299	31	1885
1 Treat No.1 Replic.1	9	550	4	58
" " " 2	8	474	7	333
" " " 3	4	149	12	427
" " " 4	9	558	6	177
	30	1731	29	995
5 Treat.No.5 Replic.1	4	613	11	1252
" " " 2	7	296	6	219
" " " 3	9	889	7	628
" " " 4	5	592	9	685
	25	2388	33	2782
6 Treat.No.6 Replic.1	5	545	9	471
" " " 2	6	279	9	640
" " " 3	8	700	8	657
" " " 4	8	680	7	185
	27	2204	33	1953
2 Treat No.2 Replic.1	6	417	9	709
" " " 2	9	1092	5	491
" " " 3	4	362	11	742
" " " 4	9	510	7	636
	28	2381	32	2578
7 Treat No.7 Replic.1	5	673	11	557
" " " 2	8	711	8	918
" " " 3	6	774	8	912
" " " 4	10	1032	6	397
	29	3190	33	2784
3 Treat No.3 Replic.1	6	484	8	510
" " " 2	8	314	8	490
" " " 3	8	792	6	520
" " " 4	7	303	9	597
	29	1893	31	2117
4 Treat No.4 Replic.1	6	228	10	171
" " " 2	9	632	6	311
" " " 3	7	772	8	673
" " " 4	5	274	11	397
	27	1906	35	1552
Grand totals:	224	17992	297	16646
Mean/palm		80.32		64.77

Difference Right - Left = 24.01%

on the 130 palms of which 60 are left-spiralled are summarized in Table 4.

Table 4. Cocos nucifera: Yield data on left- and right-spiralled palms (Data from Jamaica)

A. Right-spiralled palms

No. palms:	N u t - y i e l d s     d u r i n g								Total
	61-62:	62-63:	63-64:	64-65:	65-66:	66-67:	67-68:	68-69:	
26	1650	2170	2385	2725	2839	2900	3129	3151	20949
25	1734	2195	2374	3007	2969	2856	3500	3088	21705
19	1553	1686	1802	2126	2366	2238	2707	2497	16785
70	4747	6051	6561	7858	8174	7974	9336	8736	59437
Per palm:	67.81	86.44	93.73	112.26	116.77	113.91	133.37	124.80	106.14

B. Left-spiralled palms

26	1710	2141	2411	2650	2775	2744	2949	2869	20249
25	1618	1904	2301	2560	2692	2808	3265	2992	20140
9	495	602	598	688	888	785	1016	879	5991
60	3823	4647	5310	5898	6355	6337	7230	6740	46340
Per palm:	63.72	77.45	88.50	98.30	105.91	105.62	102.50	112.33	96.54

Note : Spirality of palms determined on the basis of the positions of two consecutive leaves

It is clear from data given in Table 4, that the right-spiralled palms produced more fruits per tree during each year of the eight-year period. On the aggregate, a right-spiralled palm produced 9.94% fruits in excess of a left-spiralled one.

4. Data from Trust Territory of Pacific Islands :

Dr. M.N. Sproat, Director of Agriculture, Trust Territory of Pacific Islands at my request weighed the copra from the fruits of 100 left-spiralled and 100 right-spiralled coconut palms during the calendar year 1963. The right-left difference of kernel yield was quite high, being 13.48 per cent (that is, 31.24-27.53 lbs. of kernel per tree per year ). Davis, 1964 a).

**B. BORASSUS FLABELLIFER LINN.**

The palmyra<sup>palm</sup> flowers only once every year in India.

Ten female palms from a village 80 km north of Calcutta whose foliar spirals were known were harvested of all the fruits. Five of them were left-spiralled and the rest right-spiralled. On an average, a right-spiralled palm produced 190.20 fruits while a left-spiralled one produced only 114.20 fruits, the difference being 68.3 per cent.

Fruits of another set of 31 palms were counted at Srikakulam (Andhra Pradesh) during the 1966 fruiting season, and the data relating to the 14 left-spiralled and 17 right-spiralled palms are presented in Table 5.

**Table 5. Borassus flabellifer: Foliar spiral and fruit-yield**

A. Foliar spiral Right			B. Foliar spiral Left		
Palm	No. of spikes	No. of fruits	Palm	No. of spikes	No. of fruits
1	19	308	1	11	146
2	18	136	2	5	52
3	7	60	3	15	108
4	9	71	4	21	98
5	11	118	5	8	91
6	18	142	6	7	77
7	12	121	7	14	133
8	37	208	8	32	179
9	14	128	9	23	159
10	22	118	10	23	191
11	36	279	11	10	100
12	14	106	12	8	61
13	not recorded	111	13	13	90
14	not recorded	159	14	16	102
<b>Total</b>	<b>217</b>	<b>2065</b>	15	17	141
mean	15.08	147.50	16	not recorded	78
			17	not recorded	38
			<b>Total</b>	<b>223</b>	<b>1844</b>
			<b>Mean</b>	<b>14.87</b>	<b>108.47</b>

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A right-spiralled palm produced on an average 147.50 fruits, and a left-spiralled palm only 108.47 fruits. The excess for the rights turns upto 35 per cent. Thus, the two populations show the similar trend.

C. ARECA CATECHU LINN.

Areca catechu shows only a single foliar spiral. Fig. 1 shows left-spiralled and right-spiralled palms. Under Calcutta conditions, it flowers mainly in March-April. A palm produces generally 2-5 spadices in the year, of which one or two may be sterile or partially developed. All the bunches produced in 54 middle-aged palms were marked during 1967 and the fruits from each bunch were counted separately. 32 of these palms were left-spiralled and 22 right-spiralled. The lefts produced, on an average, 3.14 productive spadices and the rights produced 2.59 productive bunches as shown in Table 6.

Table 6. Areca catechu Linn. : Foliar spiral and fruit-yield

Kind of palm :	<u>spadices/palm</u>		Total	Mean per
	<u>productive</u>	<u>sterile</u>	<u>fruits</u>	<u>palm</u>
Right-spiralled (22)	2.59	0.53	4104	186.55
Left-spiralled (32)	3.14	0.86	4305	134.53
<b>Total</b>	<b>3.45</b>	<b>0.72</b>	<b>8409</b>	<b>155.72</b>

Excess (number of) nuts for the Rights = 38.67%

A left-spiralled palm on an average produced 134.53 fruits while a right-spiralled palm produced 186.55 fruits. This means that the rights produced 38.67 per cent in excess of the lefts.

Foliar spiral and yield in Hibiscus cannabinus Linn.

Hibiscus cannabinus, popularly known as the Deccan hemp has been in cultivation for centuries in India as a bast fibre crop. It is a tall erect annual plant and the leaves

are distinctly alternata. From the leaf arrangement, left- and right-handed plants can be distinguished and the two kinds of plants are distributed almost equally in any large population. However, the various branches show clockwise and counter-clockwise arrangement of leaves. The flowers are usually solitary, axillary and conspicuous. Being a Malvaceous species, the petals are contorted and the direction of contortion in a flower may be clockwise or counter-clockwise, the two types of flowers occurring equally in large populations (Davis, 1964b). Left- and right-twisting flowers are shown in Fig. 2, on page 6.

There is an association between the direction of the foliar spiral of a shoot and the aestivation of the flowers. A plant/shoot whose leaves are arranged clockwise, produces a greater number of flowers having counter-clockwise contortion. Also plants with counter-clockwise leaf arrangement produce a preponderance of flowers with clockwise contortion.

Observations were made on a plot of Hibiscus cannabifolius at the Indian Statistical Institute. All the well-developed fruits from 49 left-spiralled and 50 right-spiralled plants were counted and the data presented in Table 7.

Table 7. Hibiscus cannabifolius : Foliar spiral & fruit-yield

Spiral of plants	No. of plants	Number of fruits	
		Total	Mean per plant
Left	49	1317	26.88
Right	50	1558	31.16
Total	99	2875	29.04

$$\begin{aligned} \text{Right} - \text{Left} &= 4.28 \text{ fruits/plant} \\ &= \underline{15.92} \text{ per cent.} \end{aligned}$$

A right-spiralled plant produced, on an average, 4.28 fruits (i.e. 15.92 per cent) more than that of spiralled plant. These results are in conformity

situation prevalent in the three palm species mentioned already.

#### Summary

Results of observations made on the fruit-yield and its association with foliar asymmetry in three palm species - Cocos nucifera, Borassus flabellifer and Arca catechu as well as the fibre crop, Hibiscus cannabinus are reported.

As the phyllotaxy of a palm is alternate, left- and right-spiralled palms can be made out by tracing out the position of a leaf in relation to that of its immediate older one. However, some species of palms show three, five or more obviously visible spirals which are not given any importance in this paper. Thus, all species of palms are regarded as having a single foliar spiral.

Fruit-yield data on the coconut collected in India and those received from Tanzania, Jamaica and Trust Territory of Pacific Islands showed uniformly that a right-spiralled coconut (according to the single spiral) yields significantly more fruits than a left-spiralled one. Borassus flabellifer and Arca catechu also show this trend more clearly.

In Hibiscus cannabinus there is a negative association between the foliar spiral and the aestivation of corolla. In this species too, the right-spiralled plants produce more fruits than the left-spiralled ones.

#### Reference

- Davis, T.A. (1962). The non-inheritance of asymmetry in Cocos nucifera. J. Genet., 58 : 42-50.
- Davis, T.A. (1963). The dependence of yield on asymmetry in coconut palms. J. Genet., 59 : 106-115.
- Davis, T.A. (1964a). Leaf spiral and yield  
204 : 496-497.

- Davis, T.A. (1964b). Aestivation in Malvaceae. Nature, 201 : 515-516.
- Davis, T.A. (1970). Fibonacci numbers for palm foliar spirals. Acta Botanica Neerlandica, 19 : 249-256.
- Davis, T.A. (1971a). Why Fibonacci Sequence for palm leaf spirals ? Fibonacci Quart., 9 : 237-244.
- Davis, T.A. (1971b). Right-handed, left-handed and neuter<sup>ral</sup> palms. Principes. J. Palm Soc., 15 : 63-68.
- Satyabalan, K; Ninan, O.A.; and Krishna Murar, M.M.(1964). Foliar spiral and yield in coconuts. Nature, 202 : 927-928.
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## 8. EFFECT OF CHANGING THE DIRECTION OF GROWTH ON FRUIT-YIELD IN COWPEA AND DIOSCOREA

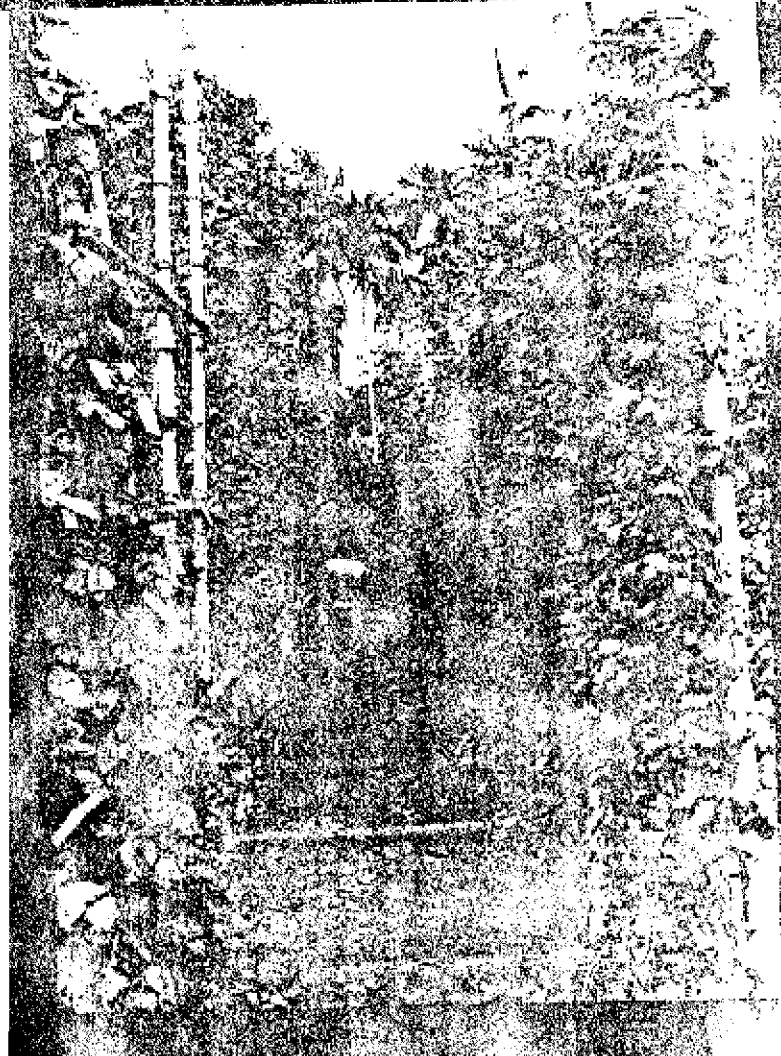
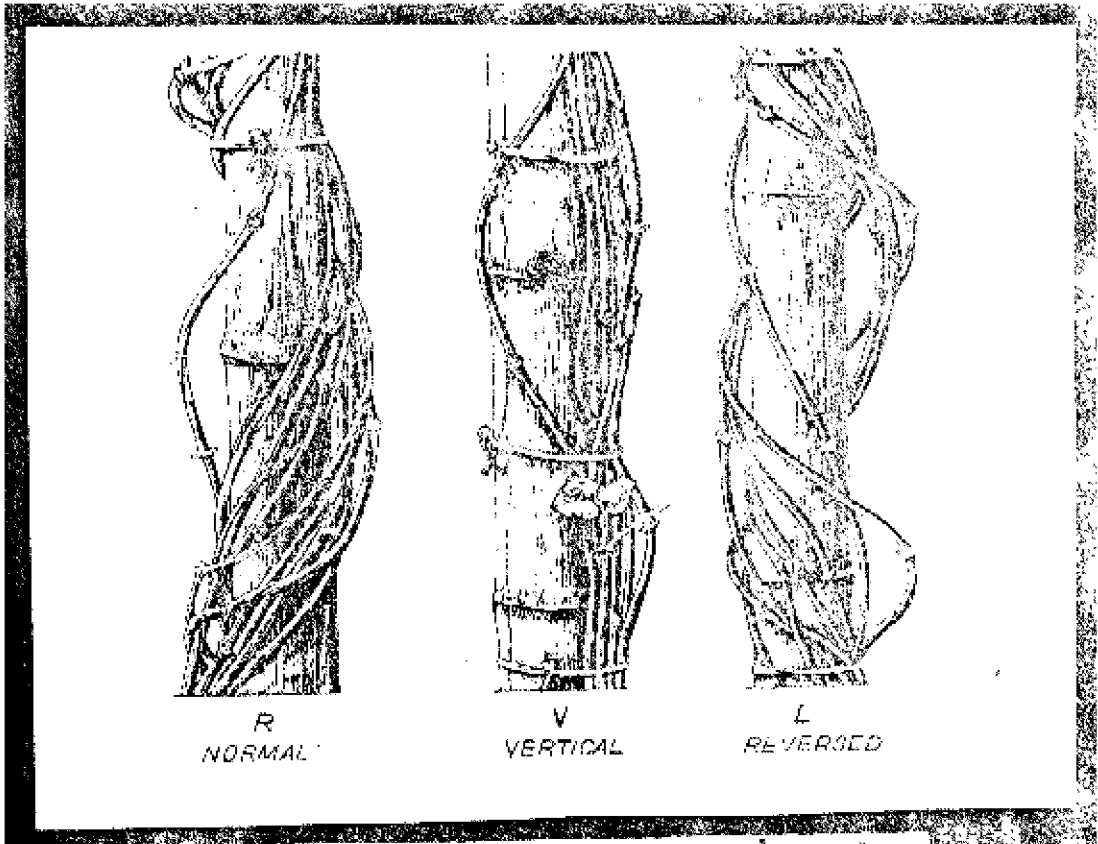
### Introduction

Many flowering plants display bilateral symmetry in their various organs and the significance of some such situations were statistically analysed (Davis and Ramanujacharyulu, 1970). Asymmetry in a plant organ is effected by various causes, and sometimes it helps the to compete with other plants efficiently in order to attain essential requirements for its growth. A weak-stemmed liana, for instance, in a tropical forest would find itself difficult to expose its leaves to the sun's rays unless it has the capacity to grow faster and produce a such longer stem that would twine over other trees, and spread its leaves above the canopy of the forest trees. The stem of such a climber has to move clockwise, counter-clockwise or irregularly. For most species, the direction of twining of the stem seems to be genetically controlled although plants like Mikania scandens, Senecio confusa etc. have some of their shoots twining clockwise and the others counter-clockwise. Over 90 per cent of the stem-twiners in and around Calcutta move counter-clockwise. It was proposed to see whether a significant change could be brought about in their productive capacity by reversing the normal direction of twining some stem twiners. For this purpose, one set of experiments was conducted on cowpea (Vigna sinensis Sndl.) which normally twines counter-clockwise and produces fruits and seeds. The other set of experiments was conducted on Dioscorea esculenta Burkill whose stem moves clockwise and produces tuberous roots. This species does not flower under Calcutta conditions. The results on the trials with Vigna sinensis are reported in some data

Dioscorea briefly reported.

Grote Reber, an eminent astro-physicist of the Commonwealth Scientific and Industrial Research Organisation, Tasmania (Australia) reported in 1960 some most striking results on his experiments with nine varieties of bean plants by reversing the direction of the stem from counter-clockwise (normal direction) to clockwise (left-handed) direction. He planted these pole beans in rows of about fifty hills each. The vines on even-numbered poles of three rows were carefully unwound and twined backward. All vines and pods were allowed to ripen, wither and dry on the poles. Then the plants were harvested and weighed. In all cases Reber found an appreciably better ratio of ounces of beans/ounces of shucks, and to a lesser ratio of ounces of beans/ounces of vines for the reversed vines compared to the normal ones. The same experiment was repeated by him with Hawaiian beans and he obtained similar results. Through the findings of another experiment with a Hawaiian bean as well as a different species (Phaseolus multiflorus), Reber confirmed in 1964 that artificial reversal of the direction of coiling of bean vines caused an increase in the weight ratio of beans to shucks.

Since Reber's experiments were not based on serious statistical considerations, it was decided to repeat the experiments. The fact that the fruit-yield in the coconut palm was found to be dependent on the direction of foliar spiral (Davis, 1963) also prompted the conduction of the present investigation with cowpea at the gardens of the Indian Statistical Institute, Calcutta.



### Materials and methods

#### A. Vigna sinensis :

Three varieties of cowpea popularly cultivated in South India were obtained from the Madras Agricultural Research Institute, Coimbatore. They are :

- I. E.C.455 ( a green vegetable type with long pods and bearing medium-sized seeds. It is a good yielder)
- II. New Era ( a seed type with medium-sized pods. Its seeds are large and is a good yielder).
- III. C.521 (a seed type with medium-sized pods and an average yielder).

The three methods tried were : (1) H (or R); plants were allowed to twine by the normal direction which is counter-clockwise (right-handed), (2) V; Plants were forced to grow vertically, and (3) L; Plants were forced to twine clockwise (left-handed). Figure 1 illustrates the three methods.

20 feet long, more or less uniform bamboo poles (base diameter about 4 inches and tapering to 2-3 inches at the top) were used as supports. The bamboos were buried in the soil to a depth of two feet. The design of the experiment chosen was Latin Square Design, and the experimental plot measured 90 ft x 45 ft. Each of the nine plots contained nine rows, and one variety occupied three rows of which in one the growth was vertical, in another, clockwise and in the third, counter-clockwise. Under each row, three poles were fixed and one plant was allowed to twine or grow on each of them.

Five seeds were sown at the base of each pole on March 25, 1966 and the seedlings were thinned to 3 each ten days later. They were further thinned to 2 seedlings per pole on April 16, and finally only one seedling was allowed per pole



exactly one month after sowing. Variety I was a fast-grower which started twining on the poles within a month of sowing. Tying of the vines on the poles with narrow cotton tapes commenced from April 23 with this variety. The other two varieties had stiffer and sturdier stalks, but produced tender vines in a further fortnight when they were tied in accordance with the design. Uniform tying was adopted also for the plants twining by the normal way (counter-clockwise). Whenever the twiners grew three inches or more above the last tie, the fresh growths were tied again. Hence, for some poles, tying was essential once every three days during certain periods. As may be presumed, the free tips of the vines forced to move clockwise and vertically always showed their urge to twine counter-clockwise. Tying was discontinued on June 10 when flowering had already commenced, and thereafter the shoots crowded at the distal end of the poles.

Variety II was the first to commence flowering on May 18. Variety III flowered first on June 3 which was followed immediately by Variety I. Because of its susceptibility to a virus disease, Variety I was badly damaged and most plants became stunted and produced crinkled and oblerotic leaves. In addition, mites also started infesting some plants, Variety I being most susceptible to it. Variety II was also sparingly attacked. The mites were, however, destroyed by hand as and when detected. With the heavy rains in July-August, the mites totally disappeared.

The plants fruited in stages and hence the ripe (dry) pods were collected once every three days and stored in paper bags. Fruit-yield from the three pl

and the numbers of good and shrivelled seeds were estimated for each treatment.

However, <sup>the</sup> weights of stems, roots and leaves were not recorded. As the ripe leaves shed at intervals, collecting and assigning them to the respective plants was almost impossible. The roots of practically all the diseased plants started rotting even before their shoots withered fully. This discouraged the collection of roots of even the healthy ones. However, the stems along with their various off-shoots could have been collected and weighed. But it was not easy to separate the individual plants since the branches of the three plants of the same treatment intertwined deeply.

#### Results

Tables 1-3 give data on the number of fruits, weight of fruits and numbers of good and shrivelled seeds respectively for each variety under each treatment for all the nine plots. Variety I performed badly and failed to produce any fruit in many plots. Also the fertility status of the experimental plot was not uniform since the plots 7-9 gave poor yields compared to the others as evidenced from data given in Table 4. From the figures of this table, the mean yield per plant is calculated as 43 fruits, weighing 56.2 gms and bearing 454 good seeds. These data also include the plants that produced no fruits. The respective figures for varieties II and III naturally should be higher.

Table 5 gives detailed yield figures individually for the three varieties. The treatments differ significantly from one another. Regarding the overall mean yield of 177 gms of a treatment, the left-handed ones are 177 gms

120	-	671	-	298	13	-	-	II N
I N	II L	II V	III V	II N	I N	III L	III N	I L
83	272	197	327	200	-	-	-	-
III N	I V	III V	I L	II L	II N	I N	III L	II V
166	73	389	-	350	246	-	1	-
III V	III N	I V	II N	I N	III L	II V	I L	II L
152	43	-	332	3	20	6	-	-
II L	II V	I N	III N	I L	III V	II N	I V	III L
482	183	6	220	1	232	178	8	6
I L	III L	II N	II L	III N	I N	III V	II V	I V
-	431	376	550	114	7	112	106	13
II N	I L	III L	I N	III V	II V	I V	II L	III N
238	7	277	-	283	267	-	162	6
I V	III V	III N	III L	II V	I L	II L	II N	I N
32	262	186	158	226	4	195	82	17

I, II, III - three varieties of cowpea. L - left, N - Right and V - vertical methods

II V 164.0	I N -	II L 818.2	I V -	III L 285.2	III N 16.6	I L -	III V -	II N -
I N 100.0	II L 368.0	II V 300.0	III V 401.7	II N 285.9	I V -	III L -	III N -	I L -
III N 199.0	I V 78.5	III V 510.7	I L -	II L 507.2	II N 378.2	I N -	III L 2.5	II V -
III V 180.0	III N 47.7	I V -	II N 508.8	I N 3.0	III L 25.0	II V 8.2	I L -	II L -
II L 803.0	II V 225.5	I N 4.7	III N 290.0	I L 1.0	III V 264.7	II N 279.2	I V 12.5	III L 6.2
I L -	III L 562.8	II N 532.9	II L 567.0	III N 166.1	I N 9.0	III V 132.5	II V 119.0	I V 9.5
II N 213.0	I L 6.1	III L 354.1	I N -	III V 339.0	II V 403.7	I V -	II L 234.1	III N 9.0
I V 79.5	III V 306.8	III V 199.8	III L 173.9	II V 351.0	I L 5.7	II L 281.8	II N 96.5	I N 20.7

II V	I N	II L	I V	III L	III N	I L	III V	II N
1205	-	7278	-	2271	118	-	-	-
132	-	648	-	94	4	-	-	-
I N	II L	II V	III V	II N	I V	III L	III N	I L
836	3137	2393	3131	2345	-	-	-	-
41	256	112	112	92	-	-	-	-
III N	I V	III V	I L	II L	II N	I N	III L	II V
1577	557	3701	-	4157	2816	-	14	-
110	135	124	-	160	269	-	-	-
III V	III N	I V	II N	I N	III L	II V	I L	II L
1346	384	-	4133	23	194	67	-	-
166	36	-	132	-	11	1	-	-
II L	II V	I N	III N	I L	III V	II N	I V	III L
6130	1840	53	2340	8	2166	1881	98	50
347	187	1	78	-	72	75	-	6
I L	III L	II N	II L	III N	I N	III V	II V	I V
-	4853	4267	6363	1164	73	1059	145	87
-	161	91	304	39	2	29	86	9
II N	I L	III L	I N	III V	II V	I V	II L	III N
2085	57	2915	-	2607	3391	-	1949	42
232	-	136	-	144	117	-	93	2
I V	III V	III N	III L	II V	I L	I L	II N	I N
189	2534	1688	1490	2712	46	2424	808	167
	136	58	39	153	1	46	37	7

## Block totals

plot	wt. of fruit (kg)	number of fruit	number of seed
1	1861.9	1364	13609
2	2080.1	1602	16514
3	2725.9	2107	22335
4	2535.4	2108	22451
5	1938.4	1445	15287
6	1267.9	924	10223
7	752.7	516	5651
8	464.6	359	4014
9	45.4	42	546
	13652.5	10467	110430

5	1.0	1	8	3.0	3	23	-	-	-	4.0	4.0	31
6	5.7	4	46	9.0	7	73	-	-	-	14.7	11	119
7	-	-	-	-	-	-	-	-	-	-	-	-
8	-	-	-	-	-	-	12.5	8	98	12.5	8	98
9	-	-	-	20.7	17	167	9.5	13	87	30.2	30	254
	18.3	17	153	137.4	121	1152	180.0	126	931	535.7	264	2736

Varlets II

1	805.9	482	6130	259.0	238	2003	164.0	120	1205	1226.9	840	9340
2	369.0	272	3137	485.1	331	3150	225.1	183	1340	1078.2	786	8127
3	818.2	671	7278	532.9	376	4267	300.0	197	2393	1651.1	1214	13938
4	567.0	550	6363	508.8	332	4133	594.0	521	5030	1659.8	1405	15526
5	507.2	350	4157	285.9	200	2345	351.0	226	2712	1144.1	776	9214
6	165.0	135	1419	378.2	246	2816	403.7	267	3391	546.9	648	7626
7	281.8	195	2424	279.2	178	1891	8.2	6	67	569.2	379	4372
8	234.1	162	1949	96.5	82	808	119.0	106	1145	449.6	350	3902
9	-	-	-	-	-	-	-	-	-	-	-	-
	3745.2	2817	32857	2825.6	1993	21405	2165.0	1626	17783	6735.8	6426	72045

Varlets III

1	76.5	86	521	199.0	166	1377	138.0	152	1346	455.5	404	3244
2	562.8	431	4853	47.7	43	384	306.8	262	2534	917.3	736	7771
3	891.1	277	2915	199.8	186	1688	510.7	309	3701	1064.6	852	8304
4	171.9	158	1490	200.0	220	2304	401.7	327	3131	265.6	705	6929
5	285.2	298	2271	166.1	114	1164	339.0	253	2607	738.5	665	6042
6	25.0	20	194	16.6	13	118	264.7	292	2166	306.3	265	2478
7	-	-	-	31.0	25	220	132.5	112	1059	163.5	137	1279
8	2.5	1	14	-	-	-	-	-	-	2.5	1	14
9	6.2	6	50	9.0	6	42	-	-	-	15.2	12	52
		1277	12308	959.2	773	7237	2135.4	1727	16544	4580.8	3777	36149
		4111	45318	3922.2	2877	29854	4480.4	3479	35258	13652.3	10467	110430

handed by 33.83%, and the verticals over the rights by 14.23%. The numbers of fruits produced by the lefts and verticals are better than that of the right-handed by 42.89% and 20.92% respectively. In the production of seeds also, the lefts and the verticals are superior to the rights by 51.80% and 18.10% respectively. Clearly, the lefts produced slightly lighter fruits and lighter seeds than those of the rights. However, when the varieties are considered individually, Variety I did not show any significant difference between treatments. The vertical vines of variety III gave a better performance than either the lefts or the rights. The statistical analysis of the data are given under.

#### Statistical Analysis

Let the three varieties of cowpea be denoted by I, II and III and the three conditions of growth by N (Normal), L (Left-twining) and V (Vertical). Combination of any variety with any condition of growth is considered to be a treatment. Thus, we have 9 different treatments denoted by (1), (2), ... (9) as follows :-

(1) I N,	(2) II N,	(3) III N,
(4) I L,	(5) II L,	(6) III L,
(7) I V	(8) II V,	(9) III V.

To test the effect of the 9 treatments, a 9 x 9 Latin Squares Design was conducted using 81 plots and the data are analysed as shown below :

(A) Fruit-yield : Number of fruits.

Let  $y_{ij}$  denote the yield (either the no. of fruits or the wt. of fruits) in the plot situated in the  $i^{th}$  row and  $j^{th}$  column.  $i = 1, 2, \dots, 9$ ;  $j = 1, 2, \dots, 9$ .



Let  $5_{ij}^k = \begin{cases} 0 & \text{if } k^{\text{th}} \text{ treatment is not applied in } (i,j)^{\text{th}} \text{ plot.} \\ 1 & \text{if } k^{\text{th}} \text{ treatment is applied in } (i,j)^{\text{th}} \text{ plot.} \end{cases}$

Let  $r =$  number of rows  $=$  number of columns  $=$  number of treatments  $= 9$ . We assume the linear additive fixed effects

model  $y_{ij} = \alpha_i + \beta_j + \sum_{k=1}^r \delta_k \tau_k + e_{ij}$  where

$\alpha_i$  = effect of  $i^{\text{th}}$  row

$\beta_j$  = effect of  $j^{\text{th}}$  column

$\tau_k$  = effect of  $k^{\text{th}}$  treatment  $1 \leq i, j, k \leq r$  and

$e_{ij} \sim N(0, \sigma^2)$   $E(e_{ij}, e_{i'j'}) = 0$  if  $i \neq i'$  or  $j \neq j'$ .

We want to test the null hypothesis  $H_0: \tau_1 = \tau_2 = \dots = \tau_9$ .

The computations and the ANOVA table are given below.

Let  $T_{i0} = \sum_{j=1}^9 y_{ij}$   $T_{0j} = \sum_{i=1}^9 y_{ij}$   $T_k = \sum_{i,j} \delta_k \tau_k y_{ij}$

and  $T_{00} = \sum_{i=1}^9 T_{i0}$

$T_{10} = 1103$   $T_{20} = 1102$   $T_{30} = 1084$

$T_{40} = 1225$   $T_{50} = 556$   $T_{60} = 1316$   $\begin{matrix} 9 \\ I \end{matrix}$

$T_{70} = 1709$   $T_{80} = 1240$   $T_{90} = 1162$   $i = 1$   $T_{10}^2 = 12956211$   $\begin{matrix} 2 \\ I \end{matrix}$

$T_{01} = 1364$   $T_{02} = 1602$   $T_{03} = 2107$

$T_{04} = 2108$   $T_{05} = 1475$   $T_{06} = 924$   $\begin{matrix} 9 \\ I \end{matrix}$

$T_{07} = 516$   $T_{08} = 359$   $T_{09} = 342$   $j = 1$   $T_{0j}^2 = 16736315$   $\begin{matrix} 0j \\ I \end{matrix}$

$T_1 = 121$   $T_2 = 1963$   $T_3 = 773$

$T_4 = 17$   $T_5 = 2817$   $T_6 = 1277$   $\begin{matrix} 9 \\ I \end{matrix}$

$T_7 = 126$   $T_8 = 1626$   $T_9 = 1757$   $k = 1$   $T_k^2 = 1981771$

$\sum_{i,j} y_{i,j}^2 = 3334125.00$   $T_{00} = 10497$

C.F. = 1360333.44

Table 6 : Analysis of Variance

Source of variation	d.f.	S.S.	M.S.S.	F	Critical (5%) table values
Rows	8	79245.56	9905.6950		
Columns	8	499257.11	62407.1388	<del>10.784</del>	<del>2.164</del>
Treatments	8	846085.11	105760.6388	10.784	2.164
a) Varieties	2	708422.89	354211.4450	36.117	3.166
b) Conditions of growth	2	28204.74	14102.3700	1.438	3.166
c) Interaction	4	109457.48	27364.3700	2.791	2.546
Error	56	549203.78	9807.2100		
Total	80	1973791.56			

Conclusions :

- (1) The 9 treatments differ significantly in their fruit-yields.
- (2) The 3 varieties of cowpea show significant differences in their fruit-yields.
- (3) The three conditions of growth show no significant differences in their fruit-yields.
- (4) There is a significant interaction between the effects of varieties and of growth conditions.

All these conclusions are valid at 5% level of significance.

(B) Wt. of fruits:

Table 7 : Analysis of variance

Source of variation	d.f.	S.S.	M.S.S.	F.	Critical Table values (at 5%)
Rows	8	146580.06	18332.51		
Columns	8	726521.74	90815.22		
Treatments	8	1489699.24	186212.45	12.0305	2.164
a) Varieties	2	1214907.59	607453.80	39.2455	3.166
b) Conditions of growth	2	36811.75	18405.88	1.1891	3.166
c) Interaction	4	237979.90	59494.97	3.8438	2.546
Error	56	866785.22	15478.31		
Total	80	3229586.26			

Conclusions:

- (1) The 9 treatments differ significantly in their effects on the weight of fruits.
- (2) The 3 varieties of cowpea differ significantly in their effects on the weight of fruits.
- (3) There are no significant differences among the 3 conditions of growth as regards their effects on the weight of the fruits.
- (4) There is a significant interaction between the effects of varieties & the effects of the conditions of growth on the weight of the fruits.

All these conclusions are made at 5% level of significance.

(c) Effects of the conditions of growth on individual varieties:

$T_{IN} = 137.4$	$T_{IL} = 21.3$	$T_{IV} = 180.0$	$T_I = 336.7$
$T_{IIN} = 2925.6$	$T_{IIL} = 3744.3$	$T_{IIV} = 1865.4$	$T_{II} = 8435.3$
$T_{IIIN} = 959.2$	$T_{IIIL} = 1486.2$	$T_{IIIV} = 2135.4$	$T_{III} = 4580.8$

$$SS_I = \frac{T_{IN}^2 + T_{IL}^2 + T_{IV}^2}{9} - \frac{T_I^2}{27} = 1499.25$$

$$SS_{II} = 196157.74$$

$$SS_{III} = 77134.70$$

$$F_I = 0.048$$

$$F_{II} = 6.337$$

$$F_{III} = 2.497$$

Critical region at 5% level of significance is  $F = 3.166$

Conclusions: (1) In varieties I and III, the 3 conditions of growth do not have significantly different effects on the weight of fruits.

(2) In the variety II, however, the 3 conditions of growth differ significantly in their effects.

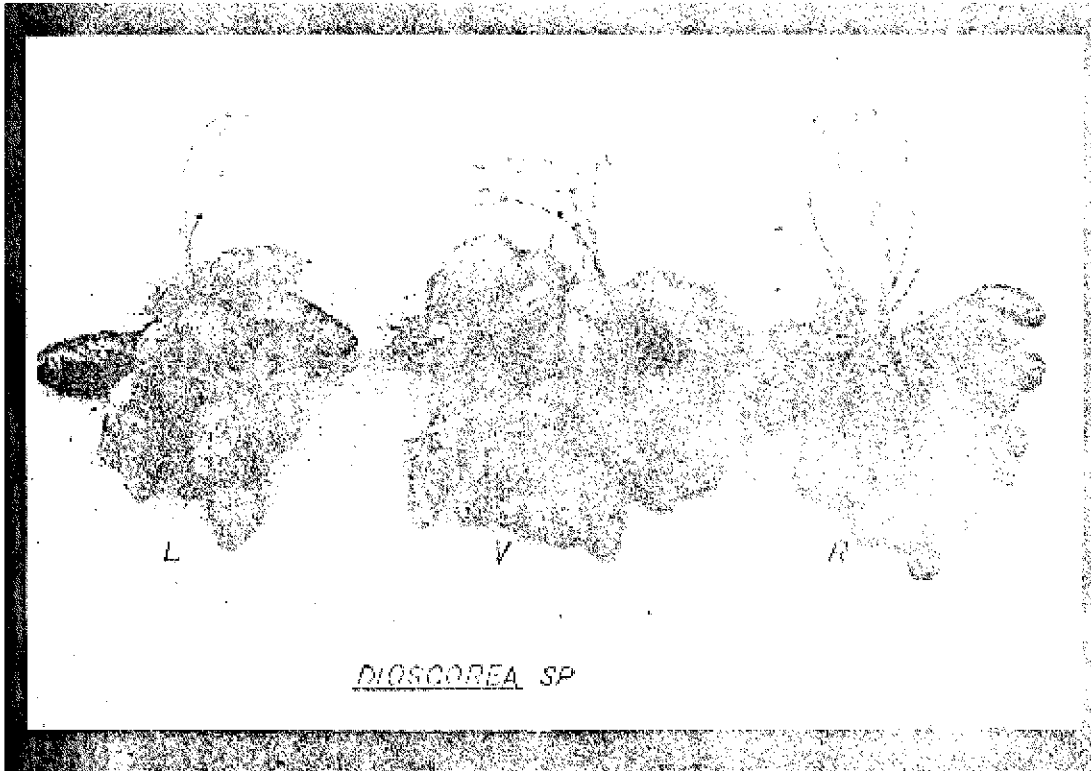
It may be recalled that variety I had a very poor performance as it was susceptible to a virus disease. The treatments Vertical and Left of variety III produced significantly more yield than the Normal ~~method~~. But the two better treatments did not differ by themselves significantly. Therefore, the three treatments of this variety did not show a significant difference. In spite of this, it is clear that the artificial change in the directions of growth in variety III and more strikingly variety II produced excess fruits by weight and number than the normal method of twining. These results are in conformity with those reported by Reber. However, the cause for this change in the yield potentials is not known.

### B. Dioscorea esculenta :

The genus Dioscorea includes species which are predominantly stem twiners. Some of them twine clockwise and others counter-clockwise (Brain and Parkill, 1936, 1939). At least five species of this group of yams are cultivated in Kerala India for their edible tubers. Dioscorea esculenta which produces medium-sized tubers is popularly cultivated in Kerala and the harvest matures during the colder months of November-February. The stem of this vigorous twiner always moves clockwise (left-handed) and it does not flower in India. Thus, this Dioscorea species differs from Vigna sinensis by twining oppositely and by producing root tubers rather than fruits.

Planting materials from one of the most common varieties of D. esculenta were obtained from Kerala in 1967 and multiplied at Calcutta. From the yield of 1968-69 crop, uniform tubers, each weighing between 125 gm and 175 gm were selected and sown in two special plots of land at the premises of the Indian Statistical Institute on 12.3.1969 according to Latin Square design. Each plot measured 14m x 3 m.

All the treatments followed with Vigna sinensis were adopted for Dioscorea also, and the twiners were made to coil on similar-sized, 15 feet long bamboo poles. Only a single tuber was planted per pole, and the tubers were kept sufficiently moist. They sprouted within a period of 2-4 weeks. Six weeks after planting, tying of the twiners was commenced with cotton tape (clockwise, counter-clockwise and vertically) according to the design. Dioscorea grew at a much faster rate than Vigna and produced a much longer stem. The length of the bamboo pole was suspended on



vines under the Vertical treatment. In this case, when the tip of the vines reached the terminus of the bamboo, the entire shoot was unwound and the older region lowered to enable the growing tip to grow along the bamboo thus cleared. As the plants matured, their leaves turned yellow and withered. They were uprooted and the tubers collected on 17.3.1970, that is one year after sowing. The number and weight of tubers per plant were recorded separately.

The average weight of tuber yield per plant for the various treatments is given below :

1. Normal vines (Left-handed twining) = 114 gms
2. Reversed vines (Right-handed twining) = 726 gms
3. Vertical vines (neutral ones) = 1161 gms

Thus, the left-handed vines are better than the right-handed ones by 7.67%, and the vertical ones are better than the lefts by 42.63%, and over the rights by 53.57%. It may be recalled that with the trials on Vigna sinensis also, one variety (Var.III) responded more favourably with the vertical treatment by yielding fruits more than those for the other two treatments.

Even though the above two experiments require to be repeated for confirmative results, it is clear that when the normal kind of asymmetry of the stem is altered, it affects significantly the fruit-yielding capacity as well.

I thank H.D. Prabhakar for helping in the analysis of the data.

#### Summary

A Latin Square design experiment was conducted at the premises of the Indian Statistical Institute, Calcutta in 1966 to study the effect of changing the di-

twine on the yield of fruits in three varieties of cowpea (Vigna sinensis). Normally all these varieties, being weak-stemmed plants and devoid of tendrils, twine counter-clockwisely (right-handed) on a support. The three methods adopted were : N (allowing the plants to twine by the usual right-handed direction); L (forcing them to twine to the left); and V (making them grow vertically, not allowing to twine along one direction or the other). Thus, the three varieties and the three methods constitute in all nine treatments. These were replicated nine times.

The plants were made to grow on long bamboo poles. The treatments were continued till the plants flowered. The ripe fruits were harvested, counted and weighed separately for each treatment. The numbers of good and shrivelled seeds for each treatment were also recorded.

Variety I performed very badly as it was affected by a virus disease and the data obtained on this variety were not given such importance. The two abnormal treatments (L & V) of varieties II & III gave significantly higher yields compared to that of the normal (R) method. For variety II, the method L gave a better yield than method V, and all the three methods of this variety differed significantly. However, for variety III, the method V produced more fruits (by number and weight) than the method L which is of course, significantly more than for method R.

Results of an experiment with Dioscorea esculenta are also briefly reported.

Reference

- Davis, F.A. (1963) : Dependence of yield on asymmetry in coconut palms. J. Genet., 53 : 186-215.
- Davis, F.A. and C. Ramanujacharyulu (1971) : Statistical analysis of bilateral symmetry in plant organs. Santhya.
- Grote Reber (1960) : Reversed bean vines. Gastroped. 25 : 122-124.
- Grote Reber (1964) : Reversed bean vines. J. Genet., 59 : 37-40.
- Prain, D. and Burkill, I.H. (1936) : An account of the genus Dioscorea in the east. I. The species which twine to the left. Ann. Royal Bot. Gard., Calcutta, 14 : 1-210.
- Prain, D. and Burkill, I.H. (1939) : An account of the genus Dioscorea in the east. II. The species which twine to the right. Ann. Royal Bot. Gard., Calcutta, 14 : 211-526.

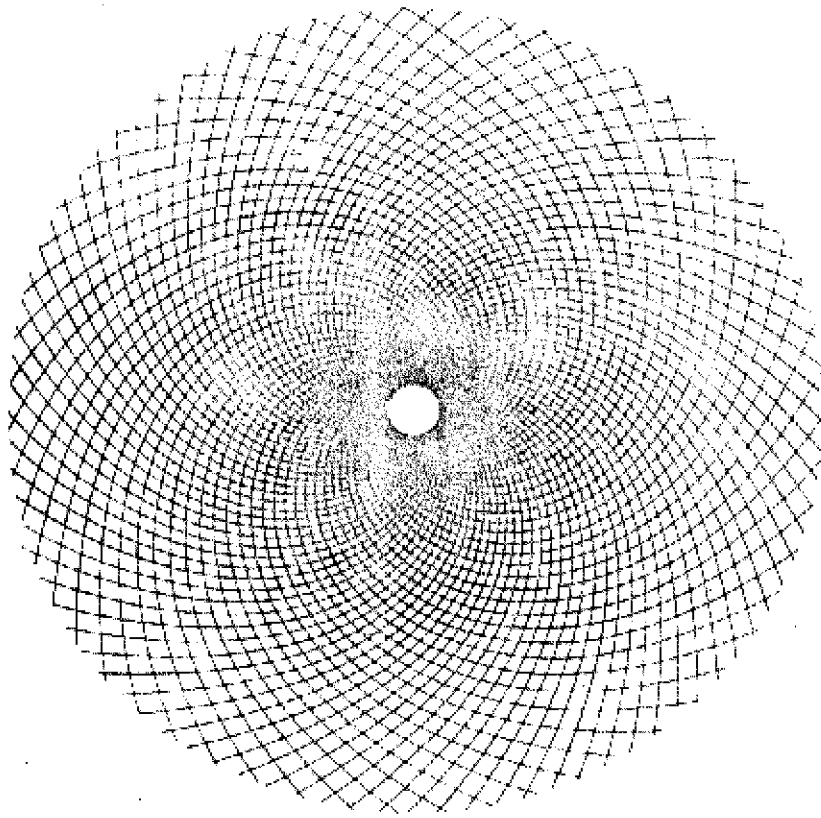
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## 9. CONSTRUCTING THE SUNFLOWER HEAD

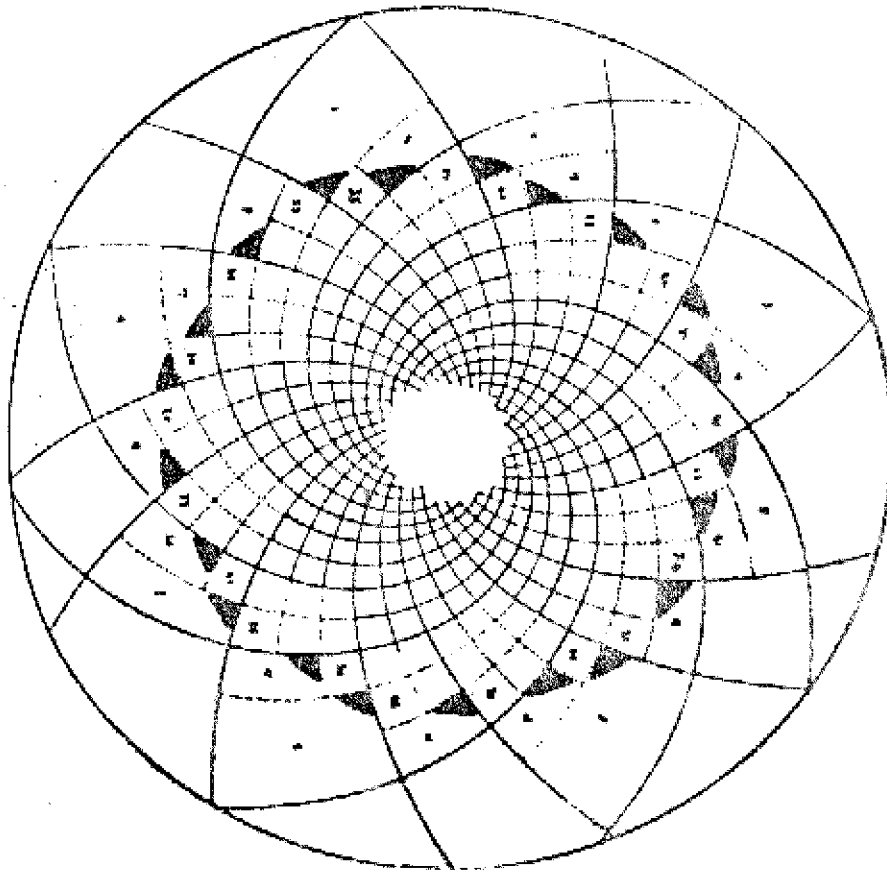
### Introduction

The sunflower plant, scientifically known as Helianthus annuus, belonging to the family Compositae is important both for its huge, attractive flower heads as well as for the edible oil that is <sup>ex</sup>tracted from the seeds (botanically fruits). The leaves of this plant are produced one after another (alternate phyllotaxis), in a single spiral, running clockwise or counter-clockwise, any two consecutive leaves making an angular deflection of about  $137.5^\circ$ . As the plant matures, the size of the later formed leaves gets reduced when the tip of the main stem flattens <sup>out</sup> into the flower-bearing disc known as capitulum. At the base of the disc, there are many reduced leaves called involucral bracts which also show spiral patterns. On the top of the disc too, numerous highly reduced, closely-set leaves (bracts) are present, each subtending a small flower in its axil. Although these bracts are also produced one after another, the time between the formation of any two <sup>consecutive</sup> bracts (and hence flowers) is considerably reduced. The oldest flowers are distributed at the periphery of the disc, and younger and younger flowers are met with as one proceeds from the periphery to the central point which represents the tip of the compressed main stem. Each of the petal-like structures seen at the periphery of the disc represents a female flower or sterile one known as ray floret. Bordered by the ray florets on the disc are the numerous, less prominent, regular, bisexual flowers called disc florets. If a perfectly developing capitulum is observed, it will be seen that the flowers start blooming one by one, a bloomed flower appearing at a place approximately  $137.5^\circ$  away from its immediate older one in



SUNFLOWER WITH 56 COUNTER-CLOCKWISE AND  
89 CLOCKWISE SPIRALS.  
(M. GARDNER, 1960)

FIG. 2

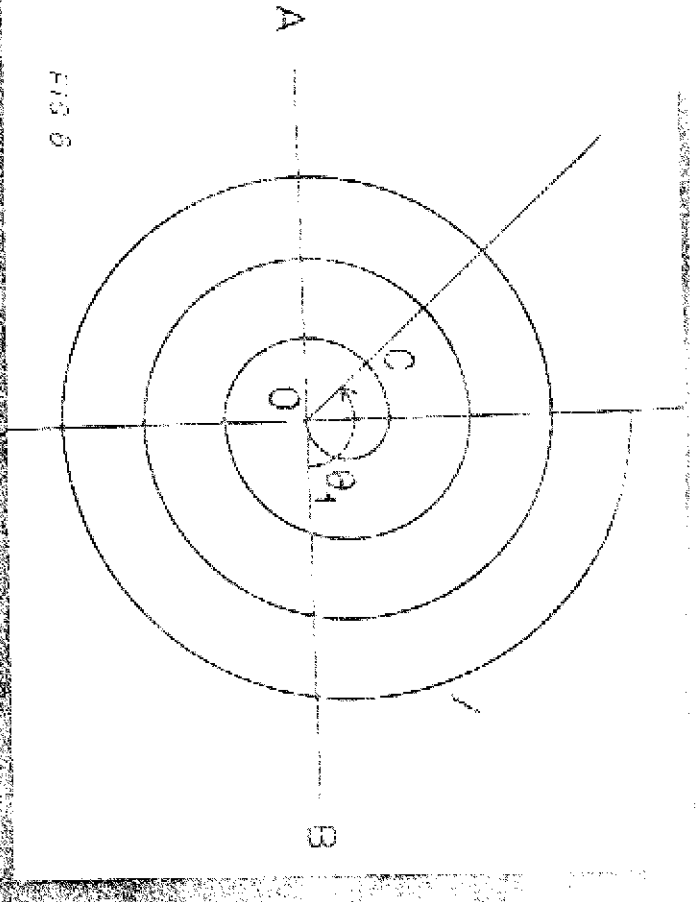
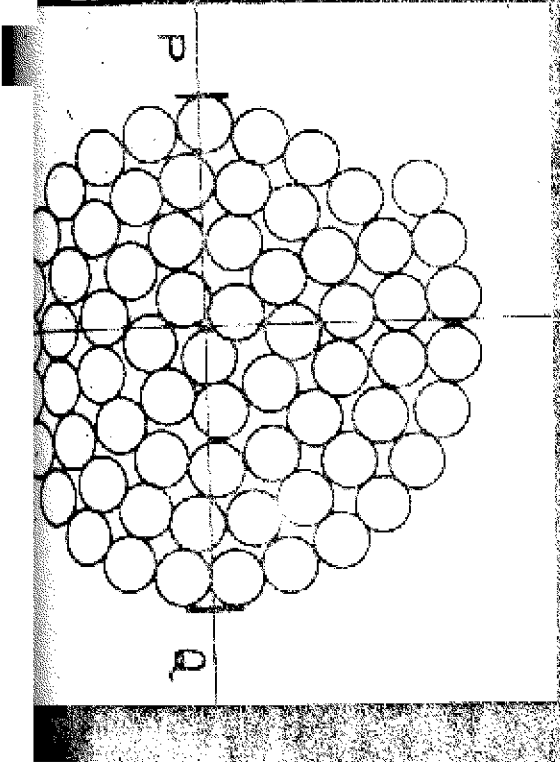
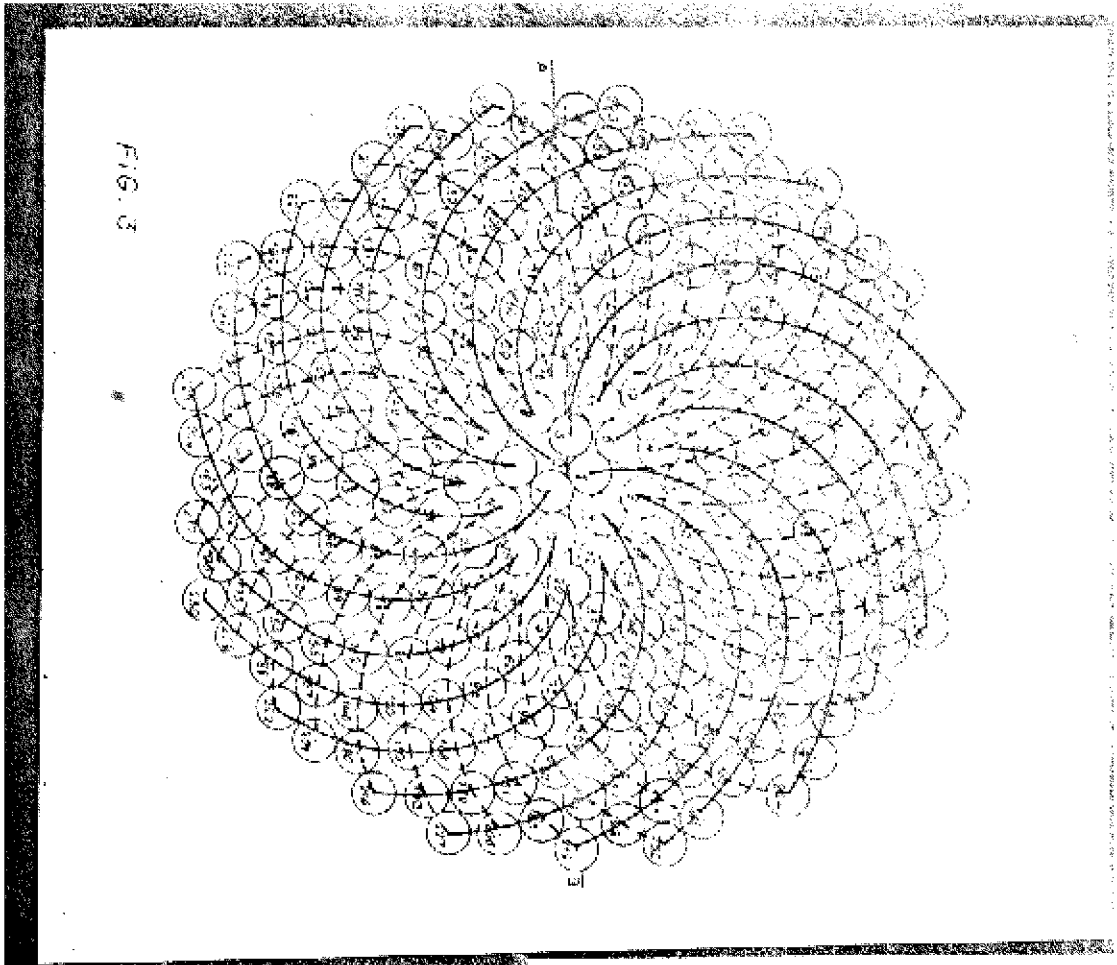


PHYLLOTAXIS ORDER OF SUNFLOWER  
(WEISSE, 1891)

the central point. In nature such an ideal head is not really to be found. Thus, the capitulum of the sunflower is a highly compressed stem whose leaves are reduced to small bracts each supporting a flower in its axil. The development, maturing and maturity of the <sup>individual</sup> flowers follow the sequence commencing from the oldest bract and moving upwards (towards the centre).

One's admiration for the aesthetic value of sunflower heads <sup>enhanced</sup> if he understands the mechanism involved in the arrangement of the individual flowers on it. Spirals or arcs in specific numbers are formed according to certain mathematical laws. From 1754, several biologists and mathematicians were attracted by the spiral patterns in nature such as in the leaf-arrangement, arrangement of flowers on the sunflower head and similar other plant organs, who gave possible explanations for the same (Bonnet, 1754; Braun, 1851; Schimper, 1836; Bravais, 1837; Hofmeister, 1868; Wright, 1873; Schwendener, 1878; De Candolle, 1881; Weiss, 1897; Schoute, 1913; 1914; Thompson, 1917; Church, 1904, 1920; Colman and Coan, 1920; Huxner, 1922; Crow, 1928; Geibel, 1928; Snow and Snow, 1934; Plantefol, 1948; Wardlaw, 1949; Richards, 1948, 1950; Kramer, 1955; Snow, 1955; Duckar et al., 1960; Sinnott, 1960; Frank Land, 1960; Coxster, 1961; Leppik, 1961, 1970; Bergamini, 1965; Gardner, 1969; Davis, 1970, 1971; Kilmner, 1971). However, none of them could explain fully well the different phenomena manifested on the capitulum of Compositae. Figures 1 and 2 are two examples of sunflower heads constructed by two of these workers in 1897 and 1969.

Many of the investigators referred to above had realised



with a fixed diameter is drawn touching AB at O. A second circle of the same diameter is drawn at an angular deflection of  $137.5^\circ$  from the line connecting the centre of the first circle and O. The second circle which just touches the first one can be placed either to the left of the first one or to its right. This decides whether the capitulum becomes left-handed or right-handed. In nature the lefts and rights are distributed randomly. In the present case the second circle is shown on the left side of the first. Successive circles of the same diameter have been drawn one after another on the left of the preceding ones at the same angular deflection of  $137.5^\circ$ . None of the subsequent circles overlap any of their neighbours, but they merely touch the margin of one or two neighbours which lie on the line proceeding to the centre. Although the subsequently formed circles in the picture seem to move away from the centre than the early formed ones, a reverse course takes place on the head. That is, flower No. 234 is the oldest and No. 1 the youngest. At the time when the second flower (circle) is differentiated at the tip of the stem, the first one rotates away from its original position by  $137.5^\circ$ . Thus, when more and more flowers are formed, the already formed ones are pushed towards the periphery with minimum space between them. Some of the earliest formed flowers turn into the ray florets and the latter ones into disc florets. Care was taken that <sup>no</sup> circle ~~was~~ <sup>falls</sup> nearer to the centre than any of the circles already drawn. It can be shown that the configuration in the capitulum does not depend on the size of the circles as long as every circle has the same diameter. Fig. 5 exhibits the following property. Start with any circle at the periphery and join the centres of adjacent circles whose numbers differ by 41. Then, the continuous-

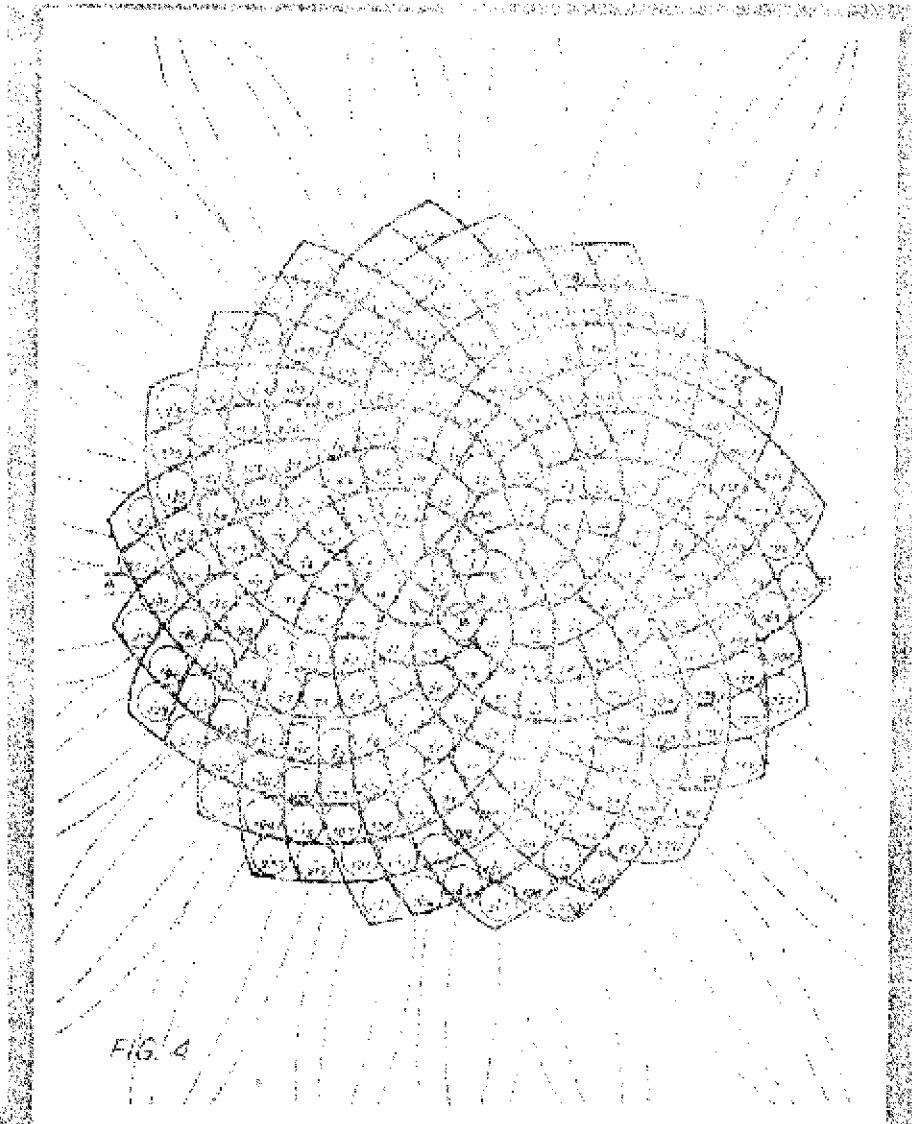


FIG. 4

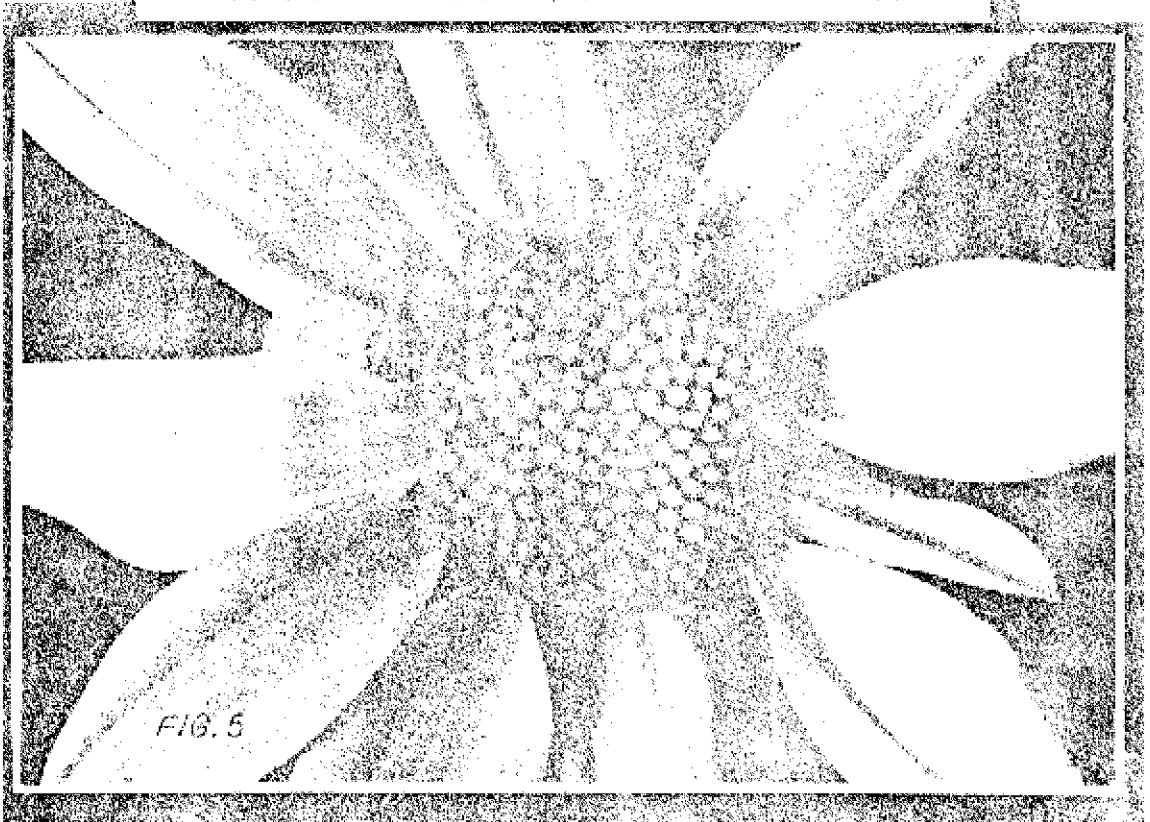


FIG. 5

line radial arcs are obtained. Similarly starting from any circle at the periphery, the circles whose numbers differ by 4 are connected. The dotted-line arcs which move opposite to the 21 arcs are obtained. The two kinds of arcs pass through all the circles.

The overall pattern of Fig. 3 is slightly modified as to bring forth the individual seeds on the capitulum boldly, and the result is seen in Fig. 4. As the radial arcs are drawn just bordering the circles, the space available for a seed is represented by each circle (parallelogram). 34 clockwise and 21 counter-clockwise arcs are clearly seen at the periphery. The 34 arcs (each after passing through 4 or 5 seeds) merge with the set of 13 arcs moving along the same direction but showing greater degree of curvature. From where the 13 arcs take over from the 34, the original 21 arcs are seen moving opposite to the 13 arcs. Thus, the <sup>sets of</sup> 34 and 21 arcs seen at the periphery of the entire head get reduced to 21 and 13. At some level still closer to the centre, arcs 13 and 8 are seen and this combination progressively gets reduced to 8 and 5, 5 and 3, and finally to 3 and 2. It is striking that in a natural capitulum one can see a similar configuration, <sup>Fig. 5.</sup> It is, therefore, emphasized that all the arcs which start from the periphery do not reach the centre as many earlier workers had erroneously depicted. Richards (1948, 1950) seems to be the only worker whose illustrations on the phyllotaxis may be considered throwing some light on this peculiarity.

It can be inferred from Fig. 4 that in capitulums bearing equal sized seeds or flowers, the numbers of visible arcs vary with the diameter of the head, a smaller one showing

numbers and larger ones higher numbers, all matching with stages in the F. Sequence. The oldest seed/flower of the capitulum in Fig. 4 is just older to 233 members. 233 is a F. number. Hence a head having 233 to 144 (next lower F. number) seeds/flowers will show 34 and 21 arcs at the periphery. Another having 89 seeds/flowers will show 21 and 13 spirals, one with 14 seeds will show 13 and 8 spirals, and so on to smaller numbers of arcs as the numbers of individual flowers per head decrease. On the same sunflower plant, the terminal head which is generally the largest will show the highest number of arcs at the periphery. But the heads produced on secondary and further orders of branches become smaller and smaller, and they show lesser and lesser numbers of arcs. Another indication for this decrease can be had from the number of ray florets seen on a capitulum. The periphery of the capitulum in Fig. 4 has 21 projections. The flower at each projection develops into a ray floret which increases the attractiveness of the flower head, a device to facilitate cross pollination. In a smaller head, the number of projections is reduced to 13, 8 and perhaps 5 and may show an equal number of ray florets. But in nature considerable variation is observed. However, if data are obtained on a large number of heads, the numbers of ray florets will cluster around some terms of the Fibonacci Sequence. Another striking similarity between this reconstructed picture and a natural capitulum is the following. If any arc is followed from the periphery, the seed at the junction where three or four kinds of arcs meet *will be found to be* slightly irregular in shape. Such irregular 'junction seeds' can be picked out from any large capitulum with developed seeds. At the centralmost part of the head, it is often possible to



and very large and highly irregular seeds.

As one proceeds <sup>ing</sup> from the periphery, the 34 spirals move clockwise and then join the 13 spirals which also move clockwise. They are followed by the 5 spirals which ultimately join the 2 spirals (marked within circles 1,3,5) both moving along the same direction. The spirals synchronising the members of alternate terms of the Fibonacci Sequence, i.e. 1, 8, 3 and 1 commencing from the periphery move counter-clockwise. This peculiarity of the spirals (spirals equalising alternate Fibonacci Numbers) moving along the same direction has a striking similarity with a basic property of the Fibonacci Numbers. The ratio between consecutive F. Numbers being steadily between the plus side and minus side of the Golden ratio (0.618 ...). The ratio of 1/1 is 1.0 which is on the plus side, 1/2 = 0.5 which is on the minus side, 2/3 = .667 is on the plus side, 3/5 = .60 is on the minus side, and so on.

One of the difficulties encountered by most earlier investigators is the following. As is obvious from Fig.2, the investigators represented the margin of a capitulum by a circle whose periphery is divided into 55 and 89 equal parts. Arithmetic spirals are drawn from the 55 points, all reaching the centre of the circle. Similarly 89 log spirals are drawn which move steeply and reach the centre. Instead of the sets of spirals numbering 55 and 89, one can choose any other sets of <sup>well matching</sup> two adjoining F. Numbers. The two sets of spirals/arcs cut each other forming parallelograms. A parallelogram at the periphery turns out to be several times larger than one near the centre. This would suggest that the size of the seeds would

vary considerably depending on the spot on the disc where the seed develops. But in nature, the seeds/<sup>flowers</sup> are almost of the same size whether they develop from the periphery or at the centre of the flower head (Fig.4). Other workers who had realised the importance of the Fibonacci angle ( $137.5^\circ$ ) between successive flowers and with generating log spirals which steadily diverge as they get extended from the centre (Fig.1). In such diagrams, the parallelograms at different regions of the head would inevitably exhibit wide disparity in their area.

However, these log spirals may hold good to represent the growing point of a palm crown or other plants where the various leaves are produced at long time intervals, and therefore, showing a gradation in the size of the leaves. In the sunflower head, such a time interval is very much narrowed down, and there are innumerable units to accommodate. Hence, a spiral with even a small log effect will cause a big difference.

The method of plotting the circles in Figs. 3 and 4 is explained thus. Assume that the various points or centres of parallelograms which are obtained by observing the Fibonacci angle between consecutive points in a pattern which show log spirals as in Fig.1 are replaced by uniform discs. The margin of disc No.1 touches O on the reference line AB. Disc No. 2 is brought to O by the shortest distance and left where it touches disc No.1 without disturbing the position of disc ~~1~~<sup>The latter.</sup>. Similarly, No.3 is dragged by the shortest track towards O and left where it touches the disc nearest to it. Similarly, discs 3, 4, 5, .... 234 are brought closer. The required

are obtained by connecting the suitable circles. The final  
 portion (Fig. 4) becomes much different from the original

Also at the lower side of the capitulum where the leaves  
 modified into involueral bracts, it is possible to trace out  
 several sets of spirals. If Fig. 5 is to represent the  
 arrangement of these involueral bracts, the oldest bract will  
 be located at the centre near circle No. 1, and the youngest  
 at the periphery. As the number of such bracts on any flower-  
 head is much less than that of the flowers on top of the disc,  
 the bracts display areas matching smaller terms in the Fibonacci  
 sequence compared to those on the top. Generally a disc showing  
 areas 34 and 21 areas at the periphery has 21 bracts, and  
 a disc having 55 and 34 areas bears 34 bracts, and so on  
 with some variation in the number. Like these involueral  
 bracts, the normal leaves themselves display areas when looked  
 at from the top of a non-flowering shoot. Thus, it is the golden  
 ratio of the angular deflection between any two leaves, bracts  
 or flowers that brings about the radial areas, their numbers  
 matching with stages in Fibonacci Sequence.

A sunflower head can also be considered to represent a  
 hypothetical configuration of the crown of a coconut palm,  
 the individual seeds would correspond to the different  
 leaves on the crown. The shape of the palm crown as well as  
 the positions of its leaves can be shown to be 'best placed'  
 according to different mathematical considerations. Efficiency factors  
 are better explained in a palm crown rather than in a sun-  
 flower head because the sunflower disc is a very flattened  
 disc and in order to appreciate the explanation of the effi-

ciency factors, the height of the cone should be larger than what is noticed in a sunflower head. From the mathematical explanation, one can see that the growth principle is the same whether it is in the formation of individual flowers on the capitulum or in the formation of leaves in a palm crown. In the next section is given the mathematical theory to explain Fig.4.

### 3. Mathematical explanation

The mathematical equation for a logarithmic spiral in polar co-ordinates is as follows :

$$(1) \quad r = ke^{a\theta}$$

where  $k$  and  $a$  are constants. Since  $k$  is only a weighting factor for  $r$ , without loss of generality we may assume the equation to be of the form,

$$(2) \quad r = e^{a\theta}$$

Fig.6 gives the logarithmic spiral where AB is a reference line and O is the origin. Depending upon the value of  $a$ , the width between successive spirals increases slowly or rapidly. Consider the case where  $a$  is very small. Then we have,

$$(3) \quad r = e^{a\theta} = \left[ 1 + a\theta + \frac{(a\theta)^2}{2!} + \frac{(a\theta)^3}{3!} + \dots \right] \approx 1 + a\theta$$

where  $\approx$  means 'approximately equal to', that is,  $r-1 \approx a\theta$ .

In other words, this logarithmic spiral behaves like an Archimedes' spiral whose equation is of the form,

$$(4) \quad r = b\theta$$

where  $b$  is a constant. Archimedes' spiral has the property that the width between successive spirals remains the same (except near the origin O).

Now consider the formation of a sunflower. Let the individual flowers come out at a constant speed of  $\lambda$  units per second along the spiral in equation (2) with a very small  $a$ . Let the second flower emerge after  $t_1$  units of time. At this stage let the angle be  $\theta_1$ . That is, the first flower is at the position marked  $O$  in Fig. 6 when the second flower starts. If the distance covered by a moving point, such as flower number 1, is denoted by  $s$  then from elementary Calculus we have

$$(5) \quad \lambda = \frac{ds}{dt} = \sqrt{r^2 + \left(\frac{dr}{d\theta}\right)^2} \cdot \frac{d\theta}{dt}$$

where in general  $\frac{dx}{dt}$  denotes the derivative of  $x$  with respect to  $t$ . At the time  $t_1$ , the distance travelled is  $\lambda t_1$ , and thus by integrating equation (5) we have,

$$(6) \quad \lambda t_1 = \sqrt{1 + a^2} \left[ \frac{e^{a\theta_1} - 1}{a} \right].$$

That is,

$$(7) \quad \theta_1 = \frac{1}{a} \log \left\{ 1 + \frac{a \lambda t_1}{\sqrt{1 + a^2}} \right\}$$

where the logarithm is taken to the base  $e$ . Since  $\lambda$  and  $a$  are mutually non-dependent, we may expand the right hand side of (7). That is,

$$(8) \quad \theta_1 = \frac{1}{a} \left\{ \frac{a \lambda t_1}{\sqrt{1 + a^2}} - \frac{1}{2} \left( \frac{a \lambda t_1}{\sqrt{1 + a^2}} \right)^2 + \dots \right\}$$

$$\approx \frac{\lambda t_1}{\sqrt{1 + a^2}} \quad (\text{since } a \text{ is assumed to be very small}).$$

Now when the second flower emerges at position  $O_1$ , the third flower starts and the first flower has travelled another  $\lambda t_1$  units of distance. If the angle which the

1st flower has travelled now makes with AB is denoted by  $\theta_2$ , then we have,

$$(9) \quad \theta_2 \approx \frac{\lambda t_2}{\sqrt{1+a^2}} = \frac{2\lambda t_1}{\sqrt{1+a^2}} = 2\theta_1.$$

In other words, the angle between successive flowers remains approximately the same as  $\theta_1$ . In drawing Fig.3 we have used this property of a logarithmic spiral when the constant  $a$  is small. We have taken  $\theta_1$  as  $137.5^\circ$  which is observed in actual sunflower heads. In a natural specimen we know that all the individual flowers or seeds are of the same dimension. This observation can be taken into account only if the spiral resembles an Archimedes' spiral where the width between successive spirals remains the same. Thus, it is noticed that the constant  $a$  has to be very small. By this process a microscopic flower head is formed as seen in Fig.7.

If the diameter of the disc of the microscopic flower, which is PQ in Fig.7, is denoted by  $H$ , then when environmental conditions are favourable, this  $H$  expands at a uniform rate  $\frac{dH}{dt} = \mu$  where  $\mu$  is a constant. Correspondingly the individual flowers, which are denoted by circles in Fig.4, also expand and finally the disc attains the form as shown in Fig.5. Now for convenience we will call the 1st flower as flower number 1 and so on. Then we can get the radial distance of the  $n$ -th flower and the angle which the  $n$ -th flower makes with the reference line AB. Let the radial distance of the  $n$ -th flower be denoted by  $r_n$  and the corresponding angle  $\theta_n$ . Then from (6) we have

$$(10) \quad \lambda t_2 = \sqrt{\frac{1+a^2}{a}} (e^{a\theta_2} - 1)$$

But

$$(11) \quad \lambda t_2 = 2 \lambda t_1 = 2 \frac{\sqrt{1+n^2}}{n} (e^{a\theta_1} - 1)$$

From (10) and (11) we have,

$$(12) \quad e^{a\theta_2} = 1 + 2 (e^{a\theta_1} - 1)$$

Proceeding in this way we may have

$$(13) \quad e^{a\theta_n} = 1 + n (e^{a\theta_1} - 1) \text{ or } \theta_n = \frac{1}{n} \log \left\{ 1 + n(e^{a\theta_1} - 1) \right\},$$

$$n \geq 2.$$

But

$$(14) \quad r_n = e^{a\theta_n} = \left[ 1 + n(e^{a\theta_1} - 1) \right] = (1 - n + ne^{a\theta_1}).$$

Equations (13) and (14) give the values of  $\theta_n$  and  $r_n$  in terms of  $\theta_1$ . We can notice a number of interesting properties from Fig.3. From equation (14) and Fig.4 we have

$$(15) \quad r_1 - r_{35} = 34(1 - e^{a\theta_1}) \quad \text{along the continuous line arcs}$$

$$r_{22} - r_{56} = 34(1 - e^{a\theta_1})$$

$$(16) \quad r_{64} - r_{85} = 21(1 - e^{a\theta_1}) \quad \text{along the dotted line arcs.}$$

$$r_{98} - r_{119} = 21(1 - e^{a\theta_1})$$

In other words, if one continuous line arc is given, then all the other similar arcs can be traced by a simple rotation. Similarly, if one dotted line arc is given, then all other similar arcs can be obtained. In Fig.4 we have several parallelograms. For example,  $r_{43}, r_{64}, r_{77}, r_{98}$  form a parallelogram and further,

$$(17) \quad \frac{r_{64} - r_{43}}{r_{77} - r_{43}} = \frac{21(1 - e^{a\theta_1})}{34(1 - e^{a\theta_1})} = \frac{21}{34}, \quad \theta \neq 0.$$

If we consider a parallelogram nearer to the origin of the configuration in Fig.4, we have for example,

$$(18) \quad \frac{r_0 - r_4}{r_{17} - r_9} = \frac{2}{8}$$

It is easy to notice that if we move from the outer perimeter to the origin of the configuration along any radial line, then at different stages one can redraw the two types of area in the following sequence (21, 34), (13, 21), (8, 13), (5, 8), (3, 5).

This section illustrates that if the individual flowers emerge at a uniform speed at fixed intervals of time along a logarithmic spiral  $r = e^{a\theta}$  with a very small  $a$  and with the initial angle of  $\theta_1 = 137.5^\circ$ , then the exact configuration of a sunflower<sup>head</sup> can be reconstructed. The results in equations (15) to (18) are due to the assumptions of a basic logarithmic spiral and the numbers 34, 21, 13, 8, 5, 3, 2 from a Fibonacci sequence appear due to  $\theta = 137.5$  because it is well-known that the ratios of a successive Fibonacci sequence namely,  $1/2, 2/3, 3/5, 5/8, 8/13, 13/21, \dots$  approach the golden ratio  $(\sqrt{5}-1)/2$  and if  $\theta_1$  is measured in radian and if  $\theta/(2\pi - \theta_1) = (\sqrt{5}-1)/2$ , then  $\theta_1$  is approximately equal to  $137.5^\circ$ .

From the above explanations and theory it is easy to associate the radial area seen in sunflower<sup>heads</sup> with the Fibonacci sequence. Now it remains to be explained why the microscopic flowers are formed along a logarithmic spiral  $r = e^{a\theta}$  with  $a$  being very small when the flower is programmed. One plausible explanation is as follows. From the theory of Fluid Dynamics it is known that if we consider fluid in uniform motion, that is, the same motion is repeated at equal intervals of time, then the law governing the motion is given by



$$(19) \quad f(t_1) f(t_2) = f(t_1 + t_2)$$

where  $t_1$  and  $t_2$  are two intervals of time and  $f$  is some unknown function. But (19) is the famous Cauchy functional equation in the Theory of Functional Equations, whose unique continuous solution is

$$(20) \quad f(t) = e^{\alpha t}$$

where  $\alpha$  is an arbitrary constant. If the fluid motion is translated into rotation and expansion, then (20) becomes

$$(21) \quad r = e^{at}$$

where  $a$  is an arbitrary constant. This shows that the logarithmic spiral in (21) may be a natural outcome of the supply of genetic material in the form of pulses at constant intervals of time obeying the law of fluid flow as explained in (19).

### Summary

Following a new method, it has been made possible to reconstruct correctly the numerous individual flowers/seeds on the sunflower head, a problem actively investigated by mathematicians and biologists alike for about a century. The head thus constructed manifests the various radial arcs and patterns that are visible on a natural flower head. The formation of individual flowers on the sunflower disc which eventually causes the appearance of arcs can be explained thus : The flowers are formed one at a time, the older ones being pushed towards the periphery of the disc and the younger ones getting filled up within the disc, and the youngest one remaining at the centre.

A flower-primordium is differentiated on a side at the apex of the axis that eventually forms the disc. The primordia of the subsequent flowers are generated at a fast rate with a constant time-interval. As the individual flowers are differentiated, the tip of the axis (or the focus of the subsequent primordium) rotates so much so, the older flowers seem to move away from the growing point in logarithmic spirals which approximate to an Archimedes' spiral. <sup>The younger of</sup> Among any two consecutive flowers, ~~the younger one~~ starts differentiating from the axis when the first flower is at an angle  $\theta_1$  such that  $\sqrt{(2\pi - \theta_1)}$  forms the golden ratio. This process continues till the genetic material is finished and the flower head is fully progressed. With favourable environmental conditions, the individual flowers expand at a uniform rate over time along with the simultaneous expansion of the disc. It is shown mathematically that the above theory can explain all the properties of a sunflower head, large or small.

#### Reference

- Bergamini, D. (1965) : Mathematics. Life Science Library.
- Desmet, C. (1754) : Recherches sur l'usage des feuilles dans les plants. Göttingen and Leiden.
- Humboldt, A. (1831) : Vergleichende Untersuchung über die Ordnung der Schuppen an den Farnkeimlingen. Nova Acta Acad. Car. Leop., 15 : 195-401.
- Moire, L. and Bravais, A. (1837) : Essai sur la disposition des feuilles curviseries. Ann. Sci. Nat. Bot. II, 7 : 42-109.
- Wright, A.H. (1904) : On the relation of phyllotaxis to mechanical laws. London.
- (1920) : On the interpretation of phenomena of phyllotaxis. New York.

- Colman, S. and Coan, C.A. (1920) : Proportional form. New York.
- Coxeter, H.S.M.(1961) : Introduction to geometry, New York.
- Crow, W.B. (1928) : Symmetry in Organisms. Amer. Nat., 62 : 207-227.
- Davis, T.A.(1970) : Fibonacci Numbers for palm foliar spirals. Acta Botanica Neerlandica, 19 : 249-256.
- \_\_\_\_\_ (1971) : Why Fibonacci Sequence for palm leaf spirals ? Fibonacci Quart., 9 : 237-244.
- \_\_\_\_\_ and Bose, T.K.(1971): Fibonacci system in aroids. Fibonacci Quart., 9 : 253-263.
- De Candolle, C. (1881): Considerations sur l'etude de la phyllotaxie. Geneva.
- Ducker, H. Wiesbaden and Leith, H. (1960) : Mathematische Probleme in der Biologie. II. FW 2, H.10 : 257-261.
- Frank Land (1960) : The language of mathematics. London.
- Gardner, M. (1969): The multiple fascinations of the Fibonacci Sequence. Sci. Amer., 220 : 116-120.
- Goebel, K. (1928) : Organographie der Pflanzen. Fischer, Jena.
- Hirner, M. (1922) : Zur Lösung des Problems der Blattstellungen. Fischer, Jena.
- Hofmeister, W. (1868): Allgemeine Morphologie der Gewächse. In Handbuch der Physiologischen Botanik 1 : 405-664. Engelmann, Leipzig.
- Hilser, W.L. (1971) : On growing pine cones and other Fibonacci fruits. McCulloch's Localized Algorithm. Math. Biosci., 11:53-57.
- Hunter, E.E. (1955): The main stream of mathematics. New York.

- Leppik, E.E. (1961) : Phyllotaxis, anthotaxis, semataxis. Acta Biotheoretica, 14 : 1-28.
- \_\_\_\_\_ (1970) : Evolutionary differentiation of the flower head of the Compositae. II. Annales Botanici Fennici, 7 : 325-352.
- Plantefol, L. (1948) : La theorie des helices foliaires multiples. Fundaments d'une theorie phyllotaxique nouvelle. Masson, Paris.
- Richards, P.J. (1948) : The geometry of phyllotaxis and its origin. Soc. Exper. Biol. Symp., II : 217-245.
- \_\_\_\_\_ (1950) : Phyllotaxis : its quantitative expression and relation to growth in the apex. Phil. Trans. Roy. Soc. London, B. 235 : 509-564.
- Schimper, C.F. (1836) : Geometrische Anordnung der um eine Achse peripherische Blattgebilde. Verhandl. Schweiz. Ges. 1836:113-117.
- Schoute, J.G. (1913, 1914) : Beiträge zur Blattetellungslehre. I. Die Theorie. II. Über verästelte Baumfarne und die Verästelung der Pteropsida im allgemeinen. Reg. Trav. Bot. Neerl., 10: 153-325, 11:95-193.
- Schwendener, S. (1878) : Mechanische Theorie der Blattstellung. Engelman, Leipzig.
- Sinnett, E.W. (1960) : Plant morphogenesis. New York.
- Snow, R. (1955) : Problems of phyllotaxis and leaf determination. Endeavour, 14 : 190-199.
- Snow, Mary and Snow, R. (1934) : The interpretation of phyllotaxis. Biol. Rev., 2 : 152-157.
- Thompson, D.W. (1917) : On growth and form. Cambridge.

- Wardlaw, C.W. (1949) : Leaf formation and phyllotaxis  
in Dryopteris aristata Druce. Ann.  
Bot., n.s. 13 : 163-198.
- Weisse, A. (1897) : Die Zahl der Randblüten an Composi-  
ten - Köpfchen. - Jahrb. Wiss. Bot.,  
30 : 453-483.
- Wright, C. (1873) : On the uses and origin of arrange-  
ments of leaves in plants. Mem. Amer.  
Acad. Arts. and Sci., 2 : 379-415.

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# 10. STATISTICAL ANALYSIS OF BILATERAL SYMMETRY IN PLANT ORGANS

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**SUMMARY.** Certain organs of several species of plants express bilateral symmetry. An attempt is made to understand the laws operating in the expression of this kind of symmetry and the relationship between the substructures.

## 1. INTRODUCTION

As Sinnott (1937) puts it '...morphology, far from being the hopelessly static discipline which some would have us believe, therefore, touches so intimately the central problem of biology that it may still be described by Darwin's words, in a famous passage of the 'Origin' as the 'very soul' of natural history'. Further, morphology does not end with the presentation of facts in the form of data as is common today, but our task is to gain knowledge of those laws which are operative in the structure and behaviour of the various members of plant kingdom.

The aim of the present studies is to assess the totality of structures relating to plant organs, to find suitable classification for them and to test statistically the various hypotheses regarding their occurrence in Nature. A broader aim envisaged is to explore the relationship between the important characteristics like yield, colours and the classified structures, and to find the selection process of structures by Nature. Further questions of interest would be to create artificially the possible structures and study the relationship between yield and structure.

In this paper observations on clockwise and counter-clockwise situations, i.e. left- and right-handedness of plant organs in a few species are described. Many of these variations were not known till recently. It is worth mentioning that none of these observations demanded the use of any serious equipment, not even a hand lens.

## 2. PRESENTATION OF DATA

In this section the various situations in plant organs where bilateral symmetry occur are explained. Data on brief or continuous observations made on the members of a few families are also presented.

2.1. *Morphology of asymmetry in plant organs.* Asymmetry in morphological structures is expressed in certain organs of many plant species. In this report, those situations where the asymmetry is manifested in the two complementary forms (bilateral symmetry) by identical organs of individual plants of the same species alone are considered. The proportions of such left-handed and right-handed leaves, flowers, stems, tendrils or fruits within a plant may be 1 : 1 as is the case observed in a majority of species, or may occur in different ratios.

In most plant species where the leaf arrangement is alternate, the single foliar spiral perceivable can be regarded as running clockwise (left-handed) or counter-clock-

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wisely. In grasses and some species of the family Scitamineae, though a single leaf is formed at each node, the leaves do not show a spiral mechanism. But they fall one over another in two vertical rows, which arrangement is known as distichous. In bananas, the two rows of leaves move spirally and both the spirals in all the known species and varieties of banana move counter-clockwisely. But in some Agavaceous species like *Cordyline rubra* where the foliar spirals (two per shoot) move either clockwise or counter-clockwise, both the kinds of shoots can be usually seen with in a plant. In most palms, the leaves are arranged in single, two, three, five or more numbers of spirals. Strikingly, the leaves of some individuals of each species veer clockwise and the others counter-clockwisely (Davis, 1962a, 1964a, 1971a). The leaf-blade (lamina) while in bud rolls margin to margin in some families, and the rolling may take place along the upper surface (convolute) or lower surface (revolute). In most grasses, while the lamina of one leaf convolutes clockwise, the next one moves counter-clockwisely, and this pattern is repeated continuously. But in Scitamineae and Araceae, the individual plants of many species do not show a regular pattern although their laminae convolute. However, in *Scindapsus officinalis*, the laminae exhibit not only clockwise and counter-clockwise convolution, but also another situation of involution (Davis, 1970). In *Cordyline rubra*, there exists a correlation between the direction of foliar spiral and the convolution of the lamina (Davis and Ghosh, 1969). In palm leaves, the numbers of leaflets on linear halves differ. In most pinnate type of palms, this difference between halves is statistically significant. In left-spiralled palms, the left half of the leaves bears more leaflets, and vice versa in right-spiralled palms (Davis, 1971b; Davis, et al, 1971). A similar situation is observable with the numbers of spines on the leaf margins of both the types of young *Agave sisalana* plants (Mitra, 1968).

Most (perhaps all) members of Malvaceae (Davis, 1966b), and Bombacaceae (Davis, 1966, 1967; Davis and Kundu, 1965; Davis and Ghosh 1970) and some of Sterculiaceae, Tiliaceae, Cochlospermaceae, Euphorbiaceae, Caricaceae, Linaceae, Plumbaginaceae, Theaceae, Palmae, Tropaeolaceae, Rutaceae and Oxalidaceae show bilateral symmetry of flowers. In a flower, all the petals twist (contort) clockwise or counter-clockwisely. While in most species, the petals form a single rotating whorl, in the multipetalled variety of *Hibiscus rosasinensis* (Davis and Ghoshal, 1965) and some species of *Camellia*, there are five spirals of petals, all twisting one way or the other. This situation is like the arrangement of leaves in the Spiral Aloe (Kofler, 1965).

The fibres of a few species of plants move spirally. Some individuals of the same species have their fibres twisting clock-wisely and the others counter-clockwisely. While in the coconut the two kinds of palms occur fairly equally (Petch, 1911), in chestnut trees, a great majority of individuals twist counter-clockwisely (van Oye, 1926).

In some xerophytes, the individual stems veer either clockwise or conversely. Thus, in *Euphorbia antiquorum*, the stem has three wings (or rarely four), and it twists either to the left or right. From each node, usually three off-shoots are produced which in turn show spiral mechanism. Some of these off-shoots twist like that of the

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trunk, and the rest differently (Davis, 1968). In another species, *Euphorbia nerifolia*, there are five ridges and at each node it produces 0-5 off-shoots. Here again some off-shoots move like that of the trunk and the others unlike it. A somewhat similar condition exists in many plants with alternate phyllotaxy.

In the flowers of *Crescentia alata*, a peculiar variation was noticed. A flower has normally 5 stamens at five fixed positions. After examining over 75,000 flowers of a particular tree at Calcutta, it was found that at each position one of the four possibilities occurred: a fully developed stamen, a staminode, a stamen fully fused with the corolla, or nothing at all. Thus, 1025 forms are possible of which only 105 could be symmetrical forms, and the rest comprised pairs of mirror image forms. Usually the number of flowers falling under one type equalled more or less that of its mirror image form.

2.2(a). *Floral asymmetry: Malvaceae*. Of the two Deccan hemp flowers shown in Fig. 1, the one on the left has its petals twisting clockwise (left-handed). When viewed apically, the inner margin of the petals of a left-handed flower curves

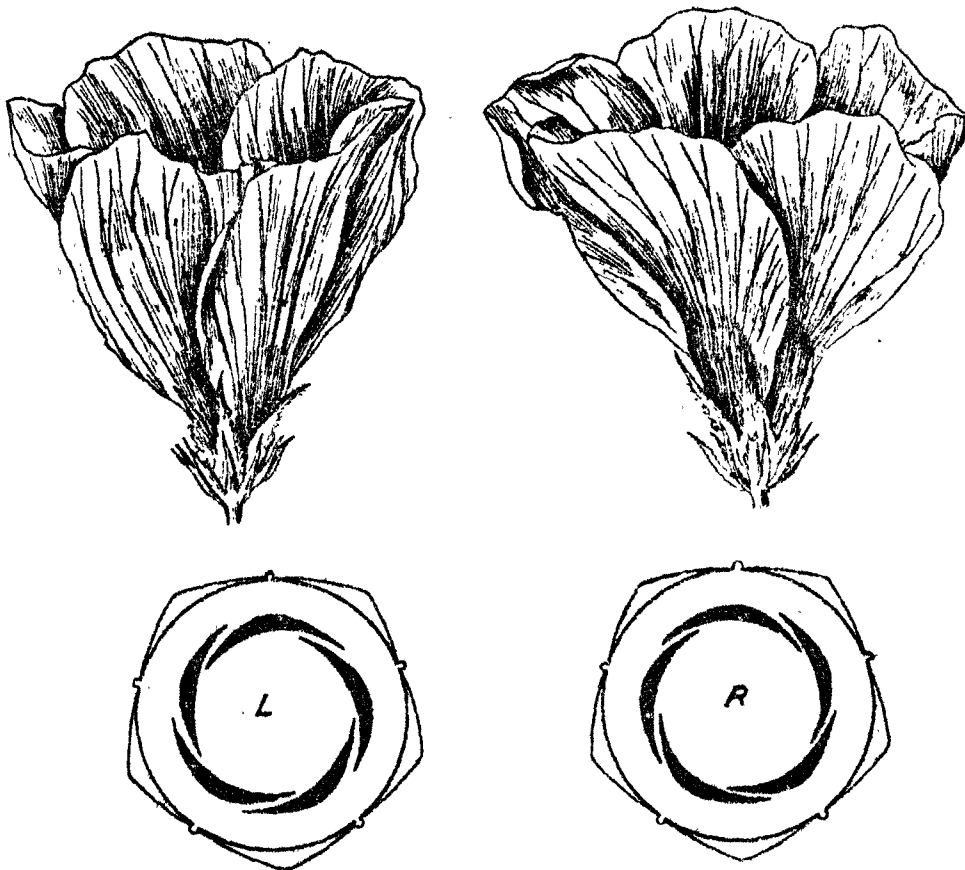


Fig. 1. Left and right-twisting flowers of Deccan hemp.

clockwise towards the periphery. In the right-handed flower, the petals curve counter-clockwise. Often it is possible to determine the spirality of a flower by examining a single petal. According to Rendle (1959), there exists a positive cor-



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relation between the asymmetric nature of a petal and twisted aestivation. In *Sida cordifolia*, each petal shows two distinct steps at the distal margin, the half that moves out first is always shorter than the other. While in *Thespesia populnea* the stigmatic end twists in accordance with the aestivation of the corolla, in *Hibiscus rosasinensis*, the monadelphous staminal tube shows clear twisting, by which the spirality of the flower can be determined.

Available flowers from 463 plants of 34 species of the family Malvaceae were examined for their aestivation (Davis and Selvaraj, 1964) and the data presented in Table 1.

TABLE 1. AESTIVATION OF FLOWERS OF MALVACEOUS SPECIES

species	no. of plants	petal-twist		$L + R$	$\chi^2$
		left	right		
1. <i>Abutilon hirtum</i>	12	1301	1371	2672	1.8338
2. <i>Abutilon indicum</i>	9	315	222	537	16.1061
3. <i>Abutilon megapotamicum</i>	2	29	31	60	0.0667
4. <i>Abutilon ochsenii</i>	1	2	4	6	0.6667
5. <i>Achania conzeilii</i>	2	168	156	324	0.4444
6. <i>Althaea rosea</i>	39	1445	1414	2859	0.3361
7. <i>Gossypium anomalum</i>	1	7	3	10	1.6000
8. <i>Gossypium arboraeum</i>	5	683	649	1332	0.8679
9. <i>Gossypium barbadense</i>	26	663	627	1290	1.0047
10. <i>Gossypium davidsonii</i>	1	13	16	29	0.3103
11. <i>Gossypium herbaceum</i>	3	8	6	14	0.2857
12. <i>Gossypium hirsutum</i>	14	397	391	788	0.0457
13. <i>Gossypium latense</i>	3	8	6	14	0.2857
14. <i>Gossypium thurberi</i>	1	3	0	3	3.0000
15. <i>Gossypium</i> sp. (wild)	2	62	67	129	0.1938
16. <i>Hibiscus cannabinus</i>	69	876	891	1767	0.1273
17. <i>Hibiscus esculentus</i>	60	255	254	509	0.0020
18. <i>Hibiscus hirtus</i>	6	30	34	64	0.2500
19. <i>Hibiscus indicus</i>	1	18	19	37	0.0270
20. <i>Hibiscus mutabilis</i>	4	72	84	156	0.9231
21. <i>Hibiscus rosasinensis</i>	55	16871	16047	32918	20.6263
22. <i>Hibiscus schizopetalus</i>	2	17	10	27	1.8148
23. <i>Hibiscus sabbdariffa</i>	93	567	574	1141	0.0429
24. <i>Hibiscus tiliaceus</i>	3	291	300	591	0.1371
25. <i>Hibiscus tortuosus</i>	1	81	80	161	0.0062
26. <i>Hibiscus tricuspis</i>	1	14	13	27	0.0370
27. <i>Hoheria lyalli</i>	1	3	6	9	1.0000
28. <i>Malachra capitata</i>	6	8892	8883	17775	0.0046
29. <i>Malvastrum</i> sp.	2	27	32	59	0.4237
30. <i>Pavonia coxi</i>	5	104	92	196	0.7347
31. <i>Pavonia odorata</i>	2	3	13	16	6.2500
32. <i>Sida cordifolia</i>	23	3187	3049	6236	3.0539
33. <i>Thespesia populnea</i>	6	2282	2394	4676	2.6826
34. <i>Urena lobata</i>	2	118	117	235	0.0043
total	463	38812	37855	76667	65.1951

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2.2(h). *Bombacaceae*. The family *Bombacaceae* was formerly included under *Malvaceae* (Hooker, 1872). The 13 species of this family examined in India showed the two kinds of twisting of the corolla. The data relating to 41, 470 flowers are presented in Table 2.

TABLE 2. LEFT- AND RIGHT-SPIRALLED TWISTING FLOWERS OF BOMBACACEAE

species	no. of plants	acstivation of corolla			$\chi^2$
		left	right	L+R	
<i>Adansonia digitata</i>	5	213	204	417	0.1942
<i>Bombax anceps</i>	2	93	94	187	0.0053
<i>Bombax ceiba</i>	27	19664	18828	38490	18.2448
<i>Bombax insignis</i>	2	46	28	74	4.3784
<i>Ceiba pentandra</i>	8	804	771	1575	0.6914
<i>Ceiba rosea</i>	1	30	28	58	0.0690
<i>Chorisia insignis</i>	1	49	48	97	0.0103
<i>Pachira aquatica</i>	1	83	102	185	1.9510
<i>Pachira cyathophora</i>	2	87	78	165	0.4909
<i>Pachira insignis</i>	1	11	14	25	0.3600
<i>Pachira longifolia</i>	1	36	32	68	0.2353
<i>Pseudobombax grandiflorum</i>	1	27	39	66	2.1818
<i>Salmalia insignis</i>	2	39	24	63	3.5714
total	54	21182	20288	41470	32.3842

$$\chi^2_{11} = 19.2726; \chi^2_{12} = 13.1116$$

2.3. *Euphorbia antiquorum*. The stem of a particular variety of *Euphorbia antiquorum* screws clockwise or counter-clockwise, and on account of this screwing habit perhaps this plant is called by the Tamils as "thirikalli" meaning the twisting cactus (Fig. 2). 1,500 main stems were examined at Coimbatore in January 1965 for



Fig. 2. Right and left-twisting spiralling stems of *Euphorbia antiquorum*.

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their spirality. Two percent of these stems reversed from one direction to the other, a tenth of which reversing twice (left to right and again back to left) as may be seen from Table 3.

TABLE 3. *EUPHORBIA ANTIQUORUM* : NATURE OF MAIN STEM

type of stem-twist	observed	percentage
Left-handeds	748	49.867
Right-handeds	722	48.133
Left turned to right	20	1.333
Right turned to left	7	0.467
Left to right to left	3	0.200
Right to left to right	—	—
total	1500	100.000

50.88 per cent of the regularly twisting stems are thus, left-handers.

A further 200 main stems were collected at random from an adjoining locality. A stem had either three or four wings at the 'internodal' region. Of these plants, 58 bore four wings and the rest three each. The stem usually produces one off-shoot each from a wing from an 'internodal' region, and thus a four-winged stem may have four off-shoots. But this number may be reduced to 3, 2, 1 or nil. Similarly, a three-winged stem may have 3, 2, 1 or no off-shoots. Stems having no off-shoot were excluded. Very rarely a wing may produce more than one off-shoot. In Table 4, details are given on the number of off-shoots produced from the 200 main stems.

TABLE 4. *EUPHORBIA ANTIQUORUM* : NO. OF OFF-SHOOTS PER MAIN STEM

main stem	4-winged stems nos. of off-shoots					3-winged stems nos. of off-shoots					
	spiral no.	4	3	2	1	total	4	3	2	1	total
left	117	22	10	5	—	37	1	51	24	4	80
right	83	12	8	—	1	21	—	43	15	4	62
total	200	34	18	5	1	58	1	94	39	8	142

Like the main stems, the off-shoots also show bilateral symmetry by twisting either clockwise or conversely. A smaller percentage of these off-shoots, however, did not show any twisting and they were accounted for as neutrals. 572 off-shoots were examined from the 200 plants and their spirality recorded. The data are given in Table 5.

TABLE 5. *EUPHORBIA ANTIQUORUM* : NATURE OF OFF-SHOOTS OF 200 PLANTS

main stem	left		off-shoots right		neutral		total	%
	total	%	total	%	total	%		
left	243	71.27	72	21.11	26	7.62	341	100.00
right	66	28.57	145	62.76	20	8.67	231	100.00
	309	54.02	217	37.94	46	8.04	572	100.00

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To examine whether the twisting of the off-shoots depends on that of the main stem, the data are split up for the 4-winged shoots and 3-winged shoots as seen in Table 6.

Table 6: *EUPHORBIA ANTIQUORUM*: ASYMMETRY OF OFF-SHOOTS IN RELATION TO KIND OF MAIN STEM

spiral of main stem	off-shoots	nature of off-shoots			
		left	right	neutral	total
<i>4-winged off-shoots (Total 198)</i>					
	observed	100	16	12	128
left	percentage	78.13	12.50	9.38	100.00
	% on all shoots	29.32	4.69	3.52	37.53
	observed	13	47	10	70
right	percentage	18.57	67.14	14.29	100.00
	% on all shoots	5.63	20.35	4.33	30.31
<i>3-winged off-shoots (Total 374)</i>					
	observed	143	56	14	213
left	percentage	67.14	26.29	6.57	100.00
	% on all shoots	41.94	16.42	4.11	62.47
	observed	53	98	10	161
right	percentage	32.02	60.87	6.21	100.00
	% on all shoots	22.94	42.42	4.33	69.69

2.4. *Euphorbia nerifolia*. Fig. 3 shows two stem pieces of *Euphorbia nerifolia*, each beset with five rows of spines, the rows running right-handed in one and left-handed in the other. The stem grows in stages, and off-shoots are produced at the junction of the stem formed during different seasons, and such a junction simulates a node.

Off-shoots ranging from 0-5 are produced from each node. However, it may be mentioned that there is a bud in the axil of every leaf or leaf scar, and very occasionally some off-shoots are also produced from these 'extra-nodal' regions of the stem.

The main stem continues to grow, generally maintaining the original direction of twisting throughout. Exceptional shoots showing reversal of stem-twist were excluded. All the off-shoots from a 'node' do not necessarily show the same kind of spirality. An off-shoot of the first order usually maintains the spirality thereafter even though it may produce shoots of the second and further orders having different spirality.

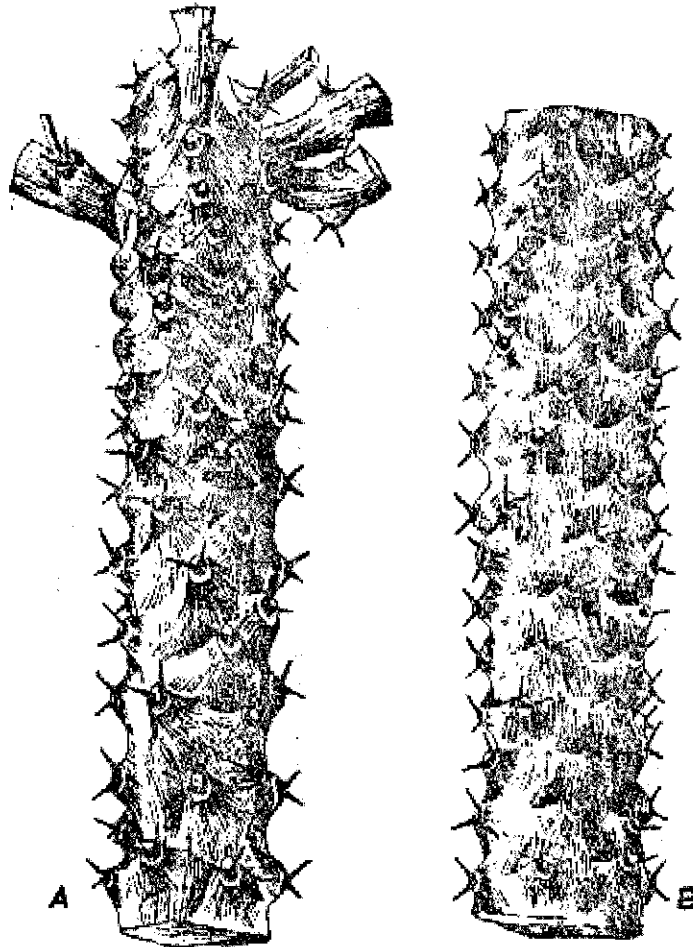


Fig. 3. Left- and right-spiralling stems of *Euphorbia nerifolia*

At the Central Arecanut Research Station, Vittal, Mysore, 36 different plants of *E. nerifolia* were observed in 1965 for the spirality of their off-shoots, and the data are presented in Table 7.

It may be seen from the data that 19 of the 36 plants bore excess left-handed off-shoots, 8 equality and 9 excess right-handed ones. On the totals, the left-handeds form 52.80 per cent, but the deviation from equality is not statistically significant,  $\chi^2 = 12.591$ .

At Khandwa, Madhya Pradesh, 240 main stems of *E. nerifolia* each having 'node' producing off-shoots ranging from 0-5 were examined. Of these, 140 or 58.91 per cent were left-handeds.

2.5. *Linum usitatissimum*. Linseed (*Linum usitatissimum*) is an economically important plant since its seeds yield the linseed oil, and the bast yields the fibre known as flax fibre of commercial importance.

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TABLE 7. *EUPHORBIA NERIIFOLIA*: LEFT AND RIGHT-HANDED SHOOTS PER PLANT

plants	off-shoots				$\chi^2$
	L	R	L+R	L-R	
1	10	10	20	—	—
2	19	15	34	4	0.471
3	9	8	17	1	0.059
4	4	5	9	— 1	0.111
5	6	6	12	—	—
6	15	14	29	1	0.034
7	11	10	21	1	0.048
8	6	8	14	— 2	0.286
9	10	9	19	1	0.053
10	8	5	13	3	0.002
11	12	7	19	5	1.316
12	8	8	16	—	—
13	9	8	17	1	0.059
14	11	6	16	5	1.470
15	10	5	15	5	1.067
16	11	6	17	5	1.470
17	9	9	18	—	—
18	21	11	32	7	1.400
19	9	8	17	1	0.058
20	12	13	25	1	0.040
21	6	9	15	— 3	0.600
22	8	5	13	3	0.692
23	6	3	9	3	1.000
24	5	7	12	— 2	0.333
25	6	4	10	2	0.400
26	4	3	7	1	0.143
27	6	7	13	1	0.077
28	6	5	11	1	0.090
29	2	4	6	2	0.600
30	7	7	14	—	—
31	1	3	4	2	1.000
32	5	5	10	—	—
33	3	2	6	—	—
34	14	17	31	— 3	0.290
35	6	6	12	—	—
36	16	15	31	1	0.032
	311	277	588	34	14.557

$$\% \text{ lefts} = 52.89 \quad \chi^2 = 1.906 \quad \chi^2_{35} = 12.591$$

The primary stem continues to grow till it flowers when it produces a few bearing lateral shoots. But at an early stage, it produces a good number of

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shoots almost from its base (Fig. 1). The single foliar spiral of the main stem be determined from the leaves or the starting positions of the first order off-shoots.

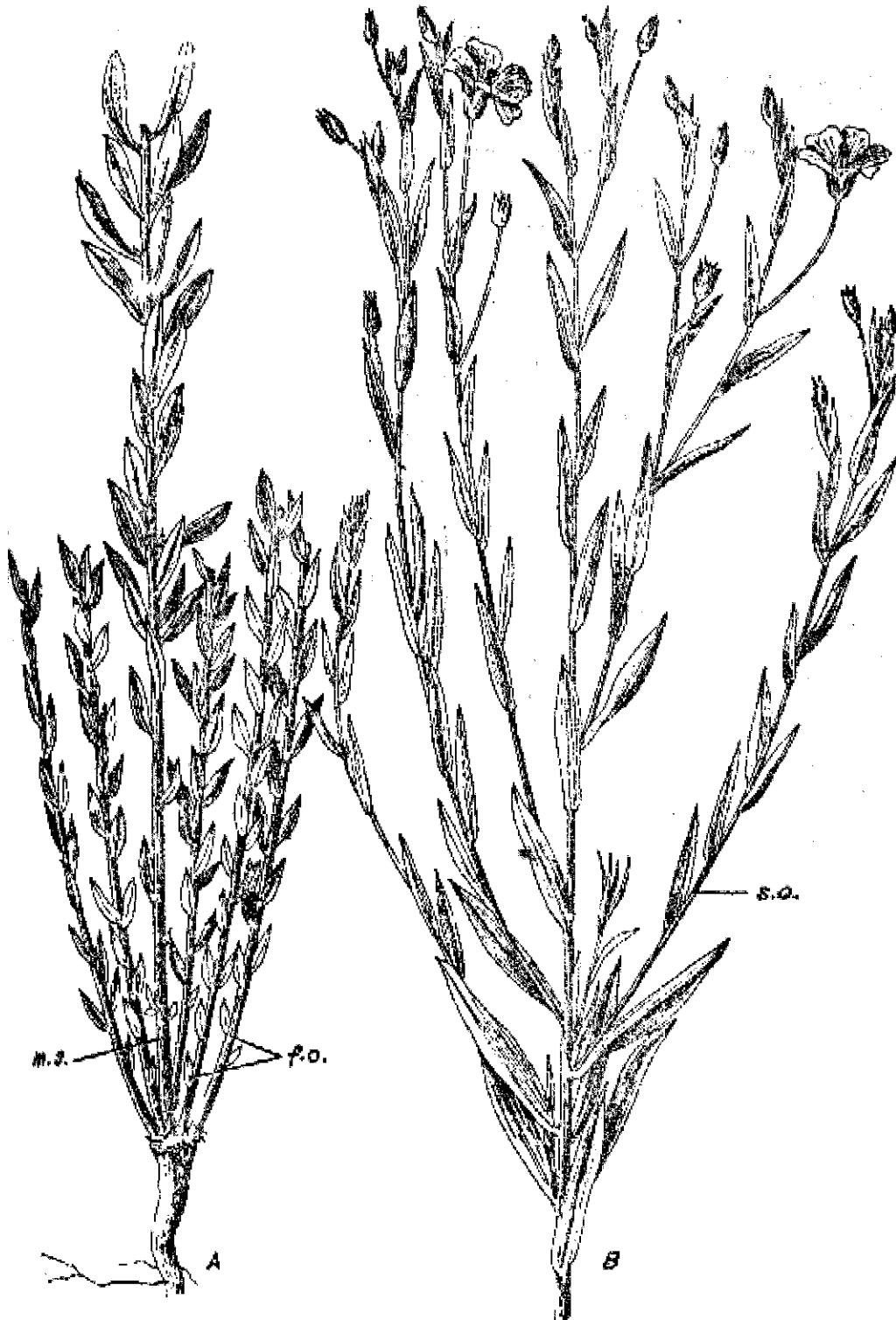


Fig. 1. Lower part of a plant (A) and a flowering shoot (B) of *L. casei* plant.

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The off-shoots grow almost as fast as the primary stem and produce lateral flowering shoots at their apices. The spirality of the first and second order off-shoots was also determined. The number of fruits borne by each off-shoot was counted. In Tables 8 and 9, the data on the numbers of first order and second order off-shoots of 22 left-spiralled and 19 right-spiralled plants are given.

TABLE 8. *LINUM USITATISSIMUM*: FOLIAR SPIRAL OF MAIN STEM AND OFF-SHOOTS

(Main stem—Left-spiralled)

plant	spiral	I order branch		II order branch		plant	spiral	I order branch		II order branch			
		L	R	L	R			L	R				
1	L	L	4	1		11	L	L	3	7			
		L	2	3				L	2	4			
		R	4	4				L	1	5	22		
		R	1	4				12	L	L	2	3	
		R	2	3						R	2	3	
		R	3	5						R	3	2	15
R	2	3	41										
2	L	L	4	2		13	L	L	2	3			
		L	2	3				L	2	3			
		L	4	2				L	3	3	16		
		R	2	3	22								
3	L	L	4	3		14	L	L	2	3	5		
		L	2	3	12								
4	L	L	2	3		15	L	L	2	4			
		R	3	2				L	3	2			
		R	1	4				R	4	1			
		R	1	4	20 $\frac{1}{2}$			R	2	3	21		
5	L	L	3	3		16	L	L	2	4			
		L	5	3				L	2	5			
		R	4	2				R	3	4			
		R	3	3				R	5	4	29		
		R	2	3				17	L	L	2	3	
		R	3	2						R	3	1	
		R	2	3						R	3	2	14
R	3	2	46										
6	L	L	1	5		18	L	L	3	5			
		R	2	3	11			L	1	4			
7	L	L	4	4				R	2	3			
		L	3	2	13			R	2	3	23		
8	L	L	1	4		19	L	L	4	2	6		
		L	1	4									
		R	3	2	15								
9	L	R	2	3		20	L	L	2	5			
		R	2	3	10			L	2	3			
10	L	R	2	3		21	L	R	1	4			
		R	2	3	10			R	3	2	10		
		L	2	4				22	L	L	4	2	
		L	2	4						L	2	4	
		L	5	3						R	2	3	
R	3	2		R	2	3	22						
R	3	3	31										

main stem L = 22

187 234 121

I order off-shoots L = 38; R = 36 (total 74)

II order off-shoots L = 187; R = 234 (total 421)



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TABLE 9. *LINUM USITATISSIMUM* : FOLIAR SPIRAL OF MAIN-STEM AND OFF-SHOOTS

(Main stem right-spiralled)

Plant	spiral	I order branch		II order branch		plant	spiral	I order branch		II order branch	
		L	R	L	R			L	R		
1	R	L	2	3		11	R	L	8	6	
		R	4	1				L	2	3	
		R	3	2	15			L	2	4	
2	R	L	3	4		12	R	L	3	2	
		L	1	4				R	4	2	
		R	4	1				R	2	3	
		R	1	5	23			R	4	3	
3	R	R	2	3		13	R	L	3	2	
		R	3	2	10			R	4	3	
4	R	R	4	4		14	R	L	3	2	
		R	2	3	13			L	3	3	
5	R	L	3	3		15	R	R	3	3	
		R	3	3				R	2	3	
		R	2	3	17			R	2	3	
6	R	L	4	4		16	R	R	3	2	
		R	3	5				R	3	2	
		R	5	1				R	3	10	
		R	7	3							
		R	4	4							
		R	6	5	51						
7	R	L	3	2		17	R	R	2	3	
		L	2	3				R	2	4	
		R	4	1	15			R	2	11	
8	R	L	3	3		18	R	R	2	3	
		R	2	3	11			R	2	6	
9	R	L	1	4		19	R	L	3	2	
		L	2	3				R	3	3	
		R	2	3				R	3	1	
		R	4	1				R	3	3	
		R	3	2				R	3	3	
		R	2	3				R	3	2	
		R	3	2	35						
		R	3	2							
10	R	L	3	2		20	R	R	2	3	5
		L	1	4				R	2	4	
		R	4	4				R	3	3	
		R	3	2	23			R	3	2	

200 198

Main stem R = 19; I order off-shoots L = 24, R = 43; (Total 67)

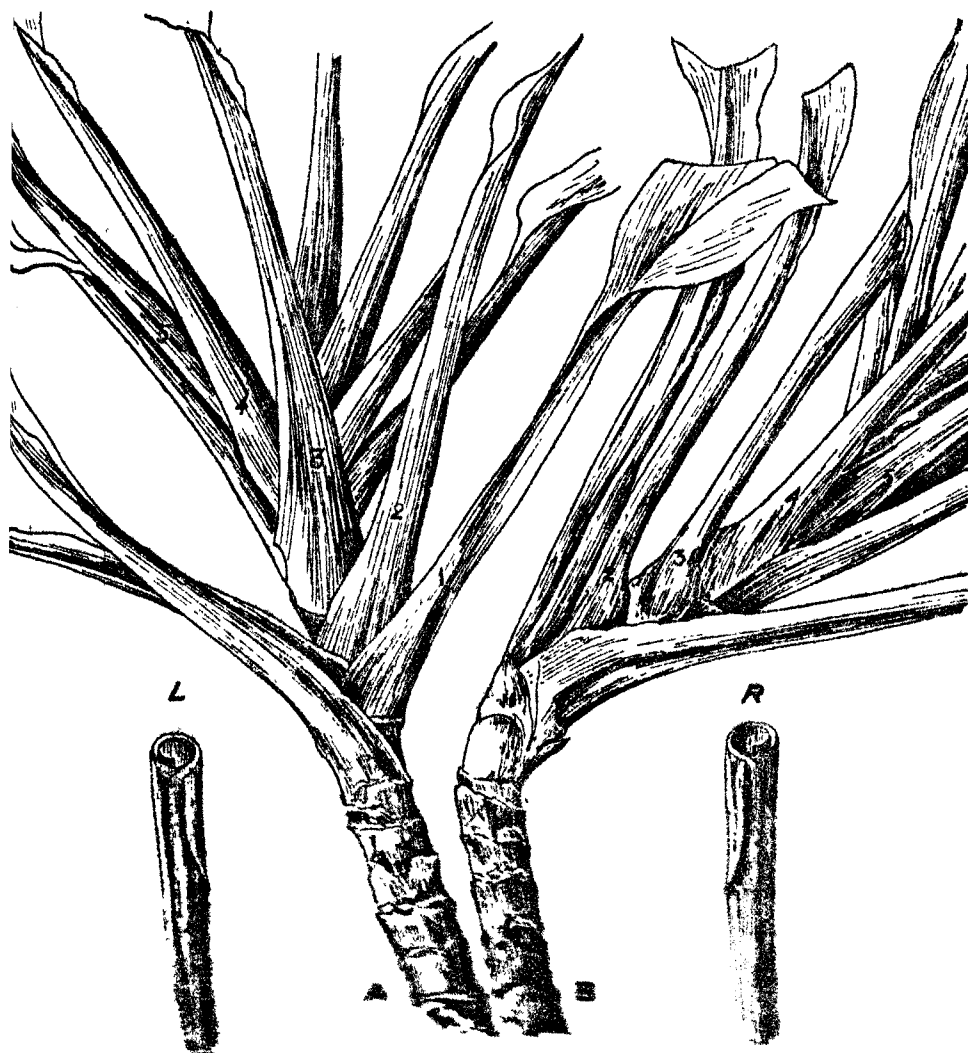
II order off-shoots

L = 200, R = 198 (Total 398).

2.6. *Cordyline rubra*. *Cordyline rubra* of Agavaceae has alternate leaves which are arranged in two spirals veering either to the left or to the right (Fig. 5).

## BILATERAL SYMMETRY IN PLANT ORGANS

plant, the two types of spirals are usually seen on different shoots. The leaf shows clear convolution before unfolding, and this rolling may be clockwise or clockwise (Davis and Ghosh, 1969).



43 shrubs of *Cordyline verna* grown at the premises of the Indian Statistical Institute were examined in 1966 for the foliar arrangement in all their shoots. From shoots of some of these plants, the convolution of the lamina of 519 leaves produced between September 1964 to April 1965 was recorded to find out whether the direction of convolution corresponded with the direction of the foliar spiral or not. 16 of the 37 shoots bore left-handed foliar spirals, and the rest, right-handed ones. The results are presented in Table 10.

TABLE 10. *CORDYLINE RUBRA* : FOLIAR SPIRAL AND PTYXIS

convolution of consecutive leaves																								total		
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	1	2	
L	L	R	R	L	R	L	R	R	R	R	R	R	L	R	R	R	R	R	R	R	R	L	L		17	
R	R	R	R	R	L	R	R	R	R	R	R	R	L	R	L	R	R	R	R	R	R	R	L		4	20
R	R	R	R	R	R	L	R	R	R	R	R	R	L	R	R	R	R	R	R	R	R	R	L		5	17
R	L	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R		2	17
R	L	L	L	R	R	L	R	R	R	R	R	L	L	R	R	R	R	R	R	R	R	R	R		9	18
L	L	L	L	L	L	R	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L		19	1
R	L	L	L	L	L	R	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L		16	3
R	L	R	R	R	R	L	L	R	R	R	R	R	R	L	R	L	R	L							5	13
R	L	L	R	R	L	L	L	L	L	L	R	R	R	R	R	R	R	R							8	8
R	R	R	R	R	L	L	R	R	R	R	R	R	R	R	R	R	R	R							14	
R	R	R	R	R	L	R	R	R	R	R	R	R	R	R	R	R	R	R	R						1	17
L	R	R	R	R	R	L	L	L	L	L	L	L	L	L	L	L	L	L							9	3
L	L	L	L	L	R	R	R	R	R	R	R	R	L	L	L	L	R	R	R						9	10
R	R	R	R	L	R	R	L	L	L	R	R	R	R	R	R	R	R	R	R						5	8
R	L	R	R	R	R	R	L	L	R	R	L	L	R	R	R	R	R	R	R	R	R	R	R		5	16
R	L	L	L	L	L	R	R	R	R	R	L	L	L	L	L	L	L	L	L						11	6
L	L	L	L	L	R	R	L	L	L	L	L	L	L	L	L	L	L	L	L						12	
R	R	L	L	L	L	Flowered																			4	2
R	R	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L						11	2
R	R	R	R	R	L	L	R	R	R																2	8
R	R	R	R	L	R	L	R	R	R	R															-	9
R	R	R	R	L	R	R	R	R																	1	8
R	L	L	L	L	L	R	L																		6	2
L	L	L	L	L	L	L	L	L																	9	-
L	L	L	L	L	L	L	L	L																	8	-
L	R	R	R	R	R	L	R	R																	2	7
R	R	R	R	R	R	R	R	R	R																-	10
L	L	L	L	L	L	L	L	L	L																11	-
L	L	L	L	L	L	L	L	L	L																10	-
L	L	L	L	L	L	L	L	L	L																10	-
L	L	L	L	L	L	L	L	R	L	L															10	1
R	R	R	R	R	R	L	L	R	R	L	R	R													3	10
R	R	R	R	L	R	R	R	R	R	R															1	10
R	R	R	R	R	R	R	R	R	R	R	R	R													-	13
R	R	R	R	R	R	R	R	R	R	R															-	9
L	L	L	L	L	L	L	L	R	L	R															9	2
R	R	R	R	R	R	R	R	R																	-	8

227 202

- 319

\* 37

observed from 10.9.1964 to 0.4.1965

VII from 11.9.1964 to 31.12.1965.

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2.7. *Scindapsus officinalis*. The leaves of *Scindapsus officinalis*, a tropical ornamental plant, are alternate and often arranged distichously. When young, the lamina rolls in one of three ways—two types of convoluted (as in *Convolvulus rostrata*), and involute, where the two halves of a lamina roll along opposite directions over the upper surface (Fig. 6). The leaf sheath also overlaps one way or the other. When the lamina rolls left-handed, the leaf sheath of the same leaf overlaps right-handed, and vice versa, if the lamina is right-handed. But when the lamina is involute, the sheaths of some leaves roll left-handedly and the others right-handedly.

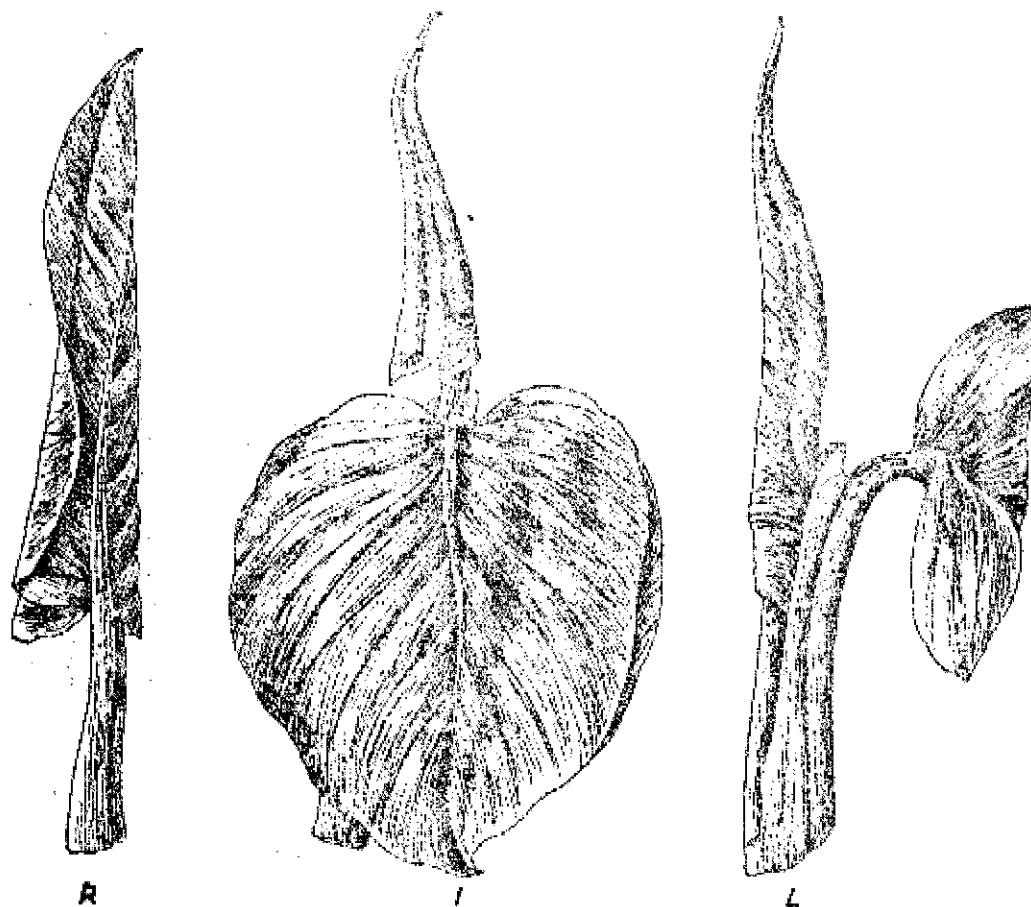


Fig. 6. *Scindapsus officinalis* leaves showing right-handed (R), involute (I) and left-handed (L) rolls of lamina.

50 shoots from three large *Scindapsus officinalis* plants growing on mango trees at the premises of the Indian Statistical Institute were labelled and the type of ptyxis on the 627 leaves produced on them during 75 days commencing from the first of May 1965 were observed. The data are presented in Table 11.

Plant 3 produced equal numbers of lefts and rights while for plants 1 and 2, the lefts are more although the differences are not statistically significant. The occurrence of involute leaves seems to vary from plant to plant, plant 1 having the

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TABLE 11. SCINDAPSUS OFFICINALIS: PREFOLIATION.  
(L = Left, R = Right, I = involute)

	L	R	I	total
<b>plant 1</b>				
1 L R I I I I I I I I I I I I I I I	1	1	18	20
2 R L L R L R	3	3	—	6
3 R I I I L R I I I R I I I I I L	3	3	10	16
4 L I I I L L I I I I I I I I R L	5	1	11	17
5 L R L R L R L R R I	4	5	1	10
6 R I R R I I I I I I R L R I I I I I	6	4	8	18
7 L R I I I L I I I R L I I I I I L	5	2	9	16
8 L R L R L I R I I I I I R I R L	5	5	7	17
	32	24	64	120
<b>plant 2</b>				
1 L R L L L L L R L R L R L	9	4	—	13
2 R I R R I I I L R I I I I	6	3	4	13
3 L R L R L I R L R L R R I	6	6	2	14
4 R R L R L R L R L R L R	6	6	—	12
5 R R L I I L L R L R L R L R	7	5	2	14
6 R L R R R L R L R I R I I I	4	5	5	14
7 R I L R R R L R L R L R	7	5	—	12
8 R I L R I R L R I R I I I I I	3	6	8	17
9 R L L I L I L L I L R L I I I I	8	2	9	17
10 R R L R L R L L L	5	4	—	9
11 L R L R L R R I I L R	4	5	3	12
12 L R L R L R R L R R L R	6	6	—	12
13 L R L R L	3	2	—	5
14 L I I R R R L I I I I I R R R L R	5	6	7	18
15 L R R L I I I I L R L R L I I	6	4	6	16
	82	68	48	198
<b>plant 3</b>				
1 L R R L R L R L R L R L R L	6	6	—	12
2 R L R I I L R I I I I I I I I R I	3	4	11	18
3 L R R L L R L R L R L R L R L R L R	8	7	1	16
4 L L R I L R L R L R R L R L R L	8	6	1	15
5 L R L R L R L	4	3	—	7
6 L R L R R L R R R R L R L	5	7	—	12
7 R L R L R L R L R L R L R	5	6	—	11
8 L L R L R L R	4	3	—	7
9 L R L I L R L I R R L R L I	6	4	4	14
10 L R R L L I L R R I R I I R L	5	6	5	16
11 L R L I L R R I I I I R R L R L	6	6	3	15
12 L R R R L R L R L R L	5	5	—	10
13 L R L R L R L R	4	4	—	8
14 R L R R I I L R L I	3	4	3	10
15 R I R L L R L R L I R I R L I	6	6	5	17
16 L R I I I I I I R I I I R L R	2	4	9	15
17 I L R I R L L I R I R L R L R	5	5	5	15
18 L R L R L R L	4	3	—	7
19 L R L R L R L	4	3	—	7
20 R L R L L I R I L I I L R L	6	4	5	15
21 L R L R L I L R L I	6	3	1	10
22 R R L R L R L	3	4	—	7
23 R L R L R L R L R L R I I	6	6	2	14
24 R L R L R L R	3	4	—	7
25 R R R R L R R R I R L R L	2	9	2	13
26 R R L R L	2	3	—	5
27 R L R L R	3	3	—	6
	137	127	57	321
total for 3 plants	241	219	163	627

ent percentage (53.33%). Since the data were collected simultaneously from the plants standing close to each other, one plant showing a very high percentage involute leaves has to be regarded as a peculiarity of this individual plant.

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2.8. *Arrangement of palm-perianth.* A palm flower usually possesses six perianth segments, generally all alike, which represent the sepals and petals of other flowers. The outer three segments may be called the sepals and the inner three, the petals. However, when the arrangement of the perianths of female flowers is carefully examined, it may be reasonable to consider that all the six perianth segments develop one after another forming a single spiral compressed into a whorl. In the female flowers of most species of palms, the aestivation of perianths vary considerably. When we consider the three inner perianths (petals), they either imbricate or twist regularly. In the imbricate flowers, one petal is completely exposed, the innermost leaf is overlapped on both sides by the other petals. Thus the middle petal has its left half exposed and the other half overlapped by the outer petal. From the position of the exposed half of the middle petal, a flower may be regarded imbricate-right or imbricate-left (Davis and Kundu, 1966). Similarly, with the regularly twisting corolla also, left-and right-handed types are observable (Davis, 1969b). Data on 9415 flowers from seven species of palms are presented in Table 12.

TABLE 12. AESTIVATION OF PETALS OF FEMALE FLOWERS IN 7 PALMS

species	corolla contorted		corolla imbricate		total
	lefts	rights	lefts	rights	
<i>Areca catechu</i>	320	273	1225	1219	3039
<i>Areca triandra</i>	9	6	182	206	403
<i>Borassus flabellifer</i>	26	38	143	143	349
<i>Coccothrinax</i>	26	18	208	188	432
<i>Phoenix paludosa</i>	42	19	62	61	184
<i>Phoenix sylvestris</i>	244	233	1083	961	2681
<i>Ptychosperma macarthurii</i>	0	1	1196	1128	2324
	805	608	4098	3704	9415

It is obvious from data given in Table 12 that the left-handed flowers (left contortion plus left imbrication) are greater than the right-handed ones. The proportion of flowers having contorted corolla to those with imbricate corolla varies very greatly with species. The percentage of contorted flowers in *Areca triandra* was only 2.7, that in *Coccothrinax* 9.2, *Borassus flabellifer* 18.0, *Areca catechu* 19.6, *Phoenix sylvestris* 23.8 and *P. paludosa* 33.7. In the case of *Ptychosperma macarthurii*, however, with the exception of a single flower, a population of 2,324 flowers had only imbricate corolla.

When all the six perianth segments of a flower are considered as a single spiral it is more appropriate to do so since the individual members develop one after another, one may observe 12 different groups according to the way the margins of a perianth segment overlap. In one type, all the members twist regularly clockwise and in another, counter-clockwise. In the neutral patterns, the perianth cycles can be

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vided into identical halves, one half exactly falling over the other half when folded along the diameter. Of the remaining patterns, two move clockwise and the others counter-clockwisely. All these patterns are illustrated in Fig. 13 with the observed and expected frequencies inscribed for each perianth pattern.

## 3. GRAPH THEORETICAL METHODS

Studies on the different morphological forms of plant organs described in the preceding sections lead to the combinatorial analysis of different possible structures of the same. These are facilitated by the use of one of the currently active fields of biology—'Graph Theory'. In this section a brief introduction to the theory as required for the present purpose is given and for other details the reader is referred to Sage (1962), Mac Mohan (1891), Polya (1962) and Ramanujacharyulu (1966).

## 3.1. Graph Theoretic results

3.1.1. A graph  $G$  is defined by a set  $X$  of points ( $n$  in number) and a set  $U$  of  $m$  pairs ( $m$  in number) of points from  $X$ . Each point of  $X$  is called a vertex and each pair (of points) in  $U$  is called an edge.

*Example 1 :*  $X : \{a, b, c, d\}$   $U : \{(a, b), (c, d), (a, c), (a, d)\}$

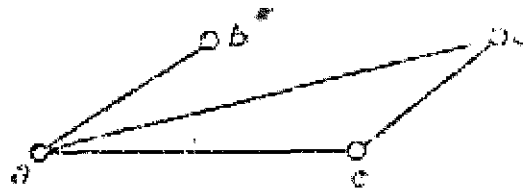


Fig. 7

The number  $m$  of edges can almost be equal to  $\frac{n(n-1)}{2}$ . In a graph  $G$ , the vertices can be used to represent the locations or sites of interest in a flower and an edge corresponds to a particular situation between the two sites on the flower.

3.1.2. The complement  $\bar{G}(X, U)$  of a graph  $G : (X, U)$  is defined as a graph with the vertex set  $X$ , but an edge appears in  $\bar{G}$  if and only if that edge did not appear in  $G : (X, U)$ .

*Example 2 :* For all our purposes we consider graphs on  $n$  vertices

$$a_i, \quad i = 0, 1, \dots, (n-1);$$

a set of edges which can be chosen from the following set

$$e_i = (a_i, a_{i+1}), \quad i = 0, 2, \dots, (n-1)$$

edges, the suffixes being read under module  $n$ . These graphs are known as 'Restricted Random Graphs' under the assumption that a graph on these  $n$  vertices is chosen with the condition that a random number of edges  $e_j$  are randomly chosen from a set of  $n$  allowed edges of the polygon.

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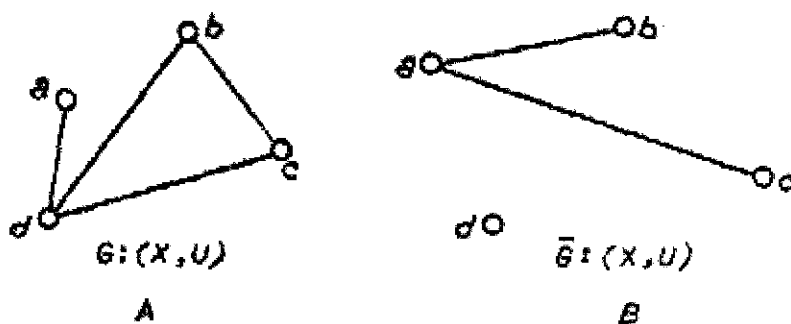


Fig. 8

3.1.3. *Colouring.* Let  $G$  be a polygon on  $n$  vertices. Let  $R$  be a set of  $s$  colours denoted by  $1, 2, \dots, s$ . A 'colouring' of the polygon is defined as assigning one and only one colour from the  $s$  colours to each edge independently. Thus there are  $s^n$  possible colourings.

3.1.4. *Cyclic rotation and patterns.* Consider a polygon  $G$  with vertices  $a_i, i = 0, 1, \dots, (n-1)$  and a colouring  $P_1$  of its  $n$  sides. Let  $P_2$  be another colouring of the polygon  $G$ . A 'cyclic rotation' of  $G$  is defined as a mapping of the vertices of  $G$  in which the vertex  $a_i$  is mapped to  $a_{i+j}$ ;  $i = 0, 1, \dots, (n-1)$ , where  $j$  is a fixed integer  $0 \leq j \leq n-1$ .

The two colourings  $P_1$  and  $P_2$  of  $G$  are said to be 'equivalent' of the same 'pattern' if given  $P_1$  the colouring  $P_2$  can be obtained by a cyclic rotation of the polygon.

*Example 3:* Let  $G$  be a polygon of 4 sides and  $R$  is set of two colours black and white:

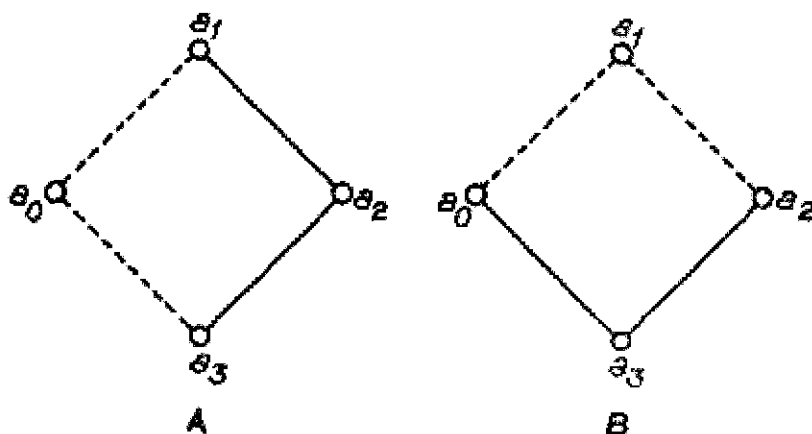


Fig. 9

In colouring  $P_1$  by writing  $a_{i+j}$  in place of  $a_i$  we get colouring  $P_2$ . Thus, these are equivalent colourings or these are of same pattern. Two patterns are distinct if they are not equivalent colouring.



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In other words, on a polygon a cyclic group is acting. One is interested in the number of distinct patterns. The solution is derived in Table 13.

TABLE 13. TABLE OF DISTINCT PATTERNS

$s$ number of colours	polygon of $n$ sides	3	4	5	6	7
	2	4	6	8	14	20
	3	11	24	51	129	315

The general formula for the number of distinct colourings to colour a polygon of  $n$  sides using  $s$  colours is as given below :

$$\frac{1}{n} (s^n + s + s + s^{d_2} + \dots + s^{d_1} + \dots + s^{d_{n-1}})$$

where  $d_i$  is the greatest common divisor between the integers  $n$  and  $i$ .

3.1.5. Evolution of restricted random coloured graphs : Now we consider the set of all possible coloured polygons which are  $s^n$  in number. Let all the graphs be given equal probability  $\frac{1}{s^n}$  of being chosen. In other words consider the development of a coloured polygon by selecting a colour out of the  $s$  colours for each side with equal probability. After colouring all the  $n$  sides we say that a Restricted Random Coloured (RRC) graph has appeared. The probability that a particular pattern appears when an (RRC) graph is chosen can be computed by obtaining the number of members in that pattern class and multiplying it by  $(1/s^n)$ . This is obtained by Ramanujacharyulu (1966); however, it is given here for computational reference for values of  $n = 3, 4, 5$  and  $6$  and  $s = 2$ .

A given pattern is an assignment of colours  $1, 2, \dots, s$  to the  $n$  cyclic edges  $e_0, e_1, \dots, e_{n-1}$ . Hence let the pattern be represented by a cyclic sequence  $f$  of integers representing the colours on these edges in that order of the cycle edges. Let the sequence  $f$  be partitioned into  $p(f)$  identical subsequences of length  $l(f)$  where  $l = l(f)$  is the least integer with this property. Then there are  $l$  equivalent colourings and the probability that an RRC graph is of observed pattern  $f$  is  $l(f)/s^n$ .

Example 4 :  $n = 4$  and 2 colours :

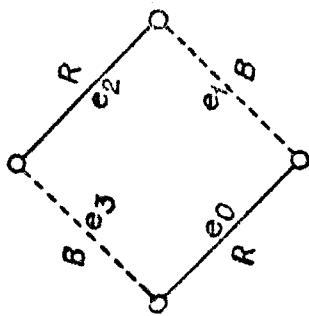


Fig. 10

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In presenting the following patterns, only patterns with not more than  $\left(\frac{n}{2}\right)$  edges in an  $n$  polygon are given as they can be obtained by complementation with respect to the polygon, the number of equivalent members in the corresponding complementary pattern classes are equal. A star on reference code denotes that the pattern is self-complementary.

A pattern  $C_{n,m}$  with  $F(n)$  equivalent members has a complementary pattern  $\bar{C}_{n,n-m}$  and the same number  $F(n)$  of equivalent members.

3.1.6. RC-Patterns: Consider once again the set of  $s^n$  possible coloured polygons of  $n$  sides in  $s$  colours.

In the above sections two colourings are said to be of the same pattern if one coloured polygon can be obtained by a cyclic rotation of the other coloured polygon.

However, this equivalence of two colouring can be defined in any required manner. In the foregoing examples as will be explained, we need the following definition of equivalence as well in case of two colourings.

The case of a polygon whose sides are coloured using two colours only in the same as that of a Restricted graph on the  $n$  cyclic vertices in which some of the cyclic edges appear (i.e. sides of one colour) and the others (sides of the other colour) do not appear.

These  $2^n$  restricted graphs are derived from the coloured polygons. Two such graphs are said to be RC-equivalent if one graph can be obtained from the other by a cyclic rotation (R) or if one graph is complement of the other with respect to the polygon.

One is interested in the number of graphs which are not RC-equivalent. Let us call them 'RC-patterns'. The general formula for RC-patterns is not yet obtained and it is evaluated here for  $n = 6$  as it is of immediate application. A self-complementary RC-equivalent pattern is called a 'neutral pattern' whereas among two RC-equivalent patterns other than self-complementary graphs, a classification of patterns into 'right' and 'left' is made in the following section viz., 3.2.2.

3.2. *Graph-theoretic approach for morphological studies.* Now we give below graph theoretic description of some of the morphological asymmetry mentioned in Section 2, which with the help of results of Section 3.1 is used to test various statistical hypotheses on the appearance of different structures in Section 4.

3.2.1. Let us consider *Euphorbia antiquorum* and *E. verticillata* discussed in Sections 2.3 and 2.4. These can in general be described as follows. There are  $n$  rows of spines spiralling either to the right or left and at a branching point there are  $n$  buds and each bud may or may not develop into a full branch again. First of all one is interested in the total number of patterns and the various possible plant structures. For this purpose let us construct a graph whose vertices  $a_0, a_1, \dots, a_{n-1}$

TABLE 14. PATTERNS AND NUMBERS OF EQUIVALENT NUMBERS

<b>PATTERN = P</b>			<i>n</i> = 3
<b>REFERENCE CODE = R</b>	$C_{3,0}$	$C_{3,1}$	
<b>NUMBER OF EQUIVALENT MEMBERS = P(n)</b>	1	3	

<b>P</b>					<i>n</i> = 4
<b>R</b>	$C_{4,0}$	$C_{4,1}$	$C_{4,2}^I$	$*C_{4,2}^{II}$	
<b>P(n)</b>	1	4	4	2	

<b>P</b>					<i>n</i> = 5
<b>R</b>	$C_{5,0}$	$C_{5,1}$	$C_{5,2}^I$	$C_{5,2}^{II}$	
<b>P(n)</b>	1	5	5	5	

<b>P</b>						<i>n</i> = 6
<b>R</b>	$C_{6,0}$	$C_{6,1}$	$C_{6,2}^I$	$C_{6,2}^{II}$	$*C_{6,2}^{III}$	
<b>P(n)</b>	1	6	8	6	3	

<b>P</b>					<i>n</i> = 6
<b>R</b>	$*C_{6,3}^I$	$*C_{6,3}^{II}$	$*C_{6,3}^{III}$	$*C_{6,3}^{IV}$	
<b>P(n)</b>	6	6	6	2	

### BILATERAL SYMMETRY IN PLANT ORGANS

represent the  $n$  interrow sites of the  $n$  buds which are circular at a branching point. Place an edge  $(a_i, a_{i+1}) = e_i$  if and only if the bud between the sides  $a_i$  and  $a_{i+1}$  develops into a full branch. Now it is clear that all possible structures of the plant correspond to the restricted random graphs discussed in Section 3.1. Hence if we assume that all possible structures have an equal probability of appearance, then the probability that a particular structure with reference to code  $C_{n,m}^i$  appears, when a single structure is observed is given by the number of members in its equivalence class divided by  $2^n$ . Tables of the required patterns and numbers are given in Section 3.1 for  $n = 3, 4, 5, 6$ .

It may be noted that if a bud has several possible states of development (which need not be measurable on an interval scale but only can be identified) which can be labelled by numbers  $1, 2, \dots, s$ , then any structure of the plant corresponds to a polygon of  $n$  sides in which a side is coloured  $j$  where  $j$  is one of  $s$  colours depending on the state of development. It may be of use to have tables for these patterns and their probabilities of appearance.

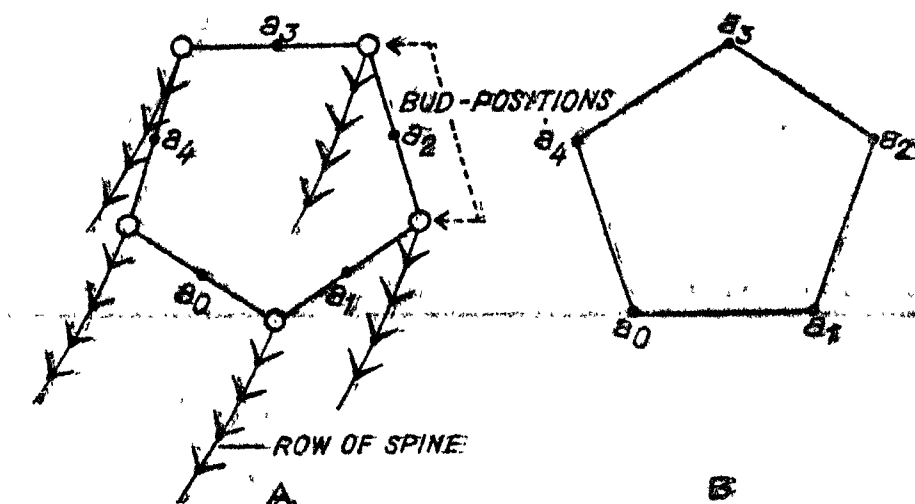


Fig. 1K

3.2.2. Here we shall consider the arrangement of the perianth lobes of the areca fruits. As described in Section 2.8, each of these flowers has six perianths. On a fruit the two ends of a perianth lobe may be exposed, or only one end is exposed while the other is overlapped by an adjacent perianth, or else both the ends may be enclosed by the two neighbouring perianths. To understand the total number of patterns of development, etc., we proceed as follows:

Consider the middle points of the perianths of a fruit. Let us construct a graph whose six vertices  $a_0, a_1, a_2, a_3, a_4, a_5$  represent the six mid-points of the six perianths. Also choose a direction of orientation around the fruit, say, clockwise. An edge  $(a_i, a_{i+1}) = e_i$  appears in the graph if and only if in the clockwise direction of movement the second end of the perianth whose mid-point is  $a_i$  is above the first end of the perianth corresponding to  $a_{i+1}$ . But the direction of orientation is arbitrary and

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or without insisting on the direction of orientation let us construct the graph. It is, for a given fruit we follow either clockwise or counter-clockwise direction for different fruits different directions of orientation can be used to draw the graph. Making the counting of structures independent of the direction of orientation brings us to consider two complementary patterns to be equivalent. Hence the number of distinct structures will be the number of RC-equivalent patterns studied in Section 2. As an example consider the following flower :

Example 5 : The two RC equivalent patterns arise because of two different orientations of the same flower in Fig. 12A.

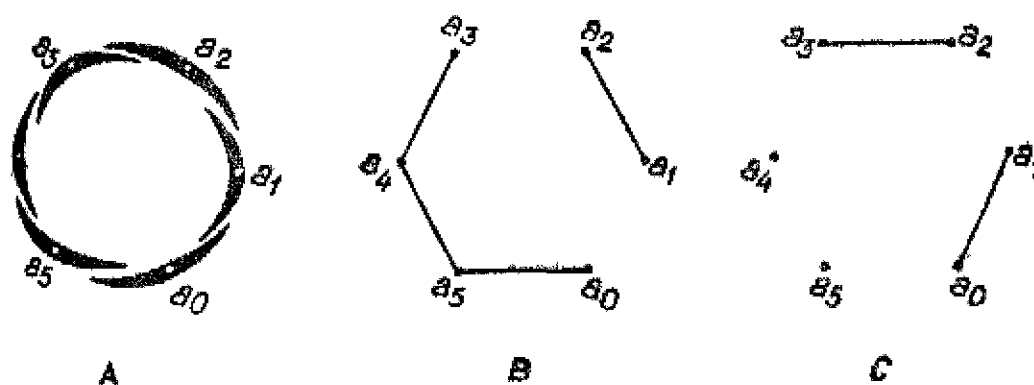


Fig. 12

TABLE 15. TABLE OF RC-EQUIVALENT PATTERNS AND MEMBERS FOR  $n = 5$

reference code	$C_{a-0}$	$C_{a-1}$	$C_{a-2}$	$C_{a-3}$	I	I	II	II	III	III
					$C_{a-2}$	$C_{a-4}$	$C_{a-4}$	$C_{a-2}$	$C_{a-2}$	$C_{a-4}$
number of equivalent members	1	1	4	4	4	8	6	6	3	3
reference code	I		II		III		IV			
	$*C_{a-2}$		$*C_{a-2}$		$*C_a$		$*C_{a-2}$			
number of equivalent members	4		6		6		2			

TABLE 16. LEFT, RIGHT AND NEUTRAL PATTERNS AND PROBABILITIES

pattern : classification	right			left			neutral
reference code	I			I			I
	$C_{a-1}$	$C_{a-1}$	$C_{a-2}$	$C_{a-1}$	$C_{a-1}$	$C_{a-2}$	$C_{a-1}$
	II	III	II	II	III	III	IV
	$C_{a-1}$	$C_{a-2}$	$C_{a-1}$	$C_{a-1}$	$C_{a-1}$	$C_{a-2}$	$C_{a-1}$
proportional probabilities	28			28			8

4 STATISTICAL ANALYSIS

In this section data on the morphology of various plant organs described under 2 are put to statistical analysis based on the theoretical results of Section 3. The tests are mainly to see whether a structure appears at random in nature, and on inter-relationship of various organs of plants with regard to twisting (or coiling) structure.

## BILATERAL SYMMETRY IN PLANT ORGANS

*Floral asymmetry in Malvaceae.* The null hypothesis taken is that the left- and right-handed flowers in each of the 34 species of Malvaceae is a statistic is  $\frac{(L-R)^2}{(L+R)}$  which follows  $\chi^2$  with 33 d.f. under null hypothesis.

Of the 34 species, 19 have excess left-handed flowers, and of these, the  $\chi^2$  value for only three species shows a significant difference from equality. None of the remaining excess right-handed shows a significant difference. The  $\chi^2$  value for the population shows a significant difference from the expected even though the lefts form only 50.62 percent of the total flowers. This significance is due mainly by the figures for *Hibiscus rosasinensis* and *Abutilon indicum*. The species alone accounts for 33.27 per cent of the total flowers studied, and the  $\chi^2$  value (20.0263) for this species largely affects the entire population, leading to an excess for the lefts. Ignoring this species, equality may be expected for the other species. Since the excess of lefts over rights is persisting in the case of *Hibiscus* even with large samples, and during different seasons, this peculiarity should be investigated.

*Floral asymmetry in Bombacaceae.* Of the 41,470 flowers from the 13 trees examined, 51.07 per cent were left-handed. But the difference between the kinds of flowers is not statistically significant, the  $\chi^2$  value with 12 d.f. to be 3.7582. However, the figures for *Bombax ceiba* show that it need significantly an excess of left-handed flowers like *Hibiscus* (Davis, 1966).

The data furnished in Tables 1 and 2 relating to the types of flowers in several species of Malvaceae and Bombacaceae discussed under the preceding two sub-headings. In the recording of the individual flowers was not maintained in a systematic order which would have enabled to find out whether the time series would follow a Bernoulli sequence, the lefts and rights being distributed randomly. The efficiency seems magnified when the data under Tables 10 and 11 are examined, while admitting that the data on floral asymmetry should have been more complete. We do not consider that the detailed data would have shown a significant departure from what one expects in a Bernoulli sequence of trials. First, the data in Tables 1 and 2 relate to the arrangement of petals in the flowers of *Millettia*, while those in Tables 10 and 11 relate to the arrangement of petals in *Millettia* and the rolling of the immature laminae in two plants belonging to different families. The parts of a flower and those of a leaf need not necessarily be correlated phenomena. Further, from one of the species mentioned under *Bombax ceiba*, the kind of twisting of flowers was recorded in the order of the several flower-bearing shoots. The data were plotted on a control chart showing the proportions of the lefts. The control chart suggested that in the population sampled, the lefts and rights were about in equal numbers on each tree (Davis and Kundu, 1965). In addition, all the flowers that were examined on *Bombax ceiba* trees were examined during one season, and their

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twisting recorded. It was found that the lefts and rights were produced more or less in a 1:1 proportion throughout the blooming period (Davis, 1966). Thus, the nature of the data in Tables 1 and 2 seems to be unique.

3.3. *Euphorbia antiquorum*. Under the null hypothesis it is assumed that there is no dependence as regards the twisting between the main stem and off-shoots. Hence the following Table 17 gives the observed and expected value in a  $2 \times 3$  table of main stem (L and R) against off-shoots (L, R and N). The symbol N denotes the neutral off-shoots which did not exhibit any twisting.

TABLE 17

main stem		off-shoots			total
		L	R	N	
left	observed	243	72	26	341
	expected	104.21	129.37	27.42	
right	observed	86	145	20	231
	expected	124.79	87.63	18.58	
Total		309	217	46	572

$\chi^2 = 18.76115 + 25.43766 + 0.07381 + 27.69520 + 37.55056 + 0.10900 = 109.62741$   
i.e. the  $\chi^2$  value is very highly significant both at 5% and 1% levels, which clearly shows the dependence of the off-shoots on the main stem with regard to the screwing. Similar values for the data relating to the 4-winged stems and 3-winged stems as given in Table 6 were calculated and in each case the  $\chi^2$  value turns to be highly significant even at the 1 per cent level as shown below :

$$4\text{-winged off-shoots } \chi^2 = 71.314$$

$$3\text{-winged off-shoots } \chi^2 = 147.984$$

As may be seen below, with the limited data obtained on *Euphorbia nerifolia*, no serious resemblance of the main stem and their off-shoots was noticed with regard to the direction of twisting.

4.4. *Euphorbia nerifolia*. As has been mentioned in Section 3.2, the possible structures of this species with 5 buds correspond to Restricted Random Graphs on 5 vertices (Fig. 11). Table 18 gives the observed data and expected frequencies under null hypothesis that all structures are equally likely.

We shall test the hypothesis that there is dependency of the branches on the mainshoot with respect to twisting by exact treatment. The conditional probability distribution of the above table is 284!298!216!230!/514!174!124!110!106! This is cumbersome to evaluate and hence we use approximate  $\chi^2$  test using Yates's corrections.

$$\chi^2 = \frac{514(174 \cdot 106 - 124 \cdot 110) - \frac{1}{2} 514^2}{298 \cdot 216 \cdot 230 \cdot 284} = 0.005559$$

## BILATERAL SYMMETRY IN PLANT ORGANS

TABLE 18. *EUPHORBIA NERIIFOLIA*: NO. OF PLANTS WITH GIVEN NUMBER OF OFF-SHOOTS

no. of off-shoots	no. of plants	expected frequency
0	16	7.594
1	80	37.970
2	52	75.940
3	54	75.940
4	30	37.970
5	11	7.594
total	243	243.008

$\chi^2$  observed is 12.03. The upper 5% value of  $\chi^2$  with 5 degrees of freedom is 11.1 and is hence significant. Thus, not all structures are equally likely for this species.

TABLE 19. *EUPHORBIA NERIIFOLIA*: LEFT-AND RIGHT-TWISTING PLANTS

no. of branches	left	expected frequency	right	expected frequency
0	9	4.218	5	3.374
1	41	21.090	39	16.872
2	36	42.180	22	33.734
3	33	42.180	18	33.734
4	16	21.090	10	16.872
5	6	4.218	5	3.374
total	135	134.976	108	107.960

1. Among the plants twisting to the left,  $\chi^2$  observed value is 32.21 and is significant enough to disprove the hypothesis that the number of branches is random or that all possible structures are equally likely.
2. Among plants twisting to the right,  $\chi^2$  observed value is 85.92 which is highly significant. Thus the data show that all structures are not equally likely.

For the same species, Table 20 contains data on plants with 5 and 6 buds observed at Khândwa, Madhya Pradesh.

TABLE 20. *EUPHORBIA NERIIFOLIA*: RELATION BETWEEN MAIN STEM AND OFF-SHOOTS

main stem	off-shoots		total
	left	right	
left	174	124	298
right	110	106	216
total	284	230	514

Table value at 5% level of  $\chi^2$  with 1 degree of freedom is 3.85 and hence the observed  $\chi^2$  is not significant. Hence we cannot reject the hypothesis that the main stem and branches twist independently.



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4.5. *Linum usitatissimum* With *Linum usitatissimum*, no clear picture can be formed as to the dependence of the foliar spiral of the off shoots with that of the primary stem. There is, however, a tendency for the first order off-shoots to show a preference to follow the foliar spiral of the primary stem. The second order off-shoots do not exhibit even this degree of affinity either with the first order off-shoots or with the primary stem.

4.6. *Scindapsus officinalis*. A perusal of the data given in Table 11 suggests that in the case of convolute leaves, there is a tendency for a leaf with left-handed convolution to be followed or preceded by one with right-handed convolution. To verify this, the type of each leaf in relation to its immediate older one was determined. The data are presented in Table 21.

TABLE 21. *SCINDAPSUS OFFICINALIS*: PTYXIS OF LAMINA

first leaf	second leaf			total
	left	right	involute	
left	20	155	44	219
right	150	21	34	205
involute	47	16	90	153
total	217	192	168	577

The hypothesis that the ptyxis of the first leaf and that of the second are statistically independent is rejected since the  $\chi^2$  value with 1 d.f. turns out to be 330.80. Therefore a left-handed lamina is generally followed or preceded by a right-handed one. However, in the case of involution, there is a greater chance for a leaf to be an involute if the immediate older one is already an involute. Data relating to the involutes were tested to see whether the involutes followed/preceded by a left-handed convolution were greater than those followed/preceded by a right-hander. It was found that the LI (left involute) or IL were occurring more frequently than the RI or IR, and statistically significantly. An involute leaf followed by another involute is significantly more than a left- or right-convolute leaf followed by an involute.

The state of the leaves of *Scindapsus officinalis* can also be represented by vertices 1, 2, ...,  $n$  on a line. Then join  $i$  to  $i+1$  by an edge if  $i$  and  $i+1$  are of different types of convolutions. Assuming that the convolution of a leaf is independent of the preceding or succeeding one, the null hypothesis becomes that all possible restricted graphs on these  $n$  labelled vertices on a line are equally likely and hence for a given graph the probability of its appearance can be evaluated. This work is deferred to a later paper.

4.7. *Arrangement of palm perianth*. Here let us consider the 316 fruits of *Areca catechu*. The possible arrangements of the six perianths are shown in Fig. 13 which give rise to the Restricted Random Graphs on six vertices described in 3.2.2.

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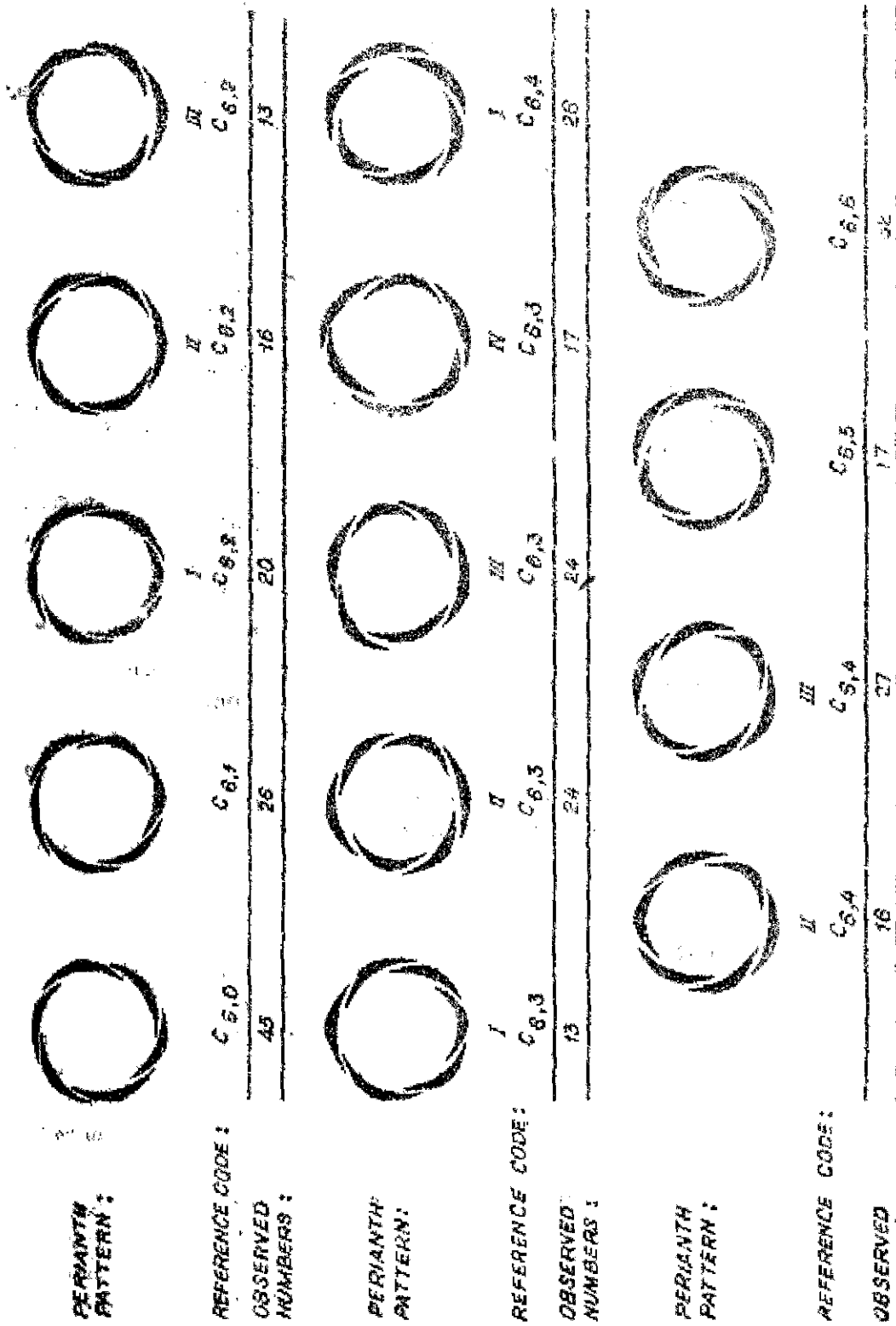


Fig. 14. The possible arrangements of the six perianth lobes in *Arabis caerulea*.

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Under the hypothesis that no specific pattern is preferred by Nature we obtain expected numbers of observations as follows :

$C_{0,0}$ and $C_{5,5}$	4.83 each
$C_{0,1}$ , $C_{1,2}$ , $C_{2,3}$	} 25.98 each
$C_{1,2}$ , $C_{2,3}$ , $C_{3,4}$ , $C_{4,5}$	
$C_{2,4}$ , $C_{3,5}$ , $C_{4,5}$	
$C_{0,2}$ and $C_{3,3}$	14.49 each
$C_{0,3}$	9.66

The  $\chi^2$  value computed as (observed—expected)<sup>2</sup>/expected summed over all is 510.39 which is quite significant at 5% level compared to (22.36) the  $\chi^2$  with 13 degrees of freedom. Hence in the course of evolution of perianths, in structures are preferred by Nature. In another species of *Areca* (*A. triandra*) it has only 3.7 per cent fruits under the  $C_{0,0}$  and  $C_{5,5}$  perianth-combinations (table 12), all patterns may occur as per expectation which would mean that no particular pattern is preferred by Nature. On the other hand, in *Psychosperma macaroti*, with only a single stray fruit under the patterns  $C_{0,0}$  and  $C_{5,5}$ , a very strong preference for certain perianth-patterns is noticed.

However, proceeding further according to the left, right and neutral classifications of structure as shown in 3.2.2, the observed numbers of patterns are respectively 141, 142 and 30 and the expected frequencies are 138.25, 138.25 and 10.75 correspondingly.

The computed  $\chi^2$  value is 5.79 and the significant tabulated value for  $\chi^2$  being 5.99 at 5% we can reject the hypothesis that the occurrence of structures is in accordance with the above left, right and neutral classifications.

## 5. SOME RESULTS

Collection and analysis of data of even what appears to be very ordinary phenomena such as bilateral symmetry in plants are not without desirable results. Numerical methods, according to Sokal and Sneath (1963), may open up a wide field in the exact measurement of evolutionary rates and may provide a more critical approach to phylogenetic problems. Encouragingly, a great awareness for evolving numerical methods even in taxonomy is fast developing.

5.1. When we study the relationship of the foliar arrangement of different organs, we find considerable variation between species even very closely related to each other. Thus, the foliar spirals of the trunk and first-order off shoots in *Prunus cerasus* are positively associated, and in *P. avium* they are negatively associated. But in *Prunus domestica*, no significant dependence was observed (Davis, 1969a). Evolutionary trait may also be attributable to certain situations concerning the aestivation of floral whorls, especially the petals and sepals. While in families like Malvaceae and Bombacaceae, the left- and right-handed flowers (according to aestivation

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petals) are randomly distributed, in some species of *Arenga* and *Caryota* where flowers are arranged in clusters of three (a female flower is surrounded by two males on opposite sides), a clear pattern is present. The two male flowers in a cluster have their sepals arranged in mirror image forms. The same is the situation with the males of all clusters. The female flower may either be a left-hander or a right-hander, but in a left-spiralled spike, majority of the female flowers are right-spiralled, and vice versa in a right-spiralled spike as evidenced from data given in Table 22 relating to *Caryota mitis* (Mitra, 1968).

TABLE 22. *CARYOTA MITIS*: AESTIVATION OF SEPALS OF FLOWER-CLUSTERS

spirality of spike	aestivation of flowers			total
	male	female	male	
	RLL		RRL	
left	6		50	56
"	17		39	56
"	13		42	55
	36		131	167
right	44		17	61
"	33		8	41
"	46		10	56
	123		35	158
Total	159		166	325

5.2: While plants with a particular type of morphological structures are endowed with greater productive capacity than those having different structures has been demonstrated with the coconut where the leaves are arranged in five spirals turning either clockwise or counter-clockwise in a palm. The left-spiralled palms in certain plantations in India, the Pacific Is. and Tanzania produce more fruits than the right-spiralled ones (Davis, 1962b, 1963, 1964c) even though the foliar asymmetry is not genetically determined. With *Vigna sinensis* which always grows counter-clockwise, the reversed vines produced more fruits than the normal ones (Reber, 1960, 1964; Davis and Mitra, 1968).

We thank Mr. S. K. De, our Artist for the pen and ink drawings.

## REFERENCES

- BOE, C. (1962): *Theory of Graphs and its Applications*. Methuen & Co. Ltd.
- DAVIS, T. A. (1962a): The non-inheritance of asymmetry in *Cocos nucifera* L. *J. Genet.*, **58**, 42-50.
- (1962b): Asymmetry and yield in *Cocos nucifera* L. *Experientia*, **18**, 321.
- (1963): The dependence of yield on asymmetry in coconut palms. *J. Genet.*, **58**, 186-215.
- (1964a). Possible geo-physical influences on asymmetry in coconut and other plants; *FAO Tech. Working Party on Coconut*, Colombo, 2, 59-69.

## SANKHYĀ : THE INDIAN JOURNAL OF STATISTICS : SERIES B

- (1964b). Aestivation in Malvaceae. *Nature*, 201, 515-516.
- (1964c): Leaf spiral and yield in coconut. *Nature*, 204, 496-497.
- (1966): Floral structure and stamens in *Bombax ceiba* L. *J. Genet.*, 59, 294-328.
- (1967): Stamen number and pollen size in levo- and dextro-rotatory flowers of Bombacaceae. *Rev. Palaeobotan. Palynol.*, 3, 133-139.
- (1968). The spirality of main stem and its relationship to that of off-shoots in *Euphorbia antiquorum* Linn. *J. Bombay Nat. Hist. Soc.*, 65, 262-286.
- (1969a): Relationship between the foliar arrangements of the trunk and off-shoots in four temperate fruit trees. *Labdev. J. Sci. Tech.*, 7B, 31-34.
- (1969b): Aestivation of coconut flowers. *Ceylon Cocan. Quart.*, 26, 123-130.
- (1970): Pre-foliation in *Scindapsus officinalis* Schott. *J. Bombay Nat. Hist. Soc.* 67, 250-258.
- (1971a): Right-handed, left-handed and neutral palms. *Principes, J. Palm Soc.*, 15, 63-68.
- (1971b): On the unequal halves of palm leaves. *Sci. & Cult.*, 37, 206-209.
- 1978, T. A. and GHOSH, R. B. (1970): Comparative morphology of *Bombax albidum* and *B. ceiba*. *Phytomorphology*, 20, 339-350.
- 1978, T. A. and GHOSH, S. S. (1969): Foliar spiral and ptyxis in *Cordyline rubra* Huef. ex Kunth. *Proc. Nat. Inst. Sci. of India*, 35, 267-272.
- 1978, T. A., GHOSH, S. S. and MITRA, A. (1971): Asymmetry in palm leaves. *J. Bombay Nat. Hist. Soc.* 68, 204-231.
- 1978, T. A. and GHOSH, K. K. (1965): Variation in the floral organs of *Hibiscus rosasinensis* L. *J. Ind. Bot. Soc.*, 45, 30-43.
- 1978, T. A. and KUNDU, A. (1965): Floral structure and stamens in *Ociba pentandra* L. Gaertn. *J. Bombay Nat. Hist. Soc.*, 62, 394-411.
- 1978, T. A. and KUNDU, A. (1966): Aestivation of perianths of *Areca catechu* Linn. fruits. *J. Bombay Nat. Hist. Soc.*, 63, 270-282.
- 1978, T. A. and MITRA, A. (1968): Direction of stem-twist and fruit-yield in *Vigna sinensis*. 56th session, *Indian Science Cong.*, Varanasi, Abst. III, 569.
- 1978, T. A. and SELVARAJ, C. (1964): Floral asymmetry in Malvaceae. *J. Bombay Nat. Hist. Soc.*, 61, 402-409.
- BOOBER, J. D. (1872): Flora of British India. VI. L. Reeve & Co. Ltd., Kent.
- LOFLEN, L. (1965): Biology and cultivation of *Aloe polyphylla*. *J. Roy. Hort. Soc.*, 90, 250-256.
- LUCMOHAN, P. A. (1891): Enumerate the necklaces with  $n$  beads each of which may have any of  $c$  colours. *Proc. Lodon Math. Soc.*, 23, 303-315.
- MITRA, A. (1968): Levo- and dextro-rotatory situations in plants and their relationship to fruit-production Ph.D. thesis, Calcutta University.
- HITCH, T. (1911): Right and left-handed coconut trees. *Ann. Royal Bot. Gard., Peradeniya*, 5, 538-539.
- HILYA, G. and others (1962): Applied combinatorial mathematics. Edited by C. F. Beckenbach. John Wiley & Sons.
- IMANUJACHARYULU, C. (1966): On colouring a polygon and restricted random graphs. *Theorie des graphes*, Rome, 333-337.
- LEBER, G. (1960) Reversed bean vines. *Castanea*, 25, 122-124.
- LEBER, G. (1964): Reversed bean vines. *J. Genet.*, 59, 37-40.
- LENDLE, A. B. (1959): The classification of flowering plants. II. Dicotyledons. University Press, Cambridge.
- LENNOTT, E. W. (1937): Morphology as a dynamic science. *Science*, 85, 61-65.
- MEKAL, R. R. and SNEATH, P. H. A. (1963): Principles of numerical taxonomy. W. H. Freeman and Co., London.
- SAN OYE (1926): Sur la torsion des troncs d'arres. *Bull. Soc., Botanique*, 11, 270-288.

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## A '2' CONFOUNDED DESIGN' FOR A MANURIAL EXPERIMENT ON COCONUT

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**SUMMARY.** A micronutrient-manurial experiment on a factorial '2' confounded design' was conducted in 1953 on a 8-hectare coconut plantation at the Central Coconut Research Station, Kayangulam (South India) as an attempt to control the Root (wilt) disease affecting the palms. The micro-nutrients Boron, Copper, Manganese, Iron, Molybdenum, Zinc, as well as Magnesium. Data on the fruit- and morphological characters were recorded on the 384 experimental palms from the inception of the experiment. The fruit-yield data alone upto and inclusive of 1960 were considered for the Analysis of Variance and the results reported. After 1960, the micro-nutrients were administered directly to the palms in liquid form by a different method.

The analysis has revealed that the healthy palms did not show any significant response to the application of any of the micro-nutrients. But palms in the early stage of the Root (wilt) disease responded favourably to the treatment combination of Boron and Iron. However, when applied alone or in combination with Copper, Iron depressed the nut-yield in this category of palms significantly. Severely diseased palms responded very favourably with Magnesium and Molybdenum when applied individually.

### 1. INTRODUCTION

Root (wilt) is the most serious disease of the coconut palm in India affecting 10 per cent of the coconuts in Kerala which is roughly about seven per cent of the total (0.64 million hectares) grown throughout India, and is responsible for an annual loss of over ten million rupees. The disease appears to be very complex in nature though indications of its viral nature are becoming more clear (Menon, 1951; Menon and Nair, 1951; Menon and Shanta, 1962; Nagaraj and Menon, 1955; Nagaraj *et al.*, 1954; Radha and Menon, 1954; Shanta and Menon, 1960; Shanta *et al.*, 1961). On account of its unknown origin, the Root (wilt) disease may be compared with other similar major diseases of the coconut in other countries such as the Lethal Yellowing (or the Unknown Disease) in Central America and Jamaica; Kaincoope Disease in Togoland; Bronze Leaf Wilt of British Guiana, West Indies and Nigeria; and Cadang-Cadang of the Philippines. The Coconut Withering Disease making its first manifestation in two provinces of Ceylon may also fall under the above

### 2. HISTORY OF THE EXPERIMENT

At the Central Coconut Research Station, Kayangulam (South India) where the Root (wilt) disease of the coconut is being investigated, the effect of certain micro-nutrients in retarding the disease or preventing healthy palms from contacting the disease is being investigated. An experiment with six micro-nutrients: Boron (B), Copper (C), Manganese (D), Iron (E), Molybdenum (F), Zinc (G) and also Magnesium (A) was conducted at this research centre from 1953.

The design of the experiment chosen is '2' confounded design'. There are 384 experimental palms in the experiment which are spread over a 8-hectare plantation along with other coconut palms which are regarded as controls. All the palms received the same amount of macro-nutrients (Nitrogen, Phosphorus and Potash). Of the experimental

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palms, a third (128) were apparently healthy at the beginning of the experiment, another 128 palms were moderately diseased, and the remaining 128 palms showed severe disease symptoms. Most of the severely diseased palms included in the experiment were producing some fruits (nuts) and/or flower-bunches even in 1960, and their condition at the time of selection was presumably within the scope of recovery. The yearly mean numbers of nuts produced by the trees of the three categories during the pre-treatment period were : healthy palms 45.97 nuts, palms showing early stage of disease 27.68 nuts, and those showing severe disease symptoms 18.75 nuts. Figure 1 explains this further.

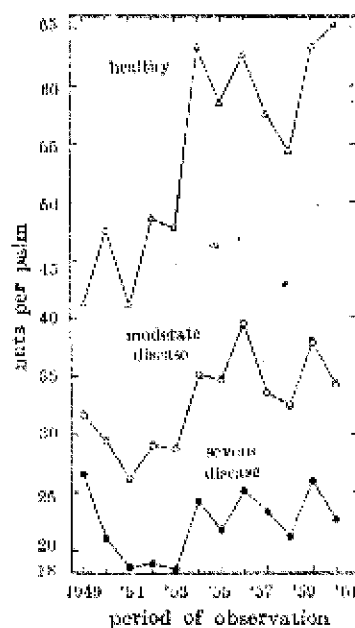


Fig. 1

*Blocks and plots* : There are 16 blocks under each category making a total of 48 blocks (vide Tables 2-4). Each block was divided into 8 plots (palms). Three blocks (one representing each category) comprising 24 palms may be regarded as one major block, and the trees of a major block are distributed more or less in one region. The 8-hectare experimental plantation consists of three almost contiguous fields as shown in Fig. 2. Field number one accommodated 3 major blocks comprising the first 24 healthy palms, 24 palms in early stage and 24 palms in late stage of disease.

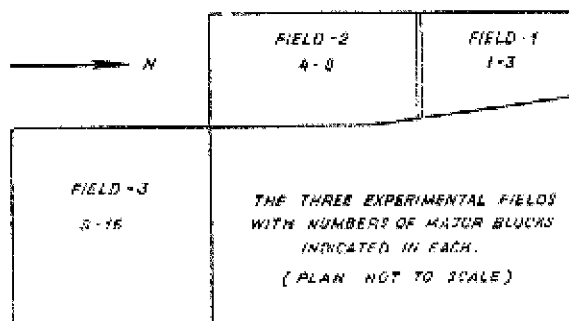


Fig. 2

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for blocks were distributed in field two, and the remaining 8 were distributed three. Thus, the 48 blocks comprising the 384 plots do not form one composite on. Though the division of blocks within a field was arbitrary, differences between fields; and thus between blocks, were suspected on certain grounds such as soil and variety of palms, soil conditions, level of water table etc. In view of the unbalancing design was decided upon which is expected to eliminate the block-to-block variation and thereby eliminate the variation between fields.

The main treatments and all possible combinations (two to seven amount to 15, plus one no-treatment), and a particular treatment was made on a set of 12 plots (plots) of which one is healthy, another with moderate disease and the remaining 10 with severe disease. Securing very uniform experimental palms of the same age and size numbers was a difficult problem. Importance was, therefore, given to (1) uniformity of the condition of the palms (healthy or diseased) under each category, (2) the spacing between them (as far from each other as possible) so that the nutrients applied to a tree were least absorbed by the neighbouring palms. Even if the palms were planted with the maximum recommended spacing of 10m, there is still to be root competition between palms since many roots of adult palms measure 10 meters in length. Accordingly, sufficient consideration could not be given to the age of the palms, and they were from 15 to 65 years in 1953 as recorded in Table 1.

Table 1 gives details on the form and quantity of the manurial salts used and related amounts of micro-nutrient elements contained in them. These salts were applied in powder form in shallow basin trenches (diameter 2 metres) taken around the base of the stem and covered with a thin layer of soil. The application was made once a year every year when the heavy South-West monsoon was just over. The experimental palms as well as the non-experimental ones standing in the experimental area received a basal nutrient dose of 0.34 kg nitrogen as groundnut cake, 0.34 kg phosphoric acid as bonemeal and 0.68 kg of potash as murate of potash (KCl) per tree per year. The pH of the soil was generally acidic, becoming strongly acidic during

TABLE 1. TREATMENTS AND DOSES OF INDIVIDUAL MICRONUTRIENTS

Symbol	salts applied	dose per tree per year (gm)	quantity of micro-nutrient element present in the dose (gm)
A	Magnesium Sulphate ( $MgSO_4 \cdot 7H_2O$ )	454	45.4 (Magnesium)
B	Borax ( $Na_2B_4O_7 \cdot 10H_2O$ )	227	25.6 (Boron)
C	Copper Sulphate ( $CuSO_4 \cdot 5H_2O$ )	227	68.1 (Copper)
D	Manganese Sulphate ( $MnSO_4 \cdot 4H_2O$ )	227	55.8 (Manganese)
E	Ferrous Sulphate ( $FeSO_4 \cdot 7H_2O$ )	227	43.4 (Iron)
F	Ammonium Molybdate $(NH_4)_6Mo_7O_{24} \cdot 4H_2O$	2	1.0 (Molybdenum)
G	Zinc Sulphate ( $ZnSO_4 \cdot 7H_2O$ )	227	51.3 (Zinc)



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monsoon, and to ameliorate this condition, about 100 kg of slaked lime per acre was spread over the soil and worked in with hand spades. In addition, a green-manure crop of sunn hemp was raised every year in these fields and at the proper time the entire plants were ploughed into the soil *in situ*. The first application of the micro-nutrients was made in September 1953.

## 3. OBSERVATIONS RECORDED

Data on the production of nuts as well as female flowers were available on these experimental palms from 1949 onwards. In addition, data on the emergence and shedding of leaves, opening of spadles, measurements of leaves and leaflets as well as the numbers of leaflets, female flowers, nuts shed prematurely and those harvested as ripe ones, appearance and progress of disease symptoms as well as incidence of major pests were collected on these palms periodically from 1953. Colour sketches depicting the condition of their crowns were prepared at the time of first application of the micro-nutrients for later comparison.

In this paper data on the fruit-yield alone are considered, and that too, for a period upto and inclusive of 1960. After 1960, the micro-nutrients were administered directly into the palm as solution by a root-injection method (Davla *et al*, 1954) instead of applying them in the soil around the stem. The fruits produced by a palm have to be regarded as the ultimate criterion of the palm's response to a treatment, since the experiment was running for a fairly long period and since a great majority of the palms were in the productive stage. The author was in charge of this manurial experiment from its inception until 1960, and hence, the data relating to this period alone are considered in this paper.

## 4. PRESENTATION OF DATA

The fruit-yield data relating to the 384 palms for a 12-year period (1949-1960) are tabulated in Tables 2 to 4. This period has been split into a 6-year pre-treatment period and a 6-year post-treatment period. Since the first annual application of micro-nutrients was made in 1953, normally the years 1953 and 1954 should have been included under the post-treatment period. But the coconut palm is unique in effectively showing the benefit or adverse effect of a manurial treatment only after two years. A flower-primordium, which is most sensitive to a treatment, matures into a nut after about two years although during this two-year period a slight effect due to a higher or lower setting or shedding of the already developed flowers and young fruits may be noticeable.

Three palms gave no nuts at all during the 12 year and they were all diseased (late stage). Three healthy and three diseased palms died through lightning and disease between 1956 and 1959. For these trees the yield averages were based on the yields for the years before their deaths. The nuts were harvested 8 times every year, and partial yields in the year when a tree died were omitted. A few other trees only started producing fruits after 1949.

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TABLE 2. EFFECT OF MICRO-NUTRIENTS ON THE FRUIT YIELD OF COCONUT PALMS: *HEALTHY PALMS*

tree no.	age (1053)	spiral	treatment	pre-treatment yield					post-treatment yield						
				1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960
58	40	L	A	36	46	11	53	12	85	16	89	6	38	45	85
56	40	R	ABCDP	15	19	15	20	13	12	12	8	39	13	13	38
120	55	R	ABCEG	32	42	49	70	69	61	69	41	54	17	48	39
104	55	L	ADPFG	108	81	61	121	59	117	91	65	65	80	74	63
55	55	L	BDE	66	77	74	83	74	97	89	81	75	67	72	58
79	55	R	BFG	44	14	19	21	38	32	28	25	21	7	5	6
54	45	R	CEP	64	56	59	69	61	84	70	79	61	67	77	62
104	45	L	CDG	88	109	92	129	107	114	104	121	116	113	132	94
56	45	R	B	63	67	90	45	61	94	57	67	101	17	113	36
19	40	R	ADP	76	46	43	66	50	47	49	67	62	56	64	53
116	55	R	AFG	54	68	63	57	43	71	52	43	66	36	62	31
62	40	L	CEG	38	17	43	39	35	59	55	38	43	1	37	42
33	45	R	CEP	60	71	29	94	54	115	26	101	3	134	35	121
33	45	R	ABCDEF	35	65	32	82	63	80	69	18	61	31	35	67
63	40	L	ABCEP	27	74	13	94	44	63	103	36	69	52	67	69
73	50	L	BDPFG	89	53	65	79	63	60	74	61	79	39	79	57
66	45	R	AB	57	46	52	63	62	61	64	44	63	68	18	65
68	45	R	DE	17	63	32	79	80	95	79	91	63	62	40	180
81	55	R	FG	65	69	44	73	56	73	66	72	56	71	61	67
48	45	R	ACEG	75	56	83	55	107	98	100	88	109	55	32	71
87	50	L	ACDP	81	59	64	80	78	87	79	62	74	39	117	62
31	40	R	BDDG	49	64	50	75	65	93	63	67	72	78	79	89
49	50	L	BCEP	55	17	53	61	56	60	56	69	68	75	71	63
3	30	L	ABDEPFG	22	22	27	26	29	42	32	49	62	14	34	45
116	40	R	C	11	65	27	64	11	26	71	39	56	67	69	72
49	25	R	ADG	63	14	46	29	21	39	104	69	89	62	69	25
96	55	R	AEP	78	63	81	69	64	99	72	73	59	57	67	100
132	20	R	BDP	nil	nil	nil	6	30	82	14	78	29	81	69	65
69	50	L	BGG	73	74	57	89	115	111	109	88	89	91	92	132
63	25	R	ABCEDE	1	4	10	10	3	11	27	33	31	17	32	61
114	25	R	ABCEFG	nil	69	nil	7	7	25	25	41	22	6	15	23
100	50	R	CDPFG	43	54	49	36	25	60	51	69	53	63	66	48
46	40	R	AG	5	52	18	20	34	43	63	58	42	51	62	116
160	50	L	BE	61	64	46	64	32	62	39	41	17	59	17	68
109	45	R	CD	98	nil	85	86	nil	64	75	61	63	68	73	58
96	65	R	ABCE	38	67	34	66	74	64	63	73	51	56	29	28
118	45	R	ADP	18	19	39	31	69	65	41	82	63	37	62	66
91	65	R	BDEG	37	53	32	61	46	62	89	48	69	51	60	102
133	50	L	CEFG	38	19	57	49	53	73	78	67	72	49	69	61
90	65	R	ABCEPFG	34	45	50	44	47	48	77	73	63	68	52	47
270	50	R	D	42	36	95	56	57	114	48	92	77	63	81	52
161	50	L	ABE	30	29	11	53	26	47	37	41	43	61	21	69
132	50	L	BCE	69	43	18	52	64	94	46	101	65	67	78	75
123	55	L	ACG	91	72	84	98	148	111	115	117	99	127	126	168
179	45	L	EPG	39	47	49	51	68	86	67	73	60	55	78	68
164	50	L	ABPFG	76	81	59	65	87	66	82	65	102	94	82	118
174	50	R	ACDEP	23	77	36	75	65	104	92	89	68	57	77	65
105	50	L	BCDEG	37	20	28	36	26	30	35	42	33	32	31	40
109	55	L	E	76	75	51	69	63	83	77	84	64	81	67	85
110	50	L	ABD	6	88	31	69	71	69	64	71	44	91	57	138
168	60	L	ACP	82	75	49	69	72	77	37	54	62	66	76	65
102	80	R	BGG	34	44	34	45	26	41	37	54	44	24	69	66
105	55	R	DTG	11	22	9	21	13	30	29	40	29	32	67	25
115	45	L	ACDDEG	2	14	12	23	15	31	33	43	26	50	49	62
108	55	L	ABEFG	17	43	21	13	41	52	26	67	7	69	46	81
106	30	L	BCDEF	19	29	9	18	22	31	24	39	26	62	51	54
102	50	R	AE	12	44	28	15	28	72	28	36	64	55	46	67
130	45	R	BG	9	12	114	8	23	31	24	40	38	37	42	69
100	25	L	CE	nil	nil	nil	53	110	46	127	81	86	173	99	160
101	25	L	ABCD	67	nil	nil	61	112	88	136	123	143	112	135	175
119	60	L	BDEP	66	50	51	69	39	72	64	79	63	81	69	74
116	50	L	CEFG	30	15	13	17	8	29	8	15	36	26	23	36
127	40	R	ADEG	40	32	31	60	66	67	66	52	46	47	62	64
114	35	L	ABCEFG	4	36	22	24	31	21	23	42	79	35	85	46

B-B; C-Cu; D-Mn; E-Fe; F-Mo; G-Zn.

having left handed foliar spiral

having right handed foliar spiral

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TABLE 2. EFFECT OF MICRO-NUTRIENTS ON THE FRUIT YIELD OF COCONUT PALMS: HEALTHY PALMS—contd.

plot no.	tree no.	age (1953)	spiral	treatment	pre-treatment yield						post-treatment yield					
					1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960
9	408	40	L	AB	82	51	31	28	48	58	47	43	58	20	Died	
	358	60	L	BD	45	48	50	44	43	55	68	78	67	61	49	61
	178	55	R	CF	8	21	17	28	11	34	26	38	32	25	58	16
	260	45	R	ABCG	33	19	25	28	17	22	24	50	24	40	31	26
	288	65	L	BCDFG	44	49	30	34	30	31	36	44	38	38	36	31
	421	45	L	ADEG	46	64	30	64	35	79	22	110	10	89	31	58
	404	50	R	CDEG	61	32	26	38	37	36	39	28	28	17	Died	
	276	40	L	ABCDEFF	15	41	35	73	50	56	77	80	69	69	63	47
	323	55	R	AC	40	68	56	24	52	41	43	70	57	65	75	60
	190	50	R	DC	52	56	38	64	62	50	30	44	40	43	54	51
	345	45	L	EF	37	35	34	27	44	48	57	65	40	64	51	48
10	463	35	L	BCDFG	4	4	12	13	33	17	129	78	115	96	142	102
	181	60	L	BCDE	65	58	71	45	70	68	72	68	46	46	78	62
	307	25	R	ABDF	43	28	19	29	34	49	42	54	11	14	16	3
	484	50	L	ABEG	78	50	61	43	70	55	68	69	65	65	50	54
	344	40	R	ACDFEG	36	74	60	32	50	68	65	50	64	61	62	nil
	388	50	R	AD	13	58	35	nil	nil	46	38	47	21	66	34	73
	388	50	L	CC	37	26	20	23	22	40	27	47	23	34	42	27
	273	30	R	DE	13	26	40	14	37	50	56	65	69	48	91	61
	249	25	R	ABCF	nil	nil	nil	nil	1	13	35	35	27	27	49	68
	392	40	R	CDEF	12	25	15	26	11	64	30	60	32	37	90	69
	282	60	L	ABFG	0	3	7	42	41	34	53	53	43	45	39	21
	249	50	R	BDFG	56	52	35	24	50	20	37	11	Died			
	264	20	L	ABCDEFGHI	11	16	14	26	31	109	70	50	107	67	109	74
	289	35	L	DC	48	25	41	43	45	112	63	81	65	21	69	54
	299	35	R	EG	17	36	55	41	42	63	70	91	83	75	93	62
	282	35	L	EF	19	24	37	47	53	69	62	73	65	60	60	73
	392	60	L	ACDE	32	36	20	46	45	53	64	51	44	50	38	21
	261	45	R	ACFG	37	68	56	27	68	101	35	109	55	56	84	81
	15	50	L	ABEF	49	79	70	64	71	83	83	78	78	67	161	76
	169	55	R	ABDG	21	40	31	38	37	60	38	31	50	43	49	44
	298	45	L	BCDFEG	7	12	21	nil	9	32	35	6	41	1	32	17
	362	60	L	F	40	56	55	44	62	68	52	50	62	51	64	69
	367	50	R	ACE	32	31	15	23	26	53	39	45	42	33	56	47
	359	65	R	ABG	40	59	32	42	36	54	35	42	44	29	54	36
	361	60	R	DEG	63	63	45	61	57	70	54	60	64	68	55	41
	354	55	R	BCD	74	40	35	55	62	37	65	108	40	80	69	62
	110	30	L	BCDFC	nil	nil	nil	20	5	100	95	35	94	13	91	72
	96	55	R	ACDFG	17	35	48	23	47	67	63	60	78	39	32	85
	365	55	R	ABDEI	nil	nil	nil	11	31	57	38	63	45	69	62	57
	241	35	L	G	nil	nil	nil	nil	nil	12	21	38	56	40	52	59
	241	45	R	ACD	56	100	94	61	98	129	89	95	104	76	106	70
	218	45	R	DEF	37	53	48	48	44	46	50	45	40	40	46	48
	188	25	R	BCF	1	22	32	34	17	30	39	35	1	4	nil	nil
	186	25	R	ABF	4	6	15	28	41	29	20	34	25	28	23	24
	4	55	L	ACDFG	44	39	33	29	37	41	45	46	38	30	47	35
	192	25	L	ABDEG	nil	nil	nil	30	35	69	69	107	102	95	112	85
	199	50	R	BCDFG	39	52	32	28	21	29	36	40	45	47	51	34
	94	55	L	ABC	27	48	45	48	47	62	53	54	56	13	62	84
	125	30	R	ADF	42	63	65	40	36	72	67	37	74	33	65	60
	113	45	L	ABCDEFGHI	60	80	64	105	49	121	126	118	114	83	127	100
	70	30	L	ABC	6	36	15	46	65	101	80	87	66	77	86	121
	102	35	R	BDG	22	81	60	69	59	103	94	112	115	40	110	93
	105	25	L	BEF	8	62	16	89	35	64	80	64	76	108	78	89
	79	30	R	CDE	58	34	30	91	131	127	157	131	128	73	123	114
	126	40	R	CEG	63	71	62	47	54	78	75	62	62	68	84	75
	133	50	R	I	60	65	82	60	41	58	55	65	60	40	60	91
	44	45	L	ABDE	66	65	40	62	68	76	61	71	51	69	60	39
	48	30	R	BCFG	nil	nil	nil	nil	1	9	20	4	15	nil	nil	nil
	28	35	L	ABFG	34	71	14	60	31	84	69	105	42	80	85	86
	148	50	J	ACFE	55	63	41	62	52	64	76	71	84	89	90	103
	3	25	R	ACFG	66	65	40	45	59	65	54	40	33	32	40	nil
	136	50	L	DEFG	33	67	41	27	46	44	45	49	40	23	41	46
	141	45	R	BCDF	30	64	41	67	34	24	60	53	49	20	48	133

## MANURIAL EXPERIMENT ON COCONUT

TABLE 3. EFFECT OF MICRO-NUTRIENTS ON THE FRUIT YIELD OF COCONUT PALMS : DISEASND PALMS (Early Stage)

age (1953)	spiral	treatment	pre-treatment yield					post-treatment yield						
			1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960
45	L	A	11	8	13	31	39	24	42	51	38	63	43	49
40	R	ABCDEF	19	28	46	28	43	60	40	27	44	28	18	60
45	R	ABCEG	60	26	15	54	29	38	17	12	13	4	1	nil
50	R	ADBEFG	71	41	68	61	59	75	88	69	52	87	90	73
50	R	BDE	7	13	8	7	12	8	11	14	9	7	13	16
45	L	BFG	5	3	nil	nil	nil	nil	nil	nil	1	1	nil	nil
55	L	CDEF	50	39	37	40	32	52	44	41	34	31	26	25
40	R	CDG	49	29	13	31	21	44	38	37	38	22	35	35
55	R	B	9	17	12	16	18	31	15	5	13	7	13	nil
50	R	ADE	18	11	13	21	10	18	19	28	16	1	13	14
55	L	AFG	36	21	26	44	51	44	34	68	46	49	34	27
45	R	CEG	56	47	66	29	20	nil	4	3	3	nil	1	nil
45	L	CDF	12	73	18	62	52	18	117	21	58	45	39	37
40	L	ABCEP	16	5	22	11	9	16	27	27	18	26	32	17
55	R	ABCDG	34	24	17	20	38	35	23	35	25	25	16	16
45	L	BDDEFG	16	23	14	21	24	48	38	36	32	39	23	23
45	R	AB	12	24	21	27	4	53	11	28	31	17	14	20
45	R	DE	53	35	27	66	44	43	56	69	52	46	49	47
30	R	FG	26	28	13	26	30	41	36	38	29	31	32	31
45	R	ACEG	20	15	7	21	17	30	19	39	21	19	13	17
45	R	ACDF	77	66	31	89	101	81	110	84	126	45	133	39
45	R	BDEG	19	8	17	16	11	21	25	30	17	20	16	9
45	R	BDEF	39	31	12	32	10	37	33	11	11	2	6	2
50	L	ABDEFG	63	37	43	67	56	76	72	71	63	57	29	77
40	L	C	84	38	48	74	56	63	47	54	50	56	48	58
30	R	ADG	71	48	39	66	24	60	38	67	63	65	58	47
45	R	AEF	17	5	2	11	3	2	27	21	15	15	5	10
50	R	BDF	29	21	19	38	31	23	33	42	27	29	27	32
50	L	BEG	nil	5	10	nil	nil	2	1	2	8	nil	nil	nil
35	L	ABCDE	35	25	12	47	7	48	38	49	34	61	38	53
45	R	ABCEG	44	10	36	62	4	26	77	29	63	44	82	61
40	L	CDDEFG	43	21	31	45	15	35	63	41	37	57	50	64
40	R	AG	54	46	33	48	16	40	62	49	47	57	61	46
50	R	BF	13	22	11	46	29	41	36	14	40	16	47	16
45	L	CD	6	18	8	26	48	64	82	68	15	19	48	40
40	R	ABCE	36	13	13	30	22	20	28	23	27	31	34	68
60	L	ADBEF	24	20	18	8	34	33	29	20	52	26	48	40
40	L	BDEG	26	38	11	48	33	38	59	58	40	53	59	51
45	L	CEFG	99	82	73	77	78	79	48	49	37	23	32	25
50	L	ABCDDEFG	29	39	29	34	48	67	32	36	44	22	24	14
50	R	D	48	27	29	19	68	25	52	46	25	42	34	2
55	R	ADE	40	27	56	37	47	62	61	40	54	54	60	43
55	R	BEF	6	50	15	52	16	58	29	58	33	33	46	41
55	L	ACG	13	36	17	25	23	33	41	34	31	27	36	27
35	R	BFG	53	59	47	43	53	79	53	123	48	74	76	84
35	L	ABDEFG	20	24	29	31	27	49	33	37	32	37	25	35
50	L	ACDEF	11	29	26	19	24	29	5	22	11	15	24	13
50	R	BCDEFG	59	15	19	30	39	40	14	15	5	1	12	34
45	L	E	3	4	5	8	6	21	21	14	7	11	22	18
50	L	ABD	14	20	17	46	37	36	27	47	42	40	54	58
50	L	ACF	16	29	16	19	22	37	34	51	33	35	47	37
35	T	BCG	1	3	1	1	nil	17	21	29	51	49	56	62
50	L	DFG	19	40	12	34	43	62	18	62	62	2	60	47
50	L	ACDEG	31	44	33	25	33	44	39	43	21	62	32	46
55	L	ABEFG	16	6	3	20	27	33	13	34	25	44	48	38
50	L	DCDEF	18	30	29	27	37	27	24	51	32	46	39	39
30	R	AF	47	3	15	8	8	32	24	36	16	14	51	29
65	L	FG	46	36	44	35	32	32	25	32	32	26	23	11
60	R	CE	35	59	23	46	30	34	10	29	34	19	25	32
45	L	ABCD	59	67	63	42	36	47	46	84	72	32	38	36
55	R	BDEF	5	37	12	10	21	23	17	12	27	4	21	7
65	R	CDEG	43	59	39	38	56	59	79	71	45	39	67	60
55	R	ADEG	19	16	11	9	7	13	6	15	18	20	22	21
55	L	ABCEFG	7	31	18	18	13	27	44	15	20	61	34	27

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TABLE 3. EFFECT OF MICRO-NUTRIENTS ON THE FRUIT YIELD OF COCONUT PALMS : DISEASED PALMS (Early Stage)—contd.

plot no.	tree no.	age (1953)	apical treatment	pre-treatment yield						post-treatment yield					
				1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960
9	412	35	L AE	14	16	14	1	nil	2	8	17	9	nil	5	3
	409	35	R BD	17	13	8	20	35	36	36	55	44	55	94	53
	423	30	R CF	nil	nil	1	1	1	14	34	31	60	39	75	75
	433	45	R ABCG	58	41	38	52	46	57	90	100	57	66	71	65
	424	25	L BDFG	nil	nil	nil	nil	nil	15	37	10	54	15	94	20
	427	50	R ADFG	4	1	7	nil	14	8	17	26	13	8	16	7
	407	35	R CDEG	36	24	17	14	37	31	23	25	20	3	Died	
	429	50	L ABCDEF	64	78	72	58	56	73	84	88	72	82	68	76
	321	60	R AC	33	22	48	30	37	27	38	49	41	44	53	44
458	35	L DG	22	32	17	15	9	nil	11	53	43	66	43	27	
335	40	R EF	21	32	26	11	3	0	10	9	22	15	18	28	
440	50	R BCDFG	5	8	8	1	1	20	10	18	14	31	15	17	
450	55	R BCDFE	48	37	27	25	65	54	62	61	49	64	49	50	
332	65	L ABDF	29	28	20	23	14	8	23	35	30	26	14	22	
446	40	L ABFG	17	26	27	28	17	47	10	61	52	28	46	42	
450	30	L ACDFEG	nil	nil	3	3	nil	39	22	9	nil	1	10	nil	
306	25	R AD	nil	nil	nil	nil	nil	nil	5	26	1	nil	2	7	
231	25	R CG	nil	4	12	4	8	7	23	11	16	nil	17	6	
301	30	L BE	32	13	25	4	6	30	12	37	8	43	36	24	
256	40	R ABCF	68	79	72	43	85	73	68	81	65	59	96	63	
397	50	L CDEF	27	64	47	51	53	59	33	68	41	42	53	58	
394	30	L ABFG	24	26	34	24	3	28	13	31	25	nil	13	10	
305	45	R BDFG	42	40	30	28	36	48	50	43	61	42	60	53	
387	35	L ABCDEG	3	1	nil	1	3	1	11	7	1	3	4	2	
293	50	R BC	50	38	13	5	1	9	12	21	16	13	16	14	
301	35	R EG	21	44	26	11	27	27	31	38	42	59	36	36	
209	20	L DE	nil	nil	nil	3	16	4	7	25	10	17	23	23	
204	50	R ACDF	20	34	49	23	33	29	40	56	27	45	31	24	
285	25	L ACDFG	nil	nil	nil	nil	nil	nil	nil	12	nil	2	nil		
268	60	R ABDF	49	40	35	36	43	54	34	50	45	45	50	32	
281	65	R ABDFG	16	21	13	18	35	17	26	25	12	14	27	16	
279	60	R BCDEFEG	33	24	35	23	24	40	20	41	13	20	28	1	
380	55	R F	17	12	13	4	nil	17	13	17	5	3	12	4	
360	55	L ACF	58	40	38	26	32	39	30	30	22	18	32	24	
371	55	R ABG	19	21	4	7	6	11	8	21	5	5	6	3	
348	35	L BFG	20	34	34	7	45	53	29	24	49	57	35	33	
363	45	L BCD	49	38	34	25	23	28	23	22	11	16	27	17	
370	30	L BCDFG	nil	8	9	1	30	31	16	51	20	40	41	29	
351	35	R ACDEF	14	23	41	41	24	33	39	50	40	25	52	15	
376	40	L ABDEF	30	21	16	24	25	37	26	51	25	42	40	43	
206	40	L G	28	24	21	33	12	26	35	35	36	39	41	42	
197	15	R ACD	nil	nil	nil	nil	2	10	21	16	13	21	25	36	
187	25	R DEF	4	10	14	2	7	16	12	29	21	10	18	8	
229	40	L BCE	38	54	49	37	60	48	39	60	48	45	43	50	
208	20	R ABF	nil	nil	nil	nil	3	nil	3	nil	nil	3	nil		
123	65	L ACEFG	93	100	87	98	93	100	113	112	88	60	117	77	
304	35	R ABDEG	8	12	4	3	5	1	9	20	10	25	5	7	
230	60	L BCDFG	26	12	17	10	26	12	38	22	44	20	20	15	
121	50	L ABC	55	30	54	17	20	18	28	35	26	32	34	20	
63	55	R ADF	35	41	49	38	37	62	50	59	65	40	67	43	
123	40	L ABCDEFG	26	13	12	26	16	19	41	53	46	48	54	47	
98	55	R AEG	35	16	36	20	30	15	38	18	30	17	43	22	
100	65	L HDG	48	22	44	36	29	60	70	56	40	29	41	18	
90	40	L BEF	17	28	36	23	13	39	27	34	31	28	26	39	
86	35	R CDE	35	13	9	17	7	19	29	27	13	19	26	11	
124	25	R CFG	nil	nil	nil	37	19	66	50	41	45	62	79	78	
27	30	R I	7	13	16	4	9	12	23	45	25	25	51	23	
153	50	L ATDE	42	46	47	63	60	49	58	62	57	62	72	41	
32	35	R BCFG	16	4	10	15	4	12	6	8	12	9	18	9	
54	25	L ABFG	nil	nil	nil	nil	nil	6	18	29	17	9	38	27	
150	35	L ABDF	66	58	40	43	39	95	118	81	98	57	130	36	
30	30	L ACDFG	97	95	53	90	84	93	105	108	112	102	111	118	
124	50	R BCFG	38	22	6	20	21	13	14	17	11	7	22	8	
35	30	L BCDF	nil	nil	nil	23	19	31	39	61	30	14	36	40	

## MANURIAL EXPERIMENT ON COCONUT

TABLE 4. EFFECT OF MICRO-NUTRIENTS ON THE FRUIT YIELD OF COCONUT PALMS: *DISEASED PALMS* (Late Stage)

tree no.	age (1953)	spiral	treatment	pre-treatment yield						post-treatment yield					
				1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960
38	45	R	A	38	52	54	69	60	57	44	48	54	37	48	50
103	50	R	ABCDE	45	7	10	21	17	39	29	36	26	28	26	23
152	45	R	ABCDE	29	21	25	40	41	32	41	46	36	25	33	25
146	50	L	ADDEFG	11	nil	nil	2	5	3	5	23	12	10	12	9
123	55	R	BDE	60	22	30	19	34	26	16	11	6	11	5	8
116	45	L	BFG	18	6	11	8	15	23	nil	4	10	3	1	nil
140	55	R	DEF	24	29	13	37	13	34	17	20	8	18	9	10
124	40	R	CDG	4	nil	nil	2	5	6	8	6	4	2	4	1
114	60	L	B	78	11	36	24	27	36	30	31	24	13	22	23
138	65	R	ADE	40	14	14	18	17	32	29	32	40	33	34	31
40	45	L	AFG	22	19	25	30	24	35	29	27	32	26	27	42
51	60	R	CEG	31	10	5	16	2	11	13	2	17	5	19	5
21	40	L	ODF	5	nil	nil	nil	1	nil	10	11	3	nil	6	nil
36	45	L	ABCDE	nil	nil	nil	nil	nil	nil	nil	nil	nil	nil	nil	nil
95	50	R	ABCDG	20	16	9	37	17	33	11	9	15	7	10	9
139	40	R	BDEFG	83	16	32	26	18	33	36	43	36	45	50	54
82	50	L	AB	41	27	26	40	34	51	40	25	38	33	25	24
109	60	L	DE	27	4	14	17	8	16	8	7	6	7	2	nil
129	40	R	BC	42	29	38	47	40	84	56	67	75	17	54	50
111	65	L	ACG	102	28	26	51	70	82	39	73	67	40	16	23
29	45	R	ACDE	nil	nil	1	3	1	4	2	1	1	1	7	4
18	55	R	BCEG	nil	1	nil	3	nil	nil	nil	nil	nil	2	nil	nil
28	55	R	BDEF	2	2	2	3	1	17	1	6	nil	nil	nil	nil
135	60	L	ABDEFG	48	18	21	48	60	24	29	24	33	42	43	40
140	45	L	C	31	47	47	49	41	54	70	50	51	44	41	40
147	35	L	ADC	5	17	10	23	10	32	16	42	12	42	30	4
12	40	R	AEP	75	44	35	57	54	49	63	60	55	47	43	42
122	55	L	BDF	16	9	10	23	32	12	30	47	22	28	31	19
26	45	L	BEG	18	2	4	18	12	13	12	11	12	24	32	35
141	35	R	ABCDE	6	7	nil	3	7	17	7	26	9	19	42	21
126	50	L	ABCDFG	5	11	nil	6	7	16	3	19	8	7	1	7
26	35	R	CDEFG	30	14	13	22	10	35	23	36	40	36	35	26
119	65	R	AG	15	14	6	8	14	20	14	24	24	15	20	20
43	45	R	BF	28	29	6	50	38	68	53	21	44	67	64	71
156	60	L	GD	14	47	5	39	40	41	61	14	40	9	49	6
162	65	R	ABCE	25	25	10	27	23	23	36	34	39	26	18	30
9	40	L	ADEF	63	37	30	40	40	42	47	52	48	44	61	55
134	65	R	BDEG	22	17	18	21	16	37	22	28	35	36	29	29
166	65	R	CEFG	16	14	7	9	30	30	13	8	26	12	3	14
77	50	L	ABCDE	12	18	14	13	13	26	26	31	23	37	27	36
208	60	R	D	6	2	nil	1	1	3						
231	50	L	ABE	25	33	18	14	19	33	16	32	7	25	25	12
244	50	L	BCF	2	5	1	7	19	11	17	34	26	14	30	41
246	60	L	ACG	6	19	8	9	6	13	3	15	12	9	17	11
205	30	R	EEG	nil	6	1	4	2	4	1	6	nil	4	5	nil
248	65	R	ABDFG	51	54	50	38	32	36	18	36	13	nil	13	31
246	60	R	ACDEF	6	14	16	18	2	17	24	19	42	23	7	29
253	35	L	BCDE	5	nil	5	12	11	13	7	3	16	11	6	4
197	55	L	E	16	26	20	33	28	48	25	31	21	31	22	23
190	65	L	ARD	27	29	15	22	2	58	14	29	43	21	42	60
236	65	L	ACF	6	19	10	16	10	25	22	20	12	14	28	24
222	50	R	BCG	10	9	11	2	16	15	15	18	3	20	14	26
226	50	R	DFG	40	49	30	29	34	17	12	39	1	2	7	4
197	60	R	ACDEG	25	19	16	7	31	26	28	29	17	10	20	14
196	60	R	ABEFG	3	9	nil	nil	1	8	3	10	11	16	4	7
220	60	R	BCDE	11	8	7	12	17	19	10	12	15	17	22	13
417	30	R	AF	nil	nil	nil	nil	nil	nil	nil	nil	nil	nil	nil	nil
347	65	R	EG	42	20	24	10	14	37	27	19	2	13	20	nil
311	60	R	CE	34	12	16	nil	1	15	nil	nil	nil	nil	1	2
368	35	L	ABCD	77	90	100	37	27	65	55	79	57	73	91	71
375	25	L	BDEF	nil	nil	nil	nil	nil	8	11	11	4	7	1	6
372	25	R	ODFG	nil	nil	nil	nil	nil	5	3	1	4	3	nil	nil
329	35	R	ADEG	nil	4	3	4	2	5	9	11	10	10	8	nil
354	66	R	ABCEFG	39	26	30	15	27	41	23	32	11	22	33	19

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TABLE 4. EFFECT OF MICRO-NUTRIENTS ON THE FRUIT YIELD OF COCONUT PALMS : DISEASED PALMS (Late Stage) - *contd.*

plot no.	tree no.	age (1953)	spiral	treatment	pre-treatment yield						post-treatment yield					
					1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960
9	431	45	R	AB	42	32	28	21	16	23	28	41	32	13	21	23
	415	65	L	BD	10	2	nil	7	nil	2	nil	Died				
	425	65	R	CF	62	11	5	5	6	10	3	6	14	9	4	6
	428	65	L	ABCG	38	9	4	9	2	18	8	16	14	11	10	7
	438	65	L	BEFG	18	23	3	6	5	10	14	28	33	12	22	18
	430	69	L	ABFG	16	11	19	3	nil	7	21	14	27	13	16	16
	434	65	R	CDEF	16	14	7	7	2	4	8	23	13	9	12	16
	437	65	L	ABCDEF	31	68	21	45	85	65	81	112	72	66	78	64
10	455	30	R	AC	nil	nil	nil	nil	nil	nil	nil	nil	nil	nil	Died	
	462	65	L	DG	9	10	11	11	1	4	10	5	8	7	7	4
	444	40	L	EF	37	28	32	13	30	21	38	31	30	39	40	17
	338	40	R	BCFG	9	4	9	10	nil	1	8	16	18	12	9	5
	467	45	L	BCDE	27	33	19	18	11	27	21	23	22	31	28	28
	343	50	R	ABDF	40	66	25	60	20	33	28	47	43	40	61	31
	340	50	L	ABEG	28	34	34	23	9	18	10	24	26	33	24	37
	336	45	R	ACDEFG	32	59	45	73	65	31	72	67	48	69	94	66
11	369	65	L	AD	49	32	37	29	35	31	39	30	36	55	34	25
	384	60	L	CG	40	22	7	nil	1	nil	8	10	28	18	36	14
	258	55	L	BE	1	1	nil	nil	nil	nil	nil	1	nil	1	7	nil
	382	60	R	ABCF	66	60	39	45	30	39	48	42	43	39	51	39
	262	60	L	CDEF	16	15	9	5	nil	9	19	8	9	9	3	12
	281	60	L	AENFG	39	15	14	27	20	26	27	31	31	29	43	28
	385	65	L	BDFG	22	20	7	9	11	12	12	16	16	4	3	2
	386	50	R	ABCDEG	27	14	23	9	4	18	38	41	2	10	28	14
12	260	45	J	BC	6	30	11	6	2	nil	2	4	7	1	nil	1
	274	30	R	EG	70	9	29	13	6	18	2	14	13	16	16	17
	260	45	R	DF	22	28	36	21	10	9	26	48	28	32	27	26
	263	50	L	ACDE	67	35	42	16	12	28	27	34	39	28	46	31
	267	55	L	ACFG	16	19	14	8	nil	4	24	13	15	10	8	9
	286	65	L	ABEF	40	66	35	11	7	26	28	27	36	40	52	23
	290	45	L	ABDG	58	49	39	63	32	39	49	54	52	67	67	62
	278	65	R	BCDEFG	59	42	46	7	16	21	3	11	20	8	13	17
13	353	60	L	F	7	6	9	11	nil	nil	3	3	Died			
	373	60	L	ACE	24	7	18	24	24	23	11	22	6	6	28	nil
	366	60	R	ABG	2	3	10	1	1	7	4	15	6	11	14	3
	419	40	L	BCG	10	6	10	8	2	7	14	17	2	nil	4	1
	373	60	R	BCD	46	25	22	23	36	38	38	24	24	19	40	17
	405	60	R	BCDEFG	13	13	18	6	14	14	7	18	16	9	11	7
	353	45	R	ACDEFG	1	1	nil	13	15	27	16	32	34	21	45	41
	374	45	R	ABDEF	29	15	18	30	11	60	20	34	19	16	26	11
14	202	45	R	G	4	10	4	10	4	4	7	3	3	1	4	4
	243	40	R	ACD	36	43	17	11	3	18	10	4	13	1	nil	nil
	269	15	R	DEF	nil	8	7	nil	nil	nil	nil	nil	nil	nil	nil	nil
	221	45	L	BCF	1	21	3	11	nil	2	3	6	11	nil	9	1
	186	45	L	ABF	18	23	6	9	26	37	32	32	35	17	36	27
	217	45	L	ACEFG	6	6	2	4	nil	9	16	7	13	21	10	11
	264	40	R	ABDEG	4	7	4	4	nil	nil	3	2	3	nil	1	1
	226	55	R	BCDFG	27	21	12	22	16	22	20	32	35	17	40	24
15	69	60	R	ABC	22	14	23	13	7	13	24	31	39	17	27	nil
	68	65	R	ADF	1	4	1	nil	nil	nil	nil	nil	nil	nil	nil	nil
	107	60	R	ABCDEF	16	15	20	9	13	18	11	28	12	5	11	6
	82	35	R	AEG	1	4	12	18	1	37	11	31	3	21	16	16
	111	35	L	BDC	nil	nil	nil	7	6	29	16	19	9	7	31	11
	85	35	L	BEF	2	8	1	1	nil	2	3	3	Died			
	62	65	L	CDE	20	8	19	4	11	12	21	22	16	7	19	6
	84	60	R	CFG	16	3	6	19	18	28	25	22	23	18	13	8
16	138	60	R	F	24	18	10	3	9	nil	Died					
	34	20	R	ABDE	nil	nil	nil	nil	5	6	18	18	11	13	21	8
	39	55	R	BCFG	21	12	23	79	9	20	16	19	23	7	13	14
	38	25	L	ABFG	nil	nil	nil	6	17	23	29	26	17	29	57	70
	147	45	L	ACEF	83	68	46	60	66	54	60	60	60	52	73	76
	113	45	R	ACDG	59	32	17	17	26	23	40	51	34	38	38	42
	154	55	R	DEFG	9	8	16	4	13	17	4	14	15	24	16	nil
	41	50	R	BCDF	18	29	10	9	15	26	22	10	12	nil	15	5

## MANURIAL EXPERIMENT ON COCONUT

on the main effects and two-factor interactions are given in Tables 5 and 6. In the statistical analysis, the main effects and the two-factor interactions considered, the higher interactions being included in the error. The actions were confounded. ABC, ADF, AEG; BDG, BEF; CDE, CFG; , ACDG, ACEF; BCDF, BCEG; DEFG and ABCDEFG.

TABLE 5. MAIN EFFECTS  
(corrected for  $\alpha$ )

treatment	effect		
	healthy palms	diseased palms	
		early stage	late stage
A	- 127	318	1476
B	598	- 167	246
C	1503	- 548	302
D	634	566	864
E	- 568	-2065*	34
F	-1148	1151	1242*
G	- 308	- 88	724

\* significant treatments

TABLE 6. TWO-FACTOR INTERACTIONS  
(corrected for  $\alpha$ )

treatment	effect		
	healthy palms	diseased palms	
		early stage	late stage
AB	2007	49	184
AC	- 788	844	- 192
BC	1401	585	- 26
AD	1978	- 231	600
BD	1971	- 411	- 720
CD	- 152	- 3	964
AE	- 385	1089	424
BE	- 604	2508*	118
CE	- 808	-2109*	- 338
DE	- 175	1262	1160
AF	- 284	- 325	- 312
BF	2092	367	- 343
CF	1846	1289	102
DF	914	- 668	- 276
EF	160	159	- 162
AG	1114	- 468	- 376
BG	1380	814	- 1128
CG	-1128	- 826	136
DG	-2105	- 840	- 450
EG	-1084	- 283	- 12
FG	- 344	381	- 640

\* significant treatments



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A correction for the yield difference between palms having left- and right-handed foliar spirals was made. Although this foliar asymmetry is non-inherited (Davis, 1962a), the left-handers have been observed to yield significantly more number of nuts than their counterparts (Davis, 1962b, 1963). Figure 3 shows the left-right yield differences of the healthy and diseased palms for the twelve-year period. Having

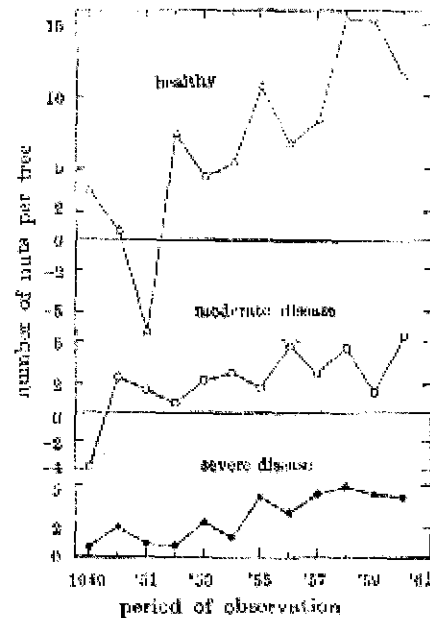


Fig. 3

noticed the difference in the yield between the left-spiralled and right-spiralled palms, it was very essential to make the correction because at the time of choosing the palms no consideration was made on the foliar spirality of the palms. 177 of the 384 palms were left-spiralled. The expectation on a basis of equality is  $192 \pm 9.8$ . The excess of rights is not significant at the 5 per cent level. Each of the 48 blocks contained 8 trees (plots), all healthy or all in the early or late stage of the disease. The numbers of blocks containing a given number of lefts are given in Table 7.

TABLE 7

lefts	0	1	2	3	4	5	6	7	8	total
blocks found	1	1	6	14	11	8	8	0	1	48
blocks expected	0.84	2.34	7.01	11.96	12.80	8.76	3.76	0.92	0.10	

The number of blocks expected with  $n$  lefts is  $\binom{8}{n} \frac{48.59^n .69^{8-n}}{128^8}$ . It is a little unexpected that even one block was found with 8 lefts, however, the variance of the number of lefts is 1.969, the expected value being  $\frac{8.177.207}{384^2} = 1.988$ .

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With regard to treatments also, disparity occurs regarding the number of the left and right palms receiving a particular treatment. With regard to treatment with E), the difference is significant,  $\chi^2$  being 8.0709 as seen below.

	L	R	L+R
E	37	27	64
e	21	43	64

$$\chi^2 = 8.0709.$$

because of the uneven distribution of the lefts and rights, it was decided to run the Analysis of Covariance with the spirality as the concomitant variable.

Since the 48 blocks are distributed in a 8-hectare estate, block differences are to occur as may be seen from the block totals given in Table 8. The block means were taken into account and the Analysis of Covariance done for each treatment separately.

TABLE 8. NUT-YIELD OF COCONUT PALMS - BLOCK TOTALS

blk	healthy palms		diseased—moderate		diseased—severe	
	pre-treatment	post-treatment	pre-treatment	post-treatment	pre-treatment	post-treatment
1	2810	2809	1437	1475	1086	614
2	2809	2785	1269	1246	921	656
3	2880	3258	1230	1772	1200	1057
4	1788	2782	1410	1857	928	1203
5	2378	2804	1721	1824	1186	1550
6	2871	3433	1643	1784	637	604
7	1897	2554	1050	1787	908	610
8	1772	3310	1455	1525	828	749
9	1876	2148	1084	2020	808	1050
10	2124	2892	1030	1491	1043	1287
11	1257	2266	1236	1413	927	1045
12	2129	2704	1033	1189	1320	1168
13	1838	2809	1150	1234	696	709
14	1730	2394	1230	1660	498	515
15	2678	4038	1304	1874	466	618
16	2185	2551	1482	2177	932	1179
total	35810	46687	21255	26317	14264	15532

## 5. STATISTICAL ANALYSIS PROCEDURE

Under this heading, the various steps used in arriving at the conclusions are laid briefly.

As already stated, this experimental data corresponds to a  $2^2$  confounded factorial manurial experiment on three groups of coconut palms (1) healthy, (2) moderately diseased and (3) severely diseased with 16 blocks of 8 plots for each group,

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one palm constituting one plot. Also, corresponding to each tree there is supplementary data regarding the spirality of the leaves. This spirality, is an environmental effect and does not depend on the treatments that are applied to the tree. A difference in the nut-yield due to right and left foliar spirality is observed, so it is necessary to take the spirality of the leaves into consideration. Thus, in the statistical analysis a concomitant variable  $X$  to represent the spirality of the leaves is introduced. For computations,  $X$  is taken as 1 if it is right, otherwise 2.

In the data it may be observed that some trees have died during the observation period. To account for this, some minor adjustments were made. If the palm died in the course of the pre- or post-treatment period, the yield for that period has been calculated on the basis of the yearly mean production for the period the palms survived.

The model  $Y = \beta X + \text{treatment-effect} + \text{block-effect}$  is assumed where  $Y$  is the increment in yield, i.e. the sum of post-treatment yields minus the sum of pre-treatment yields.

Treatment totals are calculated for  $X$  and  $Y$ , and the sum of squares for main effects and two-factor interactions are obtained by Yates' procedure. These are however influenced by the concomitant variable. Adjustment for the concomitant variable is made through standard routines of Analysis of Covariance.

The results of the Analysis of Covariance are presented in Table 9.

As clearly seen from Table 9, there exists a significant correlation between the nut-yield and the foliar spirality of the palms of the healthy and severely diseased groups. However, the moderately diseased palms do not show this dependence significantly. The fact the fruit yield depends on the foliar spiral in the coconut has already been reported (Davis, 1963).

TABLE 9. RESULTS OF ANALYSIS OF COVARIANCE

$y = \text{yield}$		$x = \text{spirality}$		
corrected sum of squares due to	degrees of freedom	$xx$	$xy$	$yy$
(1) Healthy palms :				
block	15	4.72	147.27	329630.43
treatment	28	7.66	- 545.30	348243.53
error	64	19.34	- 1254.20	1200580.60
<b>total</b>	<b>127</b>	<b>31.72</b>	<b>- 1662.23</b>	<b>1876454.56</b>

Variance estimate  $\hat{\sigma}^2 = 13485.08$       Estimate of  $\beta$  ( $\hat{\beta}$ ) = -64.8376

$F$ -statistic to test  $\mu = 0$  is  $\frac{E^{2xy}}{E_{error}}$  (Error  $ms = 6.03$ ).

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TABLE 9. RESULTS OF ANALYSIS OF COVARIANCE—*contd.*

	corrected sum of squares due to	degrees of freedom	$xx$	$xy$	$yy$
		(2)	Early disease		
block		15	4.30	-305.89	158644.22
treatment		28	6.91	-142.11	210262.28
error		84	20.72	15.36	459287.17
total		127	31.93	-432.64	827693.72

Variance estimate  $\hat{\sigma}^2 = 5896.10$  Estimate of  $\beta (\hat{\beta}) = 0.7413$

F-statistic to test  $\beta = 0$  is  $\frac{E^2xy/E_{xx}}{\text{Error } ms} = .0019$

		(3)	Late disease		
block		15	2.72	- 94.50	65497.75
treatment		28	0.58	62.88	80381.00
error		84	22.47	-517.38	240233.25
total		127	31.72	-549.00	376112.00

Variance estimate  $\hat{\sigma}^2 = 2760.84$  Estimate of  $\beta (\hat{\beta}) = 23.0264$

F-statistic to test  $\beta = 0$  is  $\frac{E^2xy/E_{xx}}{\text{Error } ms} = 4.33$

The effect  $x$  (due to foliar spirality) has been eliminated in order to find out the effect of the manurial treatment alone, and the significance or otherwise was tested by the  $F$ -test. The results are presented in Table 10.

TABLE 10. SIGNIFICANT TREATMENTS (AT 5% LEVEL,  $F_{1,85} > 3.92$ )  
MAIN TREATMENTS AND TWO-FACTOR INTERACTIONS

treatment	effect	F-value
(1) <i>Healthy palms</i>		
None significant		
(2) <i>Diseased—early stage</i>		
R	-2055	5.43153
RE	3508	8.30788
CE	-2168	6.20569
(3) <i>Diseased—late stage</i>		
A	1476	6.17821
F	1242	4.37523

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## 6 DISCUSSION OF THE RESULTS

Of the seven micro-nutrients (including Mg) tried in the experiment, five showed significant response when applied singly and/or in combination in either improving or depressing the fruit-yield of the coconut palms. No micro-nutrient was found to have any significant effect on the number of nuts of healthy palms. Palms in the early stage of disease responded very favourably with a combination of Boron and Iron (BE). The beneficial effect of Boron on the diseased coconuts became obvious even at an early stage of this experiment (Davis and Pillai, 1960). However, its beneficial effect is not noticed among severely diseased palms. Copper in combination with Iron (CE) shows severe depressing effect on early disease palms. At an early period, Copper showed some beneficial effect on healthy palms and those showing severe disease symptoms. Iron behaved differently. When applied singly, this element had severe depressive effect on moderately diseased palms. Further, Iron, in combination with Boron, showed beneficial effect while with Copper it had a depressive effect on the same category palms. The role of Iron, therefore, requires to be studied through further experiments.

Palms of the severely diseased group showed favourable response to Magnesium and Molybdenum applied singly. Analysis of yield data upto 1957 showed that Magnesium increased the nut-yield of trees of all categories, the healthy as well as the severely diseased palms showing greater response. With the present data upto 1960, this element continued to show a favourable response on all groups of palms, but significantly with the severely diseased ones. Root exudates were collected from healthy and diseased palms and their contents analysed chemically. Magnesium was found to be deficient in the root exudates of the diseased palms compared to that of healthy ones (Davis and Pillai, 1960). It would imply that diseased palms are unable to absorb as much Magnesium as healthy ones are capable of, from soils containing very low concentrations of the element. For all practical purposes, Magnesium is a macro-nutrient which is required in large quantities by the coconut. The first visible response to the soil application (as well as foliar application) was noticed on palms showing severe yellowing of the fronds. These leaves turned green steadily which eventually enabled the palms producing more fruits. It may be mentioned that the palms showing symptoms of the Withering Disease in Ceylon also showed a striking favourable response to the soil application of Magnesium (Davis, 1960; Nethasinghe, 1959; 1961a, b; Salgado and Nethasinghe, 1960).

Molybdenum has also shown a very favourable response with the palms showing severe disease symptoms. Though the palms receiving treatment F received just one gram of Molybdenum, they started showing the beneficial effect even in 1957.

## 7 LIMITATION OF THE ANALYSIS

- (1) The effect of the interactions higher than the two-factor level has not been worked out.
- (2) The experimental palms, as mentioned, are of varying age-groups, and no correction was made to this effect.

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- (3) Though the experimental palms belonged to the same tall variety of coconut, they represent more than one form or colour group. No consideration was given to these differences.
- (4) Field one (having the first 5 major blocks) was underplanted with coconut seedlings from the commencement of the experiment, whereas the other two fields were underplanted only in 1958-59.

## 8 ACKNOWLEDGMENT

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## REFERENCES

- T. A. (1962a): The non-inheritance of asymmetry in *Cocos nucifera*. *J. Genet.*, 58, 42-50.
- (1962b): Asymmetry and yield in *Cocos nucifera*. *Experientia*, 18, 321.
- (1963): The dependence of yield on asymmetry in coconut palms. *J. Genet.*, 58, 189-210.
- (1966): Coconut Withering Disease. *Bull. Coconut Research Institute, Ceylon*, 22, 1-29.
- ANANIAM, A. P. and MENON, K. P. V. (1954): Injection in coconut palms for curative purposes. I. Method of injection. *Indian Coconut J.*, 7, 49-60.
- and PILLAI, N. G. (1956): Effect of magnesium and certain micro-nutrients on Root (wilt) affected healthy coconut palms in India. *Orientalist*, 21, 669-674.
- (1960): Comparison of root exudations of coconut palms (unpublished).
- K. P. V. (1961-1961): *Annual Reports of the Central Coconut Research Station, Kayangulam, India.*
- (1961): Diseases of undetermined causes with special reference to the root (wilt) disease of coconut palm in India. *Rept. FAO Tech. Working Party on Coconut, Trivandrum*, 1, 58-84.
- and NAM, U. K. (1951-52): Scheme for the investigation of the root and leaf diseases of the coconut palm in South India—consolidated final report of work done. *Indian Coconut J.*, 5, 5-19 and 61-113.
- and SHANTRA, P. (1962): Soil transmission of the coconut wilt virus. *Curr. Sci.*, 31, 163-64.
- A. N., DAVIS, T. A. and MENON, K. P. V. (1964): Sap transfusion, a new device for virus transmission trials in palms. *Indian Coconut J.*, 7, 89-96.
- A. N. and MENON, K. P. V. (1955): Observations on root decay in coconuts, its cause and its relation to the foliar symptoms of diseases in the disease belt of Travancore-Cochin. *Indian Coconut J.*, 8, 97-105.
- (1963): Note on the aetiology of the wilt (root) disease of coconut palms in Travancore-Cochin. *Indian Coconut J.*, 9, 161-166.

## SANKHYĀ : THE INDIAN JOURNAL OF STATISTICS : SERIES B

- NETRASINGHE, D. A. (1959): Ann. Rept., Soil Chemist for 1959. *Ceylon Coconut Quart.*, 10, 17.
- (1961a): Ann. Rept., Soil Chemist for 1960. *Ceylon Coconut Quart.*, 12, 16-20.
- (1961b): Coconut nutrition and fertilizer requirements—the soil approach. *Rept. P.A.O. Tech. Working Party on Coconut*, Trivandrum, 1, 188-210.
- RADHA, K. and MENON, K. P. V. (1954): Studies on the root (wilt) disease of the coconut palm. A comparative study of the rhizosphere microflora of coconut from diseased and healthy areas. *Indian Coconut J.*, 7, 99-107.
- SALGADO, M. L. M. and NETRASINGHE, D. A. (1960): Preliminary note on Magnesium deficiency in coconut palms. *Proc. Ceylon Assn. for Advances Sci.*, 13, 14.
- SHANTA, P. and MENON, K. P. V. (1966): Cowpea (*Vigna sinensis*), an indicator plant for the coconut wilt virus. *Virology*, 12, 309-310.
- and PACHU PILLAI, K. (1969): Aetiology of the wilt (root) disease. Investigations on the virological nature. *Indian Coconut J.*, 13, 56-60.

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ASYMMETRY IN THE AESTIVATION OF PERIANTH OF PALM FRUITS

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Abstract

Palm flowers - hermaphrodite or unisexual - possess two whorls of three perianth segments each. The hermaphrodite flowers show the simplest type of aestivation since the perianth units of the whorls representing the sepals and petals are distinctly valvate. The staminate flowers have mostly imbricate calyx and valvate corolla. A careful examination of the imbricating calyx reveals the presence of right- and left-handed patterns. Flowers under these two categories of calyx arrangement are distributed more or less equally. The valvate aestivation of petals in hermaphrodite as well as staminate flowers becomes particularly handy for the emergence of stamens. The pistillate flowers, like the males, invariably have imbricate calyx which also show right- and left-handedness. The petals of pistillate flowers/fruits in species like Caryota and Arenga are valvate, others like Dictyosperma album, Ptychosperma elegans, P. macarthurii, Ptychopaphis singaporensis, Actinorhynchis callaparia, Rhopalostylis sapida show only imbricate aestivation. But in many others, some fruits are imbricating and the rest contorting corolla. The ratio of fruits with contorting corolla to those with imbricating corolla varies with species, the top positions being occupied by Phoenix sp. Clockwise and counter-clockwise rotating petals are clearly discernible among flowers/fruits beset with contorting corolla. Here again, the numbers of fruits showing the two kinds of rotations are distributed equally. There is a striking association existing between the aestivation of calyx and that of corolla in the same fruit. In species like Actinorhynchis callaparia and Rhopalostylis sapida, without

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ception, all the fruits which show left-handed calyx have right-handed corolla, and vice-versa with fruits having right-handed calyx. This association persists appreciably in Archontophoenix cunninghamiana, Salidocarpus lutescens, Dictyosperma album, Heterospatha alata, Chosperma elegans, F. macarthuri and Ptychospatha singaporensis. In several other species, such an association is not perceivable. In Strobilium and Ptychosperma palms, the flowers are arranged in clusters of three (2 males and a female) or two (males). The males have imbricate calyx and valvate corolla. The flower at the left end of the cluster in some species (Arenga pinnata) is left-handed and that at the right end is right-handed. But in Garyota and others, a reverse, the handedness of the males is noticed. The flower clusters are arranged spirally on the spike, and so, right- and left-handed flowers can be distinguished. The aestivation of calyx of the pistillate flowers in the clusters depends considerably on the spirality of the spike.

### Introduction

Palm flowers, typical of monocots, are trimerous, and their anther segments are arranged in two whorls of three units each, though exceptions where a whorl having either two or four units are occasionally met with. The flowers are generally unisexual (monoecious or dioecious), but the sub-family Coryphoideae comprises species producing hermaphrodite flowers, and the arrangement of their anthers varies considerably. Polygamous palms are rarely met with. In the absence of any serious investigation, it is customary to refer to the aestivation in palms as imbricate (Hooker, 1894; Blaxter, 1938; Patel, 1938; Raghavan and Baruah, 1956; Menon and Pandalaraj, 1958; Srinivasan and Ravappa, 1960; Lawrence, 1963 and Corner, 1966). However, a detailed examination of numerous flowers from several species has revealed the existence of further types of calyx and corolla arrangement as well. A detailed investigation has, therefore, been undertaken to study the sepals and petals in the hermaphrodite, staminate and pistillate flowers/fruits of several species of palms.

generally, three distinct kinds of aestivation are met with. The simplest of them is the valvate arrangement which is usually the condition for the corolla of staminate and hermaphrodites. In the two male flowers in Fig. 1, A & B, the petals, stamens and sepals imbricate. Even in an unopened flower, the tips of the petals do not overlap, instead they are in contact along their outer margins. Imbricate aestivation is the more common type met with in palms. Excepting those species where the corolla is valvate (*Hyphaene* sp., Fig. 8), the calyx in palm flowers is usually imbricate. Also, flowers of several species have imbricate petals. In imbricate aestivation, of the three sepals (Figs. 1, B, outer whorl) or petals (Figs. 1, C & D), the outermost one is only exposed, and the innermost one is overlapped on either end by the remaining two members of the same whorl. Thus, one end of the middle segment is overlapped by the outermost segment while its other end overlaps the innermost member partially. Two kinds of imbrications are possible based on which end of the middle perianth member is exposed. If the right end is free, the arrangement is regarded as right imbrication (Figs. 1, A and C), and if the left end is free, it is considered as left imbrication (Figs. 1, B & D). The third kind of aestivation dealt with here is contortion or twisting. Only unisexual flowers of palms have contorting calyx. But in several species, the corolla of some fruits contort. In a contorting corolla, one petal is overlapped at one end by one of its neighbours and the other end overlaps part of the other neighbour. Thus, all the petals of a contorting flower seem to rotate to the right, and in another to the left (Figs. 1, E & F). There are thus four patterns of petal-aestivation possible for most species. But some species show only the two imbricate patterns. There are also palms where the flowers have slightly or appreciably united petals both in staminate (*Enapia*) and pistillate (*Calamus*) flowers.

Observation

staminate flower

The staminate flowers of palms are much smaller than the females (ranging from 1mm x 1mm<sup>to 5 mm</sup>), and the differences in weight and size in some species reach even a two hundredfold. In the genera of sub-families Arecoideae and Caryotoideae, the staminate flowers are about the size and weight of the females, or even slightly heavier. The genus Areca, however, conforms to the general rule in having much larger and heavier female flowers. The staminate flowers are produced in different individuals of the same species as in Borassus, Latania, Phoenix, Salacca, Hyphaene and Beccarisia, or in pure male spadices along with female ones in the same individuals as in Elaeis and Attalea, or in different spikes of the same spadix where the remaining spikes are pistillate-flowered as in a rare Elaeis guineensis reported by Kunjan and John, (1970). In Chrysalidocarpus fruticosus, the terminal spike of a spadix is usually pistillate and the lateral ones staminate. The male flowers are also produced at the distal region of the same spike which bears females at the proximal end as in Coccothrinax, Areca and Arikuryroba, or they are distributed throughout the spike intermingled with female flowers as in Arenca, Chrysalidocarpus (Fig.2), Actinorhynchus, Dictyosperma, Ptychoraphis and Ptychosperma (Fig.3).

In a great majority of species, the petals of male flowers are small and which do not overlap in any way. But their sepals are invariably imbricate. The male flowers of Borassus flabellifer and Latania pinnatifida, on the other hand, have valvate sepals and tubular corolla with valvate tips. Further, in the genus Phoenix, the sepals are characteristically fused into a shallow cup, bearing three conspicuous lobes. The petals are triangular and valvate.

The staminate flowers of some species are so small that recording their characteristics is difficult and time-consuming. As for example, this is the case in Areca triandra, Chrysalidocarpus lutescens or C. madagascariensis.

scariensis measure as little as 1 mm wide and 1 mm long. Nevertheless, small numbers of flowers were examined, often with the aid of hand lens, from 19 species for the aestivation of calyx and the data are presented in Table 1.

Table 1 : Aestivation of calyx in male flowers of 19 palm species

p e e c i e s	Contortion :		Imbrication :		Total
	Left	Right	Left	Right	
<u>Pinorhytes callaparia</u>	-	-	187	180	367
<u>Chontophoenix</u> sp.	-	-	18	21	39
<u>Coca catechu</u>	-	-	20	22	42
<u>Coca triandra</u>	-	-	15	13	28
<u>Arenga obtusifolia</u>	-	-	211	210	421
<u>    pinnata</u>	1	2	716	632	1351
<u>    undulatifolia</u>	-	-	76	76	152
<u>Alyptocalyx spicatus</u>	-	-	-	150	150
<u>Caryota mitis</u>	-	-	1122	1129	2251
<u>    urens</u>	-	-	141	141	282
<u>Salidocarpus lutescens</u>	-	-	20	20	40
<u>    madagascariensis</u>	-	-	20	20	40
<u>Cocos nucifera</u>	-	-	110	145	255
<u>Actyosperma album</u>	-	-	105	110	215
<u>    terospathe alata</u>	-	-	15	16	31
<u>    ychosperma elegans</u>	-	-	20	23	43
<u>    macarthurii</u>	-	-	136	139	275
<u>    ychoraphis singaporensis</u>	-	-	75	89	164
<u>    opaloblaste</u> sp.	-	-	56	54	110
Total	1	2	3063	3190	6256

It is seen from Table 1 that only 3 flowers out of 6256 has contorting calyx. The left- and right-imbricating flowers are distributed more or less equally in each species excepting Arenga pinnata and Cocos nucifera. In A. pinnata, the lefts are in excess of the

rights and the difference is statistically significant, the  $\chi^2$  value being 5.234. In Jacobs nucifera, on the other hand, it is the right-handed that are in excess, the  $\chi^2$  value for the difference turning out to be 4.800. In Calyptranalyx spicatus (Fig.4) all the flowers examined show only one type of aestivation (right imbrication). In this species, the flowers are arranged in clusters of two, of which one is male and the other female. All the males occupy the right side in the cluster and they have the same type of aestivation. Perhaps if other spikes where the males occupy the left of the females are examined, the other type of aestivation may be available. In Arenaga, Caryota, Ptychosperma etc., the flowers are seen in clusters of three (2 males enclosing a female) or two (males) and the clusters are arranged in a spiral on the spike. Some spikes are right-handed and others left-handed. The size of the male flowers on one side is sometimes very much reduced compared to the males on the other side (Fig.5). Because of the same spiral effect, the flower clusters at the tip of the spikes possess only a single male flower, and it is often difficult to assign its position in the cluster.

#### The hermaphrodite flower

Most of the members of the sub-family Coryphoideae possess hermaphrodite flowers, of which Corypha, Licuala, Livistona, Prichardia, Sabal and Thrinax are the common ones in India. A portion of a branching spike of Prichardia pacifica bearing mature flower buds as well as bloomed flowers is seen in Fig.6. Here the three petals are highly deciduous, and they drop off as a cup when the six stamens from within the flower begin to emerge out. The hermaphrodite flowers are usually characterised by having a united calyx which forms an elongated solid stalk for the fruit. Even when young, the free ends of the calyx are valvate. The petals are also valvate whether they are deciduous or persistent (Licuala, Prichardia (Fig.8), Livistona or Corypha). Thus, the hermaphrodite flowers show the simplest kind of aestivation. Moore, Jr. (1961), on the other

hand, describes the calyx and corolla of hermaphrodite flowers thus, 'The outermost whorl of three overlapping (imbricate) sepals makes up the calyx; the next whorl of three imbricate petals together forms the corolla'.

#### The pistillate flower

The pistillate flowers have proportionately larger perianth segments. They cover the rest of the flower almost upto the stage of receptivity. In some species, the perianth segments cover the flower even at the time of receptivity when the stigmatic appendages alone project out (Phoenix paludosa). The perianth generally persistent and accrescent. Although the outer whorl of perianth of a female flower is invariably imbricate, a few exceptions are met with. In Bacaris major (Fig.7), the sepals are united into a shallow cup with three prominent fringes. In Eyphacne, the calyx lobes are valvate which are carried on a fleshy stalk (Fig.8). In very exceptional cases, the sepals are regularly twisted as in Borassus flabellifer and Archontophoenix cunninghamia. The inner whorl of perianth either imbricates or contorts. A high percentage of fruits bearing contorting corolla and others having imbricating corolla was reported in Areca and Phoenix by Davis and Kundu (1967), and Davis (1963). Like the calyx, the corolla is also valvate in Hypphaene (Fig.8). In Litsea lodigesii (Fig 9A) though at an early stage the corolla clearly imbricates or contorts, at a later stage, when the fruit enlarges, the petals show only valvate aestivation. This is brought about by the non-accrecent nature of the petals. A regular valvate corolla is seen in some Caryotoid palms of the genera Arenga, Caryota etc. In Bacaris major, the corolla is fully united into a cup.

The perianth of about 1000 female flowers/fruits each from 25 species (including Arenga pinnata and Caryota mitis) belonging to five sub-families were critically examined. The genera are prominent cup with irregularly cleft crenate margin. In Phoenix, the calyx is united into

classified below according to the aestivation of the perianth of their fruits.

1. Cupular/valvate calyx and contorting/imbricating corolla, eg. Phoenix (Fig.10);
2. Imbricating calyx and imbricating corolla, eg. Ptychosperma (Fig.3), Ptychoraphis (Fig.11 C), Actinorhysis, Rhopalocarpus, Dictyosperma;
3. Imbricating calyx and imbricating/contorting corolla eg., Areca (Figs.12 A,B), Cocos, Attalea (Fig.9 B), Heterospatha, Borassus (Fig.9 C), Chrysalidocarpus (Fig.11 B), Archontophoenix (11 A);
4. Imbricating calyx and valvate corolla, eg. Arenca, Caryota, Latania (older fruits, Fig.9 A);
5. Valvate calyx and valvate corolla, eg. Hyphaene (Fig.8);
6. Cupular calyx and cupular corolla, eg. Bactris major (Fig.7).

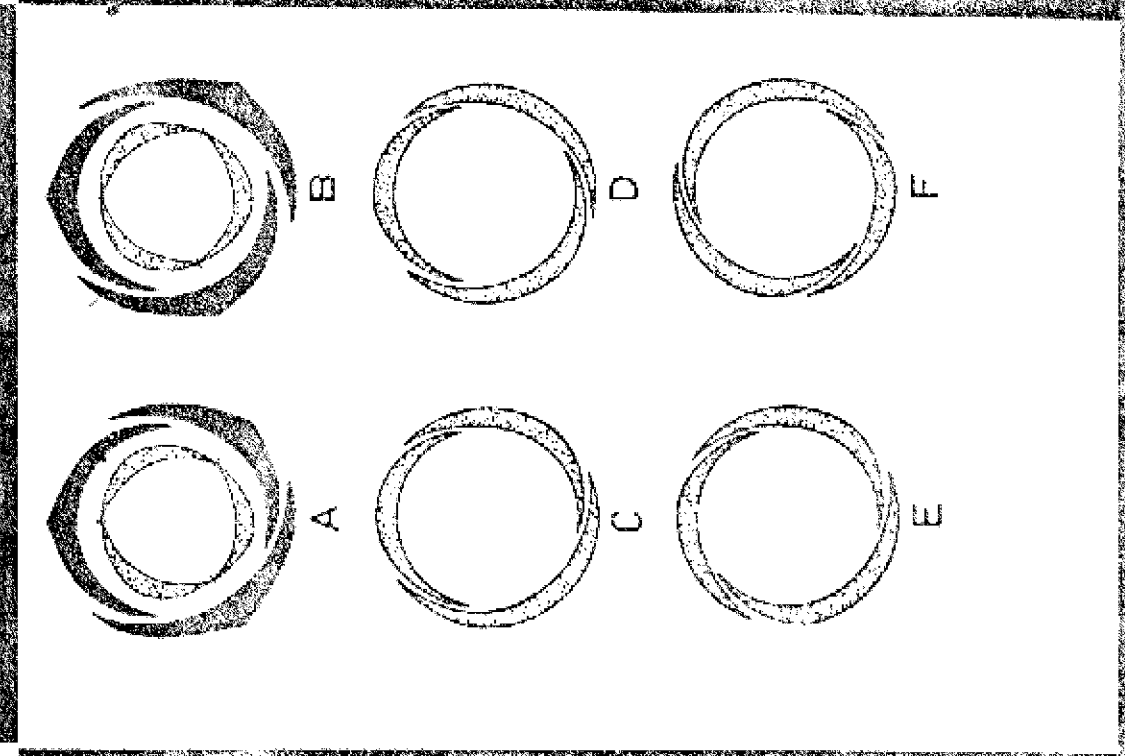
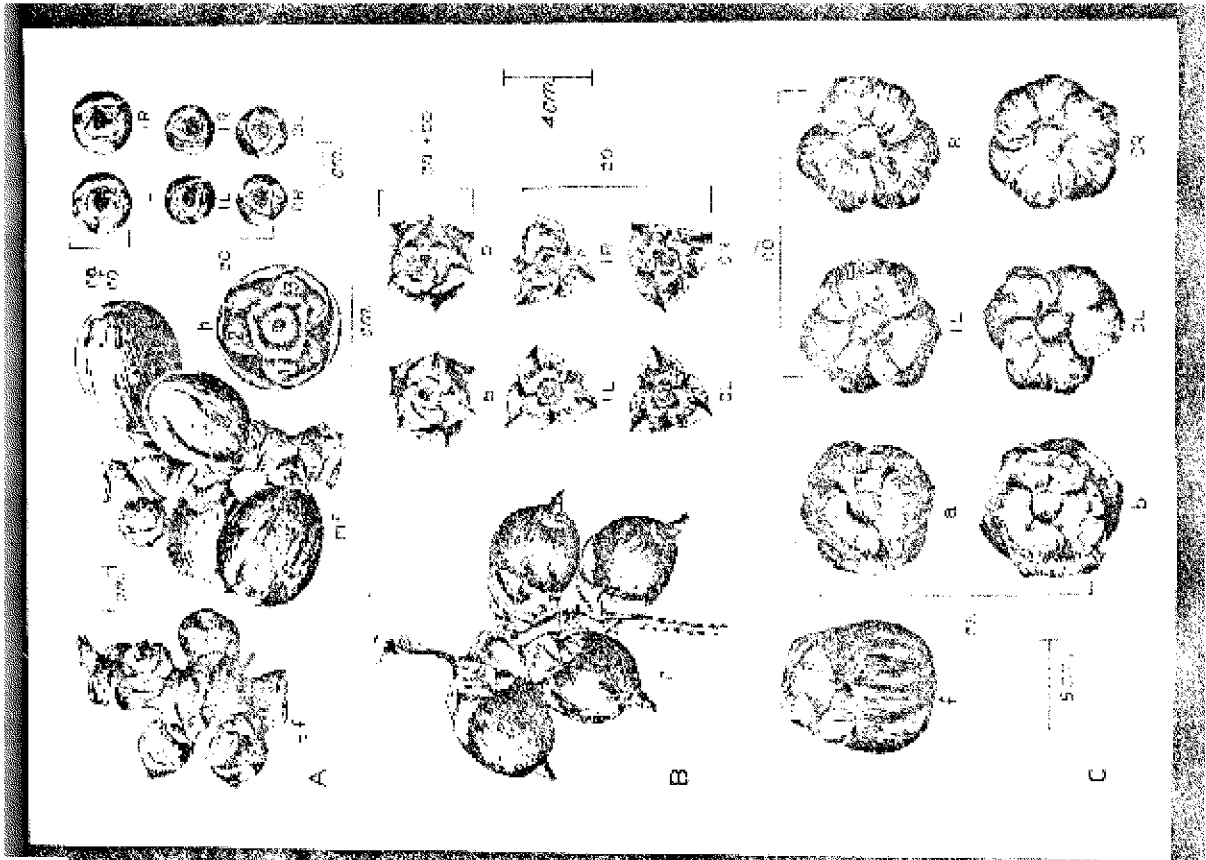
The percentage of fruits with contorted corolla to those with imbricating corolla has been recorded for some species as shown in Table 2.

Table 2

Activation of corolla in female  
flowers/fruits of 23 palm species

s p e c i e s	contortion		imbriication		Total	% contortion imb. i.
	Left	Right	Left	Right		
<u>Inoencoideae</u>						
<u>Phoenix dactylifera</u>	9	6	40	35	90	20.00
<u>P. humilis</u>	83	105	264	295	747	33.63
<u>P. paludosa</u>	178	128	459	486	1251	32.38
<u>P. reclinata</u>	178	279	547	614	1618	39.36
<u>P. rupicola</u>	17	16	74	86	193	20.62
<u>P. sylvestris</u>	403	285	1153	1026	2867	31.57
<u>P. zeylanica</u>	137	211	538	390	1476	30.85
<u>Borassoideae</u>						
<u>Borassus flabellifer</u>	44	41	141	145	371	29.72
<u>Datania lodiressii</u>	4	8	24	27	63	23.33
<u>Coccoideae</u>						
<u>Arikuryroba schizophylla</u>	16	20	67	59	162	28.57
<u>Attalea speciosa</u>	10	8	134	116	268	7.20
<u>Cocos nucifera</u>	41	43	335	341	760	12.43
<u>Arecoideae</u>						
<u>Heterospatha alata</u>	30	48	389	377	844	10.18
<u>Archontophoenix cunninghamia</u>	98	111	393	377	979	27.14
<u>Areca catechu</u>	246	229	948	928	2351	25.32
<u>A. triandra</u>	28	26	171	205	428	13.83
<u>Chrysalidocarpus lutescens</u>	57	24	120	110	311	35.22
<u>Dictyosperma album</u>	-	-	329	329	658	Nil
<u>Actinorhynchis callanaria</u>	-	-	58	62	120	Nil
<u>Ptychoraphis singaporensis</u>	-	-	226	261	487	Nil
<u>Ptychosperma elegans</u>	-	-	991	1027	2018	Nil
<u>P. macarthurii</u>	-	-	524	384	908	Nil
<u>Rhopalostylis sapida</u>	-	-	185	134	319	Nil
<u>Total</u>	1577	1588	8110	8014	19289	





Out of the above 23 species, the fruits of 17 have contorting cilia in various proportions in addition to those showing imbrication. In the last six species, the corolla of all the fruits shows imbrication. The ratio of fruits showing contortion to imbrication varies greatly from species to species.

Calyx-corolla relationship

In the staminate flowers of all the species examined as well those of Arenga pinnata, Caryota mitis and C. urens, the calyx is imbricate and the corolla remains valvate. Among the fruits where the sepals imbricate and petals either imbricate or contort, the relationship between the aestivation patterns of the calyx and corolla has been studied on fruits of 16 species. That is, the handedness of the calyx of a fruit is compared with the handedness of its corolla. The data are shown in Table 3.

Table 3 : Page 11

Table 3 : Calyx-corolla association in 16 palm species

p a l m s	Sepals Left Imbri:		Sepals Right Imbri:		Total
	Petals	Petals	Petals	Petals	
	Left	Right	Left	Right	
<u>Borassoidae</u>					
<u>Borassus flabellifer</u>	99	94	81	90	364
<u>Lactinia lodigeani</u>	20	21	16	14	71
<u>Coccoideae</u>					
<u>Arikuryroba schizophylla</u>	30	41	53	38	162
<u>Attalea speciosa</u>	54	66	90	58	268
<u>Cocos nucifera</u>	191	244	143	185	760
<u>Arecoideae</u>					
<u>Areca catechu</u>	602	618	592	539	2351
<u>A. triandra</u>	95	105	102	126	428
<u>Archontophoenix cunninghamia</u>	99	384	392	104	979
<u>Chrysalidocarpus lutescens</u>	55	99	122	35	311
<u>Heterospathe alata</u>	137	335	262	134	868
<u>Ptychosperma elegant</u>	23	1002	968	25	2018
<u>P. macarthurii</u>	30	557	490	27	912
<u>Ptychoraphia singaporensis</u>	4	257	222	4	487
<u>Dictyosperma album</u>	4	329	325	-	658
<u>Actinorhysis calligaris</u>	-	61	58	-	119
<u>Rhopalostylis papida</u>	-	134	182	-	316
Total	1443	4144	4126	1379	11092

N.B. The figures under column petals Left include those with left-imbrication as well as left-contortion where present. Similarly the figures under column petals Right include left-imbrication and left-contortion.

In the first seven species, the petal arrangement has no particular association with that of sepal arrangement. That is, where the petals are imbricate to the left, in about half the number of fruits, the petals are left-handed, and in the rest they are right-handed. A mirror picture is noticed on fruits having right-handed sepals. In the

At seven species, there exists a negative association. That is, where the sepals imbricate to the left, a majority of the flowers have right-handed petals. Vice versa is the situation where the sepals imbricate to the right. This association reaches its maximum in Actinomytis callaparia and Rhopalostylis saride in none of whose flowers the sepals and petals are similarly handed.

#### Aestivation of sepals and spirality of spike

In the 16 species mentioned in Table 3, the perianth segments are either imbricate or contort, and the distribution of flowers/fruits on the spike with regard to the aestivation is entirely random. In the genera Arenga and Caryota, and in general all the Caryotoids and Ptychospermates, a significant association between the types of aestivation of a particular flower and its position in the flower cluster exists.

In Arenga and Caryota, both the male and female flowers show imbricate sepals and valvate petals, and the flowers are borne in clusters of three or two. They are arranged on the spike more or less along a line which is perpendicular to the linear axis of the spike. The positions of the three flowers in a cluster are determined by holding the spike with the distal end up. The male flower located to the left of the female is regarded as the left flower and that to its right as right flower. In Arenga pinnata, the left flower invariably shows left-handed imbrication and the right flower, right-handed imbrication. On the contrary, in Caryota mitis, the male flower on the left invariably has right-handed imbrication and the flower on the right, left-handed imbrication. This dependence of the aestivation of the stern of sepals of male flowers on their position within the flower cluster is not influenced by the spirality of the spike. (The flower clusters are arranged spirally on the spike, running clockwise or counter-clockwise). The female flowers of Arenga pinnata, Caryota mitis, C. urens, Chrysalidocarpus lutescens and Ptychosperma macarthurii and others, show a definite dependence on the spirality of the spike.

in regard to their sepal activation. If the spike is left-spiralled, a majority of female flowers will have their sepals imbricating to the left, and if right-spiralled, a majority of the flowers will have right-imbricating sepals. Some data on the sepal activation of flowers in clusters are presented in Tables 4 and 5.

Table 4

Aranga and Caryota : Activation of sepals of male flowers in relation to their positions in cluster

Spirality: Clusters: and no. of examined spike	Activation of left & right male flowers				
	LI & RI	LI & LI	RI & RI	RI & LI	
<u>A. Aranga pinnata</u>					
Left 10:1172	1116	10	40	6	
Right 10:1067	1020	22	23	2	
20:2239	2136	32	63	8	
<u>B. Caryota mitis</u>					
Left 5:627	627	-	-	-	
Right 5:311	311	-	-	-	
10:938	938	-	-	-	

Table 5

Aranga and Caryota : Activation of sepals of female flowers in relation to spirality of the spike

Spirality and: no. of spike examined	Clusters: examined	Imbrication		Contortion		total
		left	right	left	right	
<u>A. Aranga pinnata</u>						
Left	7	407	124	-	1	532
Right	7	125	335	-	-	460
	14	532	459	-	1	992
<u>B. Caryota mitis</u>						
Left	5	465	162	-	-	627
Right	5	61	250	-	-	311
	10	526	412	-	-	938

It is seen from Table 4 that out of 2239-flower clusters examined from twenty spikes (ten each from left- and right-spiralled ones) of Arenga, in 95.44% of clusters, the male flowers on the left side bore left imbricate calyx and the flowers on the right had right imbricate calyx. The other three combinations account for less than 5 per cent of the total clusters. In Caryota mitis, out of 938 flower clusters examined from an equal number of spikes, all the male flowers on the left bore only right-imbricating calyx and those on the right had only left-imbricating calyx. In Arenga pinnata (Table 5) out of 532 female flowers examined from 7 left-spiralled spikes, the calyx of 76.50% imbricated to the left and in the rest, it imbricated to the right. Similarly, out of the 460 female flowers from an equal number of right spiralled spikes, the calyx of only 27.17% flowers imbricated to the left and the rest imbricated to the right. There was an exceptional flower having a right-contorting calyx. In Caryota mitis, out of 627 female flowers of left-spiralled spikes, the calyx of 76.16% had left-imbrication. Similarly, a great majority of the female flowers of right-handed spikes had right-imbrication. Thus, the male flowers in Arenga and Caryota show reversed aestivation, but the females of both the genera behave similarly (with regard to their aestivation).

#### Variation in the aestivation of perianth

From the data given in Table . it is seen that about five per cent of the flower clusters examined from Arenga pinnata deviated from the normal pattern. But in some other individuals a much higher percentage of the variation is met with.

In Arenga pinnata, the space between the individual flower clusters differ considerably. In such spikes where the spacing is abnormal, the lower sets of clusters show considerable variation in the perianth arrangement. There is also a possibility of both the males in a cluster showing a similar type of imbrication or showing a reversed situation than the usual. Such a variation was recorded from 12 spikes of another palm and the data are presented in Table 6.

Table 6

pinnata : Aestivation of sepals of left and right male flowers

Polarity and position of spike	Clusters examined	Aestivation of left and right flowers			
		LI & RI	LI & LI	RI & RI	RI & LI
6	301	60	65	166	10
12	349	28	221	93	7
12	650	88	286	259	17

Majority of the clusters have identical males. Moreover, of 301 clusters of left-spiralled spikes, in 55.15 per cent, both males have right-handed imbrication. But in 63.32 per cent of right-spiralled spike, both the flowers have left-handed imbrication. Thus, the male pairs showing similar type of calyx imbrication are negatively associated with the spirality of the spike.

A flower cluster of Arenga pinnata can display one of the following conditions : three fully developed flowers ( 2 males and a female ), only two developed males, two underdeveloped males and a developed female, two developed males and an underdeveloped female, one male and one female, or only one male. The above variation largely depends on the position of the spadix on the tree and position of the cluster on the spike (Sasu, 1972).

#### Discussion

The valvate aestivation of corolla in the staminate and pistillate flowers greatly facilitates the opening of petals and synchronous emergence of stamens. The unfolding of petals is caused by a number of factors. The cumulative effect of the enlargement of petals and lengthening of their filaments pushes the petals sideways. Efficient pressure develops. With the tip of petals moving outwards, their base tends to move in. This process is further facilitated by the free margin of the tangentially curved and imbricate petals whose normal tendency is to converge. Thus, the imbricate aestivation of calyx of staminate flower has a role in pressing the

petals apart. Such a lever mechanism can be more effective where the petals are much longer than the sepals as is the case in most species (fig. 2). There is a striking device which further helps in the unfolding of the petals. A little above the base of the petal, a horizontal ridge of a mass of large cells suddenly appears a few hours before the flower blooms. The rapid enlargement of three ridges (one for each petal) within an otherwise filled up cavity, presses the petals towards a periphery. Such an enlarged ridge is clearly seen in species like Schlotheimia macarthurii. In Cocos nucifera, the ridge looks divided into two halves by the stout filament of the stamen that is placed opposite the petal. The fleshy ridge thus, in function, resembles the ligules of gramineae. When young, the margins of the valvate petals are kept in position by two rows of large cells which form the abscission layer. These large cells start withering when the anthers mature. The weakening of this binding abscission layer helps the petals to detach from each other easily. In species like Prichardia pacifica, where the individual petals do not spread out, the three petals are pulled upward in a united condition by the expanding stamens. Thus, the petals are deciduous. The timely weakening of an abscission layer at the base of the petal helps it to be pushed upward. From a mechanical point of view, a petal which is not tangentially curved but having a narrow base, is better suited for spreading apart than one which is curved (as is the case with imbricating petals) and having a wider attachment at the base. In this context Moore Jr.'s (1961) view of male flowers having imbricate petals will run into difficulties while explaining the mode of their unfolding. Dicotyledonous flowers with their not stiff petals may have different mechanisms for blooming.

Often the unisexual flowers in the same spadix bloom at different times, the males blooming before the females reach the receptive stage as in Cocos, Areca etc. But in hermaphrodite flowers, both the male and female phases overlap with the unfolding of petals. This is perhaps an essential condition since the stigma gets no further



tection from the petals when once they open. In the rare hermaphro-  
dite flowers of Cocos nucifera recorded by Davis et al. (1954), the  
female phases of the same flower continued to alternate. The over-  
lapping of the perianth in these hermaphrodite flowers was cal-  
culated to be similar to that in normal female flowers. Along one (or two) margin a  
fold was formed as a result of the expansion of the ovary and partly  
the curving outward of the margins of petals, through which the stigma  
emerged. However, the tip of the petals continued to cover the stigma  
as well as bulk of the ovary until the female phase commenced. Large  
anther lobes, coupled with their imbricate or contorting margins help  
the gynaecium to develop under excellent protection till receptivity.  
Frequently too, the meristematic portion of the developing fruit is  
effectively protected by the imbricating petals. Thus, imbricate/con-  
torted aestivation of the fruits is an advantage over valvate aestivation.

The phyllotaxy of palms is alternate, and so, the perianth  
parts of their flower are produced one after another. Although the  
sepals (or petals) are produced apparently in a whorl, in some  
cases it is possible to make out the sequence of production. In effect,  
the imbricate arrangement of the perianth demonstrate this. Further,  
Ptychosperma macarthurii and to some extent in Ptychoraphis singa-  
pensis (Fig. 110), the outermost sepal is smaller than the middle  
one which is smaller than the innermost one. Similarly, the petals  
also show a progressive difference in some cases. Thus, the sepals  
and petals should have the same type of imbrication in a flower/fruit as  
they represent any consecutive six leaves on a shoot. But only a smaller  
number of fruits have such a perianth arrangement. In about fifty percent  
of the fruits of many species, the sepals move along one direction while  
the petals move oppositely. In species like Actinorhynchus callanana  
Boerhaavia diffusa, without an exception, all the fruits have  
the sepals and petals turning oppositely. The advantage of such an  
aestivation to the fruit is not known yet. Where the petals contort,  
the lag between the formation of any two consecutive petals is

much reduced. Here again, the directions of coiling of the  
and twisting of petals are opposite to each other in above fifty  
of the fruits. Davis and Ramanujacharyulu. (1971) have worked  
the theoretical possibilities of the various kinds of aestivation  
son catchu and verified the figures with data obtained by exami-  
several fruits.

The aestivation of calyx in Ptychospermate and Caryotoid  
shows how the asymmetry of sepals depends on the position of the  
in a cluster. In this group of palms, flower clusters are dis-  
tributed throughout the spikes in a single spiral running clockwise or  
counter-clockwise. The aestivation of majority of female flowers is  
governed by the spirality of the spike. But that of the male flowers  
is not. In Aranga sp., for example, the male flower on the left side  
of the cluster (on any kind of spike on any individual palm) has its  
sepals imbricating left-handedly, while the male flower on the right  
is right-handed. A reversed aestivation is noticed with the male  
flowers in Garroa sp. The flower clusters have to be regarded as the  
reduced lateral off-shoots of the main spikes. Each off-shoot  
bears a female flower at the base whose perianth arrangement associ-  
ates with the spirality of the spike. The next flower (male) of the  
lateral shoot is placed either to the left of the female or to its  
right. The third flower, also male, occupies the other side of the  
female. There is an unknown mechanism which brings about a left-handed  
aestivation for the left flower in some species (Aranga pinnata), and  
right-handed imbrication to the right flower. The mirror image pattern  
of calyx in the two male flowers of a cluster suggests that the  
flowers are formed in adjoining positions of a scorpioid cyme, or that  
of dichotomous branching taking place at the very early stage  
of differentiation. Corner (1966) has given a useful diagram of how  
a cluster of panicle of bisexual flowers can be reduced to a mere cluster  
of one or two flowers. It is often reduced to a single flower.

Literature cited

- su, S.K. 1972. Floral biology of palms (unpublished).
- Stetter, E. 1926. The palms of British India and Ceylon. London.
- Turner, E.J.H. 1966. The natural history of palms. London.
- Vis, T.A. 1969. Acctivation of coconut flowers. Ceylon Coconut  
Spert., 20 : 123-130.
- \_\_\_\_\_ and Kundu, A. 1966. Acctivation of perianth of Areca catechu  
Linn.fruits. J.Sambay Nat.High.Soc., 53:270-282.
- \_\_\_\_\_ and Ramenujacharyulu, S. 1971. Statistical analysis of asy-  
mmetry in plant organs. Sandhya, B 33 :
- \_\_\_\_\_ Anandan, A.P. and Menon, K.P.V. 1954. Hermaphroditism in  
Cocos nucifera L. Indian Coconut J., 7:133-142.
- Hooker, J.D. 1894. Palmeae by Beccari, O. & Hooker, J.D. Flora of  
British India. Kent.
- Manjun, M.M. and John, P.J. 1970. A new member to the palm family in  
Kerala. Coconut Bull., Ernakulam, 1 : 7-9.
- Lawrence, G.E.M. 1963. Taxonomy of vascular plants. New York.
- Menon, K.P.V. and Pandelai, K.M. 1958. The coconut palm, a monograph.  
Ernakulam.
- More, Jr. H.E. 1961. Botany and classification of palms. The Am.  
Horticultural Mag., 40 : 17-26.
- Marthy, K.H. and Savappa, K.V.A. 1960. Floral biology of areca (Areca  
catechu Linn.). Arecanut J. 11 : 51-55.
- Netel, J.S. 1938. The coconut, a monograph. Madras.
- Behavani, V. and Karub, E.K. 1956. On certain aspects of the morpho-  
logy of arecanuts (Areca catechu Linn.),  
Arecanut J., 7, 21-28.

