

INDIAN STATISTICAL INSTITUTE

Telegram : STATISTICA, CALCUTTA-35
Telephones : 56-8222 (9 lines)

203, BARRACKPORE TRUNK ROAD
CALCUTTA-26

Professor T. A. Davis
Biometric Research Unit

24 September 1962

Dr. Grote Reber,
"Stowell", CSIRO,
Stowell Avenue,
Hobart, Tasmania,
Australia.

Dear Dr. Reber,

Hope you had my letter No. Bio/TAD/1026 dated May 2, 1962.
I am enclosing a typed copy of my paper appearing in the next issue
of "Journal of Genetics" which I hope will interest you. I have
quoted your publication liberally. But I am not sure of the year
of publication of your paper in Castanea. Please confirm whether
1961 is correct or not. Also please give your comments on my
paper. If you have further papers on this line, please send me
copies.

Yours sincerely,

T. A. Davis
(T. A. Davis) 8419/62

THE DEPENDENCE OF YIELD ON ASYMMETRY IN COCONUT PALMS

By T. A. Davis
Indian Statistical Institute
Calcutta-35

Introduction

The main result here recorded is that coconut (*Cocos nucifera*) trees with a left-handed foliar spiral, yield, on an average, more nuts per year than those with a right-handed spiral. It is of course, likely that similar results will be obtained in other organisms. However, as the result appears to be unprecedented, I have published the data rather more fully than would be justifiable were I dealing with the effects of a manurial treatment or a gene substitution.

I previously (Davis, 1962a) mentioned that the leaves of coconut palms are arranged in five right-handed or left-handed spirals, that the two types of trees are almost equally common, and that the difference is certainly not inherited, and probably not determined genetically. In view of the finding, that asymmetry has an important effect on yield, I add some further data on the genetics and frequency of the two types, which confirm my former results.

History of the experiment

In India about 7,200 square kilometres (1.77 million acres) are under coconuts, this being 20 percent of the world area. Two-thirds of the Indian area is in the state of Kerala, and over 10 percent of the Kerala area is affected by a major disease, the root (wilt), responsible for an annual loss of some ten million rupees. It was desired to find out how far certain 'micronutrients' could prevent or control this disease. For this purpose an experiment was set up at the Central Coconut Research Station, Kayangulam. Half the trees were treated with Mg(A), half with B(B), half with Cu(C), half with Mn(D), half with Fe(F), half with Mo(F) and half with Zn(G). The design is a "2⁷ confounded design" comprising 128 treatments, for example treatment A D E G means treatment with Mg, Mn, Fe and Zn only. Each such treatment was applied to three trees, one healthy, one in the early stage, and one in the late stage of the disease. Thus the experiment involved 384 trees. Each of these trees, and many other trees standing in a 8 hectare (20 acres) field, received a basal manurial dose of 0.75 lb nitrogen as groundnut cake, 0.75 lb phosphoric acid as bone meal, and 1.5 lb of potash as "muriate of potash"(KCl) per year. The whole area received an annual dressing of 2 cwt slaked lime per acre, and each year a green manure crop was raised and incorporated uniformly into the soil.

The treatments were applied annually in shallow trenches round the bases of the stems. The experimental trees were so selected that none stood close to another. There are 16 main plots each containing 8 healthy trees, 8 with the early symptoms of disease, and 8 in the late stage. It was not possible to find, in each plot, isolated trees of the desired health category and the same age. More importance was attached to the category of the trees, and the age varied from 20 to 65 years.

From 1953 to 1960 I was in charge of this experiment, and can vouch for the accuracy of the data. There are records of the spreading and shedding of every leaf, measurements of leaves and counts of leaflets, opening of spadices, numbers of female flowers, numbers of nuts matured, etc. However the weight of nuts from individual trees was not recorded. Besides this, data on the yield of nuts from each tree from 1949 to 1952 inclusive are available. I do not doubt that they are substantially correct, but have reason to think that some nuts were stolen. The micronutrients were first applied in September 1953, and it was first intended to continue it for 5 years only. However since no significant effect of any treatment was found, it was decided to continue it for another five years.

As the data on nut yields were available, I decided to see whether the non-inherited asymmetry had anything to do with the yield. Each palm was classified for its leaf spiral and I found, to my very great surprise, the large effects shown in Figs. 1 to 3. Before discussing these it will be desirable to describe some tests made for possible bias.

Tests for bias

The trees were chosen without regard to their spirality. 177 of the 384 were Lefts. In future I shall use the words Lefts and Rights to mean trees with left-handed or right-handed foliar spirals. The expectation on a basis of equality is 192 ± 9.8 . The excess of Rights is not significant at the 5 percent level. Each of the 48 sub-plots contained 8 trees, all healthy or all in the early or late stages of the disease. The numbers of sub-plots containing a given number of Lefts are given in Table 1.

Table 1

Lefts	0	1	2	3	4	5	6	7	8
Plots found	1	1	6	14	14	8	3	0	1
Plots expected	0.34	2.34	7.01	11.98	12.80	8.76	3.75	0.92	0.10

The number of plots expected with n lefts is $\binom{8}{n} \frac{48.59^n \cdot 69^{8-n}}{128^8}$

It is a little unexpected that even one plot was found with 8 Lefts, however the variance of the number of Lefts is 1.969, the expected value being $\frac{8 \times 177 \times 207}{384^2} = 1.988$. Thus the Lefts and Rights were adequately randomized as

between blocks. With regard to treatments I have only tested randomness for the healthy palms, as these alone showed a significant excess of nuts on Lefts. Among the 128 healthy trees 29 Lefts and 35 Rights received treatments A, 29 Lefts and 35 Rights did not. This we get in Table 2(a), where a means treatment A not received.

Table 2

(a)		(b)		(c)		(d)	
L	R	L	R	L	R	L	R
A 29	35	B 32	32	C 28	36	D 27	37
a 29	35	b 26	38	c 30	34	d 31	33
$\chi^2 = 0$		$\chi^2 = 1.1350$		$\chi^2 = 0.1261$		$\chi^2 = 0.5044$	

(e)		(f)		(g)	
L	R	L	R	L	R
E 37	27	F 33	31	G 31	33
e 21	43	f 25	39	g 27	37
$\chi^2 = 8.0709$		$\chi^2 = 2.0177$		$\chi^2 = 0.5044$	

Only one of these values, taken by itself, is significant of bias.

The total $\chi^2 = 12.3585$, giving $P = .10$, which is not significant. In spite of the curious association of Lefts with an iron supplement, I think the randomization was adequate.

Treatment of exceptions

The yields of all 384 trees from 1949 to 1960 were tabulated. The tables contain 6144 entries, and I hope to publish them when the analysis of various interactions is completed. The data have been condensed in Tables 3, 4 and 5, and the graphs show further features.

Three of the 384 trees, one Left and two Rights, gave no nuts at all during these years. They were all diseased. Had they been included they would have slightly increased the excess yield of Lefts over the Rights. Thus, had they been included the evidence for the superiority of Lefts would be slightly stronger. Of the remaining 381, 3 healthy and 3 diseased trees died through lightning and disease.

years before their deaths. The nuts are harvested 8 times per year, and partial yields in the year when a tree died are omitted. A few other trees only started producing after 1949. These trees were treated like those which died. But in the case of the 128 healthy trees this adjustment only affects the pre-treatment yield, while it is the post-treatment yields which are more accurate and differ more significantly between Lefts and Rights. As it happens two of the healthy palms which died were Rights and one a Left. If the data had not been adjusted, the yield of the Lefts would therefore have been relatively higher.

The difference of yield between Lefts and Rights

In each of the 6 comparisons made in Table 6 it will be seen that the mean number of nuts on the Lefts exceeds that on the Rights. This is clearly shown in Figs. 1 to 4.

Table 6. Annual yields

Category	Number	12 years 1949 - 1960		6 years 1955 - 1960	
		Mean	Variance estimate	Mean	Variance estimate
Healthy	L 58	57.69	437.42	65.60	616.46
	R 70	49.82	366.74	54.28	455.17
Early diseased	L 60	32.95	292.12	36.54	323.24
	R 66	30.55	375.34	33.10	524.715
Late diseased	L 56	22.05	266.56	23.63	314.68
	R 64	20.04	186.59	20.33	239.12

The significance of these differences, as shown by the t test, is given in Table 7. The distributions of the means are near enough to normality to make the t test unobjectionable. However, it somewhat under-estimates the significance,

Table 7. Significance of Left-Right differences

Comparison	d. of freedom	t	P
Healthy 12 years	126	2.22	0.15
" 6 years	126	2.77	.0041
Early diseased 12 years	124	0.733	.234
" " 6 years	124	0.933	.18
Late diseased 12 years	118	0.736	.21
" " 6 years	118	1.09	.14

because, as will be seen from Fig. 1 to 3, during the last period of 6 years, in which the data are most reliable, the Lefts in each group surpassed the Rights in every year. Since the yields of a given tree in successive years are highly correlated, and, as the result of alternation in some trees, those in years n and n + 2 probably still more highly correlated, the excesses in different years are not independent. So it would be difficult to calculate how much the figure of .0038 would be reduced if the data for each year were considered.

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 overall probability that, the Rights produce as many or more nuts as Lefts is about .00014, and still less if the supplementary information from the first 6 years and from the concordance of different years is taken into consideration. Probably P would be about 10^{-5} . However there is no doubt of the significance of the result, and it is more important to show that Lefts yield more than Rights in other breeds and climates.

Fig. 5 shows the distributions of the yields of healthy Lefts and Rights from 1955 to 1960. If a population had been made up of half of each, its variance would have been 600.0, of which the difference between the means of Lefts and Rights contributes 64.07 or 10.7 percent. Among the healthy trees after treatment the Lefts gave 20.9 percent more nuts than the Rights. But it is perhaps more instructive to consider a population composed of equal numbers of Lefts and Rights. It would have a mean annual yield of 59.94 nuts. It is quite possible to cull the Rights as seedlings before transplantation. In this particular case this procedure would have increased the yield to 65.60, that is to say by 5.66 nuts per year, or 9.4 percent. This could be a considerable economic advantage. But before such a procedure can be recommended, it will be necessary to show that:

- (a) The increased number of nuts is not offset by a diminished yield of copra.
- (b) That the results obtained in one plantation in Kerala are also obtained elsewhere.
- (c) That the effect is not one of the type discovered by Roy (1960) and Lefts being stimulated by Rights, and Rights depressed by Lefts when they are grown in a mixture.

I hope to investigate these possibilities.

Differences in the leaves of Lefts and Rights

The higher nut yield of the Lefts is very probably due, at least in part to the fact that they possess more leaves. In 1953, when micronutrients were first applied, the total numbers of green leaves were counted. Each leaf was numbered with weather proof paint, and only the numbers of fully opened leaves (that is to say those whose lowest leaflets have emerged from the clasping leaf-sheath) were included. A tree usually has about five leaves which are not fully opened but partially visible above the sheath. The date of emergence of each leaf was also recorded.

Table 8 gives means and variances of leaf numbers. For the healthy trees the mean difference is 1.60 leaves, and quite significant. This means that Lefts have on an average 5.4 percent more leaves than Rights.

Table 8. Number of green leaves per palm

Particulars	Mean		Variance		t	P
	Left	Right	Left	Right		
1) Healthy palms	31.19	29.59	17.88	15.23	2.23	.014
2) Moderately diseased	29.18	28.25	22.12	18.12	1.17	.12
3) Severely diseased	26.16	25.40	19.85	18.88	0.97	.17

The differences for the diseased trees are in the same direction but not significant. Since they bear 20.9 percent more nuts, the greater number of leaves can hardly account for all of this excess.

The next step is to compare the leaves. I have as yet no data on stomata or chloroplasts, however table 9 compares 6 characters. 1583 leaves from 55 healthy trees (experimental trees), selected at random, were measured for their total length, length of lamina region and petiole, length and width of longest leaflet, and the number of their leaflets counted. Of these, 24 trees were Lefts. In each tree about 30 consecutive leaves were examined. As normally a tree takes a little over two years to produce 30 leaves, the data given in table 9 may be free from any bias due to seasonal variations.

Table 9. Coconut leaf : Summary of 6 characters

Characters	Means		$\bar{x}_1 - \bar{x}_2$	Variances		t	P
	\bar{x}_1	\bar{x}_2		s_1^2	s_2^2		
1. Total length	420.31 cm	407.14 cm	-4.83 cm	195.3504	182.6724	6.9486	.001
2. Lengths of petiole	101.55 "	106.09 "	-4.54 "	28.4510	28.7752	16.7466	.001
3. Lengths of green region	300.76 "	301.05 "	-0.29 "	761.2023	1258.0989	0.1774	0.8584
4. No. of leaflets on one half	108.19Nos.	109.59Nos.	-1.40 Nos.	19.8396	14.4354	6.7437	.001
5. Longest leaflet:							
i) Length	108.19 cm	106.84 cm	+1.35 cm.	63.1031	56.9374	3.4500	.001
ii) Width	5.29 "	5.30 "	-0.01 "	0.2672	0.3747	0.3534	0.723

Suffix 1 denotes Lefts

Suffix 2 denotes Rights

n_1 = 693 leaves (from 24 palms)

n_2 = 890 leaves (from 31 palms)

The total length of the leaf is the distance from the broadened leaf base to the tip of the central axis which ends usually with a single leaflet or somewhat prolonged into a small whip (Venkatanarayana, 1957). The region from the leaf base to the base of the lowest leaflet is regarded as the petiole and that from the base of the lowest leaflet to the base of the topmost one forms the green leaf region or the leaflet-bearing region. This length has been obtained by subtracting the length of the petiole from the total length of the leaf. The number of leaflets is usually counted for one side. But the leaflets of both the sides are not the same in number. While making the counts, no specific side was preferred, and it is presumed that the probability of counting both sides is equal and therefore the difference between sides, might not have vitiated the results significantly. The length as well as width of the leaflets increase when proceeding from the lowest leaflet (nearer to leaf base) and at about the third of the leaflet-bearing region from the base, the longest and presumably the widest leaflets are met with. It is customary to measure the length and width of this leaflet for estimating the green leaf area.

Table 9 contains some leaf measurements. While the overall length of the leaf of a Right is greater than that of a Left by 4.83 cm, the length of the green leaf portion which is the vital part of the leaf, is practically the same for both the types. The difference, therefore, is brought about by the significantly longer petiole in the case of the Right. Patel (1938) considers the longer petiole to be decidedly an undesirable character since it is positively correlated with longer peduncles of inflorescence. Further, longer leaves are associated with palms living under over-crowded situations, and where there is lack of light. A leaf of a Right has 1.4 leaflets over the other on one side and this works out to be 1.29 percent. But a Left is superior by possessing 1.26 percent more width of the longest leaflet. Thus, the green leaf area of a leaf of the Left may be regarded as equivalent to that of its counterpart. Therefore the excess 1.6 leaves per palm of the Left is significantly more than the Right. Normally this should contribute to some extent the production of the extra number of nuts.

The extra number of leaves of the Lefts normally should enhance the number of their bunches, although a greater number of bunches need not necessarily denote a greater number of nuts. The numbers of leaves shed by all the healthy and diseased (experimental) palms during the 12 months in 1958 are given in table 10.

Table 10. Number of leaves shed during 1958

Particulars	Left handers			Right handers		
	mean	max.	min.	mean	max.	min.
Healthy palms	13.59	17	11	13.58	16	9
Moderately diseased	13.23	16	7	13.23	17	9
Severely diseased	12.65	16	10	12.36	16	7

Among the healthy group, the Lefts and Rights had shed the same number of leaves. As there is a positive correlation between the leaves shed and leaves produced in coconut, it may be presumed that the rate of production of leaves in the Lefts and Rights is the same when once the stage to possess the normal numbers of leaves is reached. This may therefore mean that the leaves of the Lefts remain green on the crown for a longer period.

New genetical data

Besides the data (Davis 1962a) for trees both of whose parents are known, I give data on 308 seedlings from 5 mothers in a large nursery, sown in 1960 and examined in 1961. The pollen parents are of course unknown, but presumably were about equal numbers of Lefts and Rights. Table 11 shows no significant heredity.

Table 11. Leaf spirals of progeny obtained by open pollination

Seed parent and its spiral	Bunch No.	Spiral of progeny		% lefts	
		L	R		
1 L	1	nil	1		
	2	4	5		
	3	8	4		
Total for the tree		3	12	10	54.55
2 L	1	10	5		
	2	9	9		
	3	1	4		
	4	15	20		
Total for the tree		4	35	38	47.95
3 R	1	2	nil		
	2	3	4		
	3	10	6		
	4	2	4		
	5	1	nil		
	6	1	2		
	7	4	4		
	8	6	8		
Total for the tree		8	29	28	50.88
4 R	1	6	6		
	2	8	15		
	3	5	8		
	4	14	12		
	5	10	14		
Total for the tree		5	43	55	43.88
5 L	1	10	7		
	2	12	12		
	3	9	8		
Total for the tree		3	31	27	53.45
Grand total for 5 trees		23	150	158	48.70

The 3 left seed parents gave 78 L, 75 R, the 2 Rights gave 72 L, 83 R, $X^2_1 = 0.632$, so the slight tendency to resemble the seed parent is quite insignificant.

However in view of our ignorance it is worth while to enquire whether there is any evidence of somatic segregation within bunches. The values of χ^2 for heterogeneity for the 5 trees are:

$$\chi_2^2 = 2.262$$

$$\chi_3^2 = 3.058$$

$$\chi_7^2 = 5.411$$

$$\chi_4^2 = 2.097$$

$$\chi_2^2 = 0.302,$$

totalling $\chi_{18}^2 = 13.13$, $P = .78$. It is possible that further work might show a significant tendency to equality within bunches. There is no suggestion of segregation between bunches.

Table 12 gives data on asexual reproduction in exceptional palms scattered over most of the coconut-producing area of India and observed by myself since 1960. Double shoots in a coconut are possible due at least to three causes. In a fruit only one seed usually develops, the other two aborting at an early stage. But in exceptional cases where two seeds remain fertile, two shoots (one from each seed) are possible from a fruit. Even in the case of fruits with only one developed seed, two or more shoots are possible due to polyembryony. Further, when the single shoot branches at an early stage, two shoots from a fruit are possible, and this phenomenon is called suckering. I have also mechanically divided the single shoots in two nuts

Table 12. Double shoots, Branching/Suckering

		L	R	Total shoots	L-R
Double shoots	20 twins	1	1	40	-
	7 "	2	0	14	+14
	6 "	0	2	12	-12
Branching	2 trees	1	2	6	- 2
	2 "	2	1	6	+ 2
	1 tree	3	0	3	+ 3
	1 "	0	4	4	- 4
	3 trees	3	2	15	+ 3
	1 tree	3	3	6	-
	1 "	4	2	6	+ 2
	1 "	2	5	7	- 3
"Bulbil shoots" mother L	16	4	20	+12	
Total	46	77	62	139	+15

Tall selfed (mother L)	16	16	32
Spicata (B.7) L x Tall (B.4) R	14	11	25
Tall (B.4) R x Spicata (B.7) L	6	6	12

inducing two shoots in each case (Davis, 1960). I have studied the direction of leaf spiral in 33 such double shoots. Of these, twenty shoots had one left and the other right. But in seven others, both the shoots had left spirals while in six others both were rights. On a random basis, for 33 pairs of twins, the position will be,

Spiral	Observed	Expected
LL	7	8.25
LR	20	16.5
RR	6	6.25

There is a slight excess of unlike pairs, but this is not significant.

$$\chi_{1c}^2 = 1.09$$

I also give the spiral directions of the various shoots of branching and suckering palms examined by me. The shoots per palm ranged from three to seven. However, I have observed coconut palms with as many as 27 shoots, but their leaf spirals could not be examined. For the sets of 3, the following is the situation,

Spiral	Observed	Expected
LLL	1	0.625
LLR	2	1.875
LRR	2	1.875
RRR	0	0

Similarly for the sets of 4, 5, 6 and 7 the orders can be tabulated. There is no indication of the character being inherited. I consider that in a palm with more than one shoot, even if one shoot shows a different leaf spiral, it suggests the non-genetical nature of the character. Since these are the vegetative shoots, they can be layered (Davis, 1961 b) and propagated into individuals. In which case one could get clones with different spirals. However, another phenomenon occurs in the coconut where the flower bunches instead of developing into spadices revert to vegetative shoots, occurrence of which has been recorded by many. In one such tree where the mother was a Left, I found 16 of the "progenies" out of 20 behaving like the mother. Thus the bulbil-shoots have a strong resemblance to the "mother", $\chi^2_c = 6.05$. More accurately, the probability of getting 16 or more out of 20 resembling the parent is $6,196 \times 2^{-20}$, or 0.00591. So it is fairly sure that there is real resemblance. But I feel it may be hasty to come to conclusions from a single case. I propose examining more of such abnormal palms.

Self-pollination also can be effected artificially in the tall variety. Since the viability of the pollen can be easily retained for over a week under normal desiccation, within which period the female phase of the same spadix is sure to commence. Of course, retaining the viability of the pollen is no longer a problem since under deep-freezing, pollens remain viable even for a year. At the Agricultural Research Station at Nileshwar, Kerala, there are progenies obtained by controlled self-pollination. Second generations of these palms are also being obtained by further self-pollination. Out of the 16 progeny I examined at Nileshwar of a tree subjected to self-pollination, exactly half the number possessed a left spiral. Spicata is a peculiar variety of Cocos nucifera where the spadix remains unbranched and which bears a greater number of female flowers than males (Jacob, 1941). When this was crossed with an ordinary tall (B 4) having different leaf spirals, out of 25 progeny, 14 were Lefts. And when tall (B 4) was crossed with the spicata, exactly half progeny were Lefts.

Among palms, Hyphaene thebaica, H. coriacea and H. indica have the normal capacity to branch. There is a controversy with regard to their mode of branching. According to some it is dichotomous branching, while others consider the buds to be axillary. I am inclined to believe the latter view. This can perhaps be better understood if the branching which is rather common in Chrysalidocarpus lutescens, a suckering palm, is traced. Recently I observed the branches of a few palms of Hyphaene thebaica growing at the Botanical Garden, Howrah, and noted that the leaf spiral in different branches differed. There is also no order of this irregularity.

Having enough data to prove that the leaf asymmetry in the coconut is non-inherited, I made an attempt to see whether the direction of leaf spirals could be changed by artificial means. I started mechanically dividing the growing points of young seedlings. In a seedling having a left-spiral, when the division was effected, growth continued through only one half and this subsequent shoot had a right spiral. While many shoots behaved like this, in some, the same direction was maintained. These shoots were again and again divided till most of them died. Thus I saw that during some divisions, the direction of spiral in the subsequent shoot changed while in others not. I may further mention that the leaf spirals of the different shoots of the two twins I have induced artificially are of opposite directions. It is more interesting that one of the dwarf (green) palms at the Indian Institute, Calcutta has on its stem clear indication of change of the leaf spiral from left to right at a point about 0.7 m above ground level and where a prominent abnormal swelling is visible which I believe is the result of severe mechanical injury.

Frequency of Lefts and Rights

I had earlier reported my observation on 3028 palms gathered from eight small regions in Calcutta, Madras and Kerala. The Lefts accounted for 52.05 percent, and some peculiarity was observed between the smaller groups. The difference of the totals was significant ($P = .020$) by the usual criterion. This would not be so if the ratios in the different groups were significantly heterogeneous. But X^2 as a test of homogeneity was not very high in spite of one exceptional population. So I decided to observe a large number of trees (over 10,000) first, to establish the existence of the excess of lefts with higher probability, secondly to establish whether exceptional populations are common, and thirdly to detect regional or racial differences, if they exist.

Data given in table 13 are about the tall variety of coconut collected personally by myself from five of the coconut growing states at centres mentioned below; West Bengal : Calcutta, Howrah and 24 Parganas; Orissa : Cuttack, Sakhigopal and Puri; Andhra Pradesh : Anakapalle, Visakhapatnam and Waltair; Madras : Madras city, Madurai, Kanyakumari and Nagercoil; Kerala : Kayangulam, Ernakulam, Kozhikode, Nileshwar and Kasaragod; and Mysore : Mangalore. The palms observed include bearing

Table 13. Distribution of lefts and rights in India
(Data collected by author)

Place	Lefts	Rights	L+R	L-R
1. West Bengal	867	829	1696	-38
2. Orissa	712	734	1446	-22
3. Andhra Pradesh	679	521	1200	+158
4. North Madras	672	695	1367	-23
5. Central Madras	522	513	1035	+9
6. South Madras	537	507	1044	+30
7. South Kerala	523	504	1027	+19
8. Central Kerala	474	493	967	-19
9. North Kerala	793	703	1496	+90
10. Mysore	207	203	410	+4
Total	5986	5702	11688	+284

and non-bearing palms and even young seedlings. I consider my observations to be fairly accurate, since I am familiar with alternative methods of determining the leaf spiral if I met with doubt by one method. Out of the total of 11,688 palms examined, 51.214 percent are Lefts. Though the Lefts are in excess, it may be mentioned that this figure is slightly less than what I got earlier on a much smaller population. The sub-figures are almost evenly distributed except that for Andhra where the Lefts are 56.583 percent. However, X^2 on the total is 47.78 and hence P is less than 10^{-7} .

I had also arranged to collect similar data (on tall variety) from a few more centres in India and the data are presented in table 14. The workers to whom the requests were made to observe the leaf-spirals and familiar with the crop, and clear instructions were given as to the method of making the observation. Out of 3,268 palms

Table No. 14. Distribution of lefts and rights in India
(Data obtained through others)

Place	Lefts	Rights	L+R	L-R
1. Assam : Karimganj	254	252	506	+2
2. Madras : Kanyakumari	311	303	614	+8
3. Kerala : Neyyattinkara	189	231	420	-42
" : Kayangulam	421	358	779	+63
" : Kumarakom	215	185	400	+30
4. Maharashtra				
5. Gujarat : Bhavnagar	302	247	549	+55
Total	1692	1576	3268	+116

thus examined, the Lefts form 51.774 percent. In five out of six centres, it was the Lefts that were in excess though in small degrees. Thus when the Indian figures are pooled (tables 13 and 14) we get 51.337 percent of the 14,956 palms as Lefts and an excess of Lefts in 12 out of 16 populations.

Leaf data from abroad

Since the distribution of the two types of palms in India has been observed to be almost in equal proportions, I was interested to see how the palms in the rest of the world behave with regard to this leaf character. The coconut is distributed almost throughout the tropics, and the main regions according to Leo Schnurmacher (1938) are : Malayan Archipelago, consisting of the Philippines, Netherlands - Indies (now Indonesia), Sarawak, Papua, New Guinea, Timor and Gambia; South East Asia comprising Malaya, Siam and Indochina; India and Ceylon; Pacific Territories (Gilbert and Ellice Islands, Nauru, Mariana, Carolins and Marshall Islands, Solomon Is., New Caledonia, Fiji, Samoa, Tonga and Cook Is., French Oceania and Guam); East Africa and neighbouring states such as Mozambique, Madagascar, Tanganyika, Kenya, Zanzibar, Seychelles and Mauritius; West Africa, chiefly Gold coast, Nigeria, Dahomey, Guinea, Togoland, Angola etc.; West Indies consisting of Trinidad, Tobago, Jamaica, Grenada, St. Vincent, Virgin Islands, Puerto Rico, St. Lucia and St. Kitts; Central and South America such as Mexico, Br. Guiana, Panama, Honduras, Columbia and Surinam.

Research organisations are not so far set up in all the above-mentioned countries or regions. But I am in contact with about 40 organisations covering most of the major coconut producing countries. I am glad that over 75 percent of the organisations responded to my request favourably by furnishing me with the data asked for by actual counts. In a few countries, the information was obtained through more than one agency. I took care to furnish detailed procedures including sketches to these agencies in order to collect uniform data, and I am satisfied that with a single exception (Br. Honduras), my explanation proved clear enough to be followed without confusion.

I have given in table 15 the figures received from the various countries and that obtained from India, and they are arranged geographically starting from Tonga Islands in the Pacific Ocean, going west-ward via Indian Ocean, Africa, Atlantic Ocean and the Americas. The sums of the Lefts and Rights are almost equal. Of these figures, the one received from Andaman Islands are very peculiar, since the Lefts are only 37.35 percent. When I requested for more data from a different locality, the subsequent figures also showed the same peculiarity with a slightly increased intensity. Thus the world totals give 50.76% Lefts without the Andamans which percentage is reduced to 49.85 when the figures for Andamans are considered. However, the frequencies of Lefts and Rights in all the countries (from which data has been obtained) is almost one half in each case, in spite of this character being non-inherited. On the other hand the total American figure is 57.18% Lefts. But that for British Guiana is 63.51% which is as aberrant as the Andamans sample. A glance at the columns showing the differences of Lefts and Rights in table 15 will show that a slight excess of Rights is perceivable for countries starting from Tonga Islands roughly up to Ceylon. But beyond this, the Lefts are on the increase and the intensity goes on increasing as we proceed towards America. The gradual drift in the proportion of the Lefts and Rights with distance (longitudinally) is unexpected and an explanation perhaps is worth trying for. Though I do not deny the possibility of slight inaccuracies in the figures received from abroad I do not think that this gradual change with distance is due to any inaccurate observation.

Table 15. Distribution of lefts and rights. World totals

Country	Lefts	Rights	L+R	L-R	$\frac{L-R}{L+R}$
1. Tonga Is.	234	266	500	-32	-.064
2. American Samoa	516	484	1000	+32	+.032
3. Western Samoa	96	104	200	-8	-.040
4. Fiji	223	277	500	-54	-.108
5. New Hebrides	265	235	500	+30	+.060
6. New Caledonia	216	334	550	-118	-.215
7. Br. Solomon Is. Protectorate	1461	1621	3082	-160	-.052
8. Trust Territory of Pacific Is.	247	275	522	-28	-.054
9. Papua and New Guinea	406	398	804	+8	+.010
10. Netherlands New Guinea	272	228	500	+44	+.088
11. Philippines	726	774	1500	-48	-.032
12. North Borneo	244	332	576	-88	-.153
13. Sarawak	275	325	600	-50	-.083
14. South Vietnam	1833	1478	3311	+355	+.107
15. Malaya	272	228	500	+44	+.088
16. Andaman Is. (India)	903	1597	2500	-694	-.278?
17. Assam (India)	254	252	506	+2	+.004
18. East Pakistan	499	586	1085	-87	-.080
19. Ceylon	347	353	700	-6	-.009
20. India : Bengal, Orissa, Andhra	2258	2084	4342	+174	+.040
21. " : Madras	2042	2018	4060	+24	+.059
22. " : Kerala	2615	2474	5089	+141	+.028
23. " : Mysore, Gujarat & Maharashtra	768	691	1459	+77	+.053
24. Mauritius	15	19	34	-4	-.118?
25. Zanzibar	244	216	460	+28	+.061
26. Nigeria	222	278	500	-56	-.112
27. Dahomey	520	510	1030	+10	+.010
28. Ghana	568	557	1125	+11	+.010
29. Ivory Coast	505	554	1059	-49	-.046
30. Sierra Leone	784	749	1533	+35	+.023
31. Suriname	475	335	810	+140	+.173
32. Br. Guiana	416	239	655	+177	+.270?
33. Jamaica	467	443	910	+24	+.026
Total	21188	21314	42502	-126	-.003

The dwarf and other "varieties"

There are only two main varieties of coconut, the tall and the dwarf, although an intermediate is also noticed in some localities (the King coconut in Ceylon, Gangabondam in Andhra, India). The tall variety is characterised by its prodigious height, longevity up to about one hundred years and regular bearing habits. It takes about seven years to commence flowering and is a highly cross pollinated variety. / the other hand starts bearing by the third year of planting and largely breeds true to type, since self-pollination is possible. It grows to only half the tall, and dies by about the sixtieth year. Cultivation of this variety on a large scale is not preferred on account of its poor copra.

I have given in table 16 data relating to the leaf spirals of the dwarf variety, the semi-dwarf (serial numbers 8 and 9) and a few other "varieties". The Lefts on the total of 1263 palms account only for 47.83 percent. When only the dwarf palms are considered (numbers 1 to 7), the Lefts are slightly less, 47.21 percent. Of the seven centres, five have excess Rights, one Left and the seventh is almost neutral. Of the two American figures, while Jamaica has 54.74 percent Lefts, Suriname has 54.68 percent Rights and this do not seem to be in conformity with the figures for the tall variety.

Table 16. Dwarf and other varieties of coconut
(Distribution of Lefts and Rights)

Place	Lefts	Rights	L+R	L-R
1. Dwarf : Jamaica	104	86	190	+18
2. Dwarf : Trust Territory of Pacific Is.	16	20	36	-4
3. Dwarf : Zanzibar	15	25	40	-10
4. Dwarf : Surinam	218	263	481	-45
5. Dwarf : India, Kayangulam	72	71	143	+1
6. Dwarf : India, Kasaragod	31	41	72	-10
7. Dwarf : India, Calcutta and Madras	34	42	76	-8
8. King Coconut	8	13	21	-5
9. Gangabondam	14	18	32	-4
10. Tall x Dwarf cross	54	53	107	+1
11. "Spicata" x Tall	3	1	4	+2
12. Tall x "Spicata"	6	6	12	-
13. Other exotic races	30	21	51	+9
Total	605	660	1265	-55

From the above table, it is fairly clear that the dwarfs have an excess of Rights. The progenies between the tall and the dwarf show almost a non-aligned position. But this being a single case comprising a smaller number of seedlings it may be regarded as a chance occurrence.

Discussion

Further data confirm that the direction of the leaf spiral is not inherited. One can also add with some assurance that it is not genetically determined. For there are cases of genetical determination without heredity, for example sex in human beings and many animals, and heterostylism in plants where illegitimate pollinations are completely sterile. The data of Tables 11 and 12 also suggest that it is not due to extra nuclear segregation. I am investigating asymmetry in other plant species, and this may suggest reason why Lefts and Rights occur in nearly equal numbers. I also hope to discuss the world distribution more fully.

The slight excess of Lefts in most populations could be explained as follows, if a young seedling had exactly equal probabilities of being a Left or a Right. The Lefts have more leaves and a larger leaf area. This may enable them to resist diseases and pests better, and if the most vigorous seedlings are selected, Lefts may be preferentially chosen. Both natural and artificial selections may operate.

I hope later to correlate other characters with the direction of the foliar spirals. These include girth of stem and height at given ages, the number of leaves in seedlings, the yield of toddy or sweet sap from inflorescences and possibly the hydrostatic pressure developed by the roots, which can exceed 12 metres of water (Davis, 1961). From the economic point of view the annual yield of copra and its oil content are still more important.

A number of scientific colleagues have been kind enough to write to me as to my results. Professor R.D. Preston, F.R.S. writes "The connection between the yield of coconut palms and the tilt of the conducting tissue is very intriguing indeed and is so unexpected as to be on the verge of the credible. Since the sign of the spiral is not inherited then one is compelled to assume that the orientation of the conducting tissue affects the disposal of the materials being conducted and I know of no mechanism which would incline me a priori to have believed such a phenomenon". The fibres in a coconut stem are arranged somewhat spirally, the twist corresponding to that of the leaf spirals. Patch (1911) was among the first

to report this. This applies to the fibres on the outer stele, but inner layers may tend to twist in the reverse direction. I have not so far succeeded in observing the presence or absence of a spiral organization either in the cell surfaces or the cytoplasm. The late Sir Ronald A. Fisher, F.R.S. was kind enough to examine my numerical data and to satisfy himself of their statistical significance. He wrote "He (Davis) is mistaken if he thinks that I think that he has nearly completed the elucidation of a very queer situation". Professor Haldane, F.R.S. makes the following suggestion "The larger molecules of which palms are built, and in particular the cellulose fibres, are asymmetrical, and often arranged in spirals. But the direction of the foliar spiral may be a matter of "chance", that is to say determined by causes unconnected with the molecular asymmetry. The asymmetrical molecules may however fit more readily onto the growing tissues of trees with left-handed spirals". Dr. R.C. Snow, F.R.S. is also of opinion that the arrangement of leaves at an early stage may depend entirely on external causes.

I describe below some fantastic results on beans reported by the Astro-Physicist, Grote Reber (1961) which are comparable with the results on coconuts. Nine different kinds of pole beans (Hawaiian bean whose Linnaean name was not mentioned) were planted in rows of about fifty hills each. All nine kinds twined about in the same direction as a right-handed screw thread. The vines on even numbered poles of three rows were carefully unwound and twined backwards. The runner was loosely tied about two inches below the tip, and this process was repeated whenever the runner had grown eight to ten inches. All vines and pods were allowed to ripen, wither and dry on the poles and subsequently harvested. The field data on each hill consist of, number and weight of pods, number and weight of beans, weight of shucks, number and weight of vines. In all cases there is an appreciably better ratio of ounces of beans/ounces of shucks, and to a lesser extent ounces of beans/ounces of vines for the reversed vines compared to the normal vines. Apparently this training of the vines causes an increase in ratio of fruit to supporting structure. The same experiment was performed in a qualitative way both on Maui, Hawaii and Kempton, Tasmania, Australia, with similar results. The reversed vines gave somewhat better production of green beans in these cases. It was reported that the vine turned the same way in both the norther and southern hemispheres.

Dr. Snow raised a doubt whether the extra number of nuts may not be due to the mistake of the person who harvests them, "since the bunches hang to the Kathodic side of each leaf, it is easier for a right-handed man to cut them off in a left-spiralled tree, and he tends to miss some bunches in the right-spiralled". But the answer is simple. Even if a few ripe nuts remain uncut they will be accounted for either as shed nuts or during the subsequent harvest. The nuts of a tree are accounted for for a continuous period of 12 years, and the trees are harvested eight times in the year.

So far I have not weighed the copra of the two types of trees. Only if the increase in the number of nuts is proportionately seen in the weight of copra, can the superiority of the Lefts may be regarded as valuable. My yield data relate to a small locality in Kerala and I do not claim that this will be the situation elsewhere.

Summary

Further data confirm that the direction of leaf spirals in Cocos nucifera is non-inherited. In all probability it is also not genetically determined.

Fresh data on the frequency of Lefts and Rights from India as well as 23 other countries are reported. A slight excess of Lefts is noticed in most populations, but on the totals, the two groups do not differ significantly. However, in the case of a few countries, abnormal figures were received which show significant differences between the Lefts and Rights.

The Lefts give 20.9 percent excess yield of nuts over their counterpart, although it is based on a non-inherited character, and that is quite inexplicable. Among diseased palms also the difference is in the positive direction, but not significant by itself. The number as well as total area of the leaves of the Lefts are greater, and this may account, in part, for the increased yield of nuts of the Lefts. It is not known whether the increase in the number of nuts of the Lefts is associated with a proportionate increase in the weight of copra.

Acknowledgment

A portion of the data presented in this paper relates to another experiment I was conducting at the Central Coconut Research Station, Kayangulam, Kerala (India). I am grateful to the Indian Central Coconut Committee and Dr. K.P.V. Menon, Director, Coconut Research, Kayangulam for enabling me to collect these data. I am obliged to the Joint Director, Coconut Research, Kasaragod and the Superintendent, Agricultural Research Station, Mlleshwar with whose cooperation I could gather most of the information contained in tables 11, 12 and 16. I am specially thankful to the various foreign and Indian colleagues who supplied me very promptly with the valuable data on the frequency presented in tables 14-16. But for Professor J.B.S. Haldane, F.R.S., I would not have realised the full significance of the present findings. He is also responsible for the statistical treatment of most of the data.

Reference

1. Davis, T.A. (1960) : Clonal propagation in coconuts. Curr. Sci., 29, 273.
2. _____ (1961a) : High root-pressures in palms. Nature, 192, 277-278.
3. _____ (1961b) : Importance des racines aeriennes du cocotier. Oleagineux, 16, 653-661.
4. _____ (1962a) : The non-inheritance of asymmetry in Cocos nucifera. J. Genet., 58, 42-50.
5. _____ (1962b) : Asymmetry and yield in coconut. Experiment.
6. Jacob, K.C. (1941) : A new variety of coconut palm (Cocos nucifera L. Var. spicata K.C.Jacob) J. Bombay Nat. Hist. Soc., 41, 906-907.
7. Leo Schürmacher, Inc. (1956) : Review of coconut products for 1956. Manila.
8. Patel, J.S. (1938) : The coconut - a monograph. Govt. Press, Madras.
9. Petch, T. (1911) : Right and left-handed coconut trees. Ann. Royal Bot. Gard. Peradeniya. 5, 538-539.
10. Reber, R. (1961) : Reversed bean vines. Castanea, 25, 122-124.
11. Roy, S.K. (1960) : Interaction between rice varieties. J. Genet., 57, 137-152.
12. Venkatanarayana, G. (1957) : On certain aspects of the development of the leaf of Cocos nucifera L. Phytomor. 7, 297-305.

ASYMMETRY AND YIELD IN COCOS NUCIFERA L.

The leaves of Cocos nucifera L. are arranged in a right-handed or left-handed spiral, the angle between corresponding leaves in successive whorls being about 30°. The frequency of lefts among 3,028 trees in India was 52.05% (Davis, 1962) and among 13,842 trees elsewhere it was 52.90%. The asymmetry is not inherited (Davis, 1962) and has been regarded as trivial.

Of the 384 trees used at the Central Coconut Research Station, Kayangulam, Kerala (India) for trials of micronutrients, 177 were left-spiralled. They were divided into three groups, healthy, moderately affected by a major Root (wilt) disease, and severely affected. The mean number of nuts per year borne by the right-spiralled and left-spiralled trees in these groups between 1955 and 1960 inclusive are shown in Table 1.

Average number of nuts produced per tree per year

condition of trees	no. of trees		nuts per tree/year	
	right	left	right	left
Healthy	70	58	53.93	65.25
Moderate disease	67	61	32.60	35.98
Severe disease	70	58	18.58	23.15

The figures for the healthy trees give $t = 2,721$ (126 degrees of freedom). The probability for a difference of that magnitude or more to occur being small ($P = 0.0076$), the assumption that left-spiralled trees give higher yields, is strongly substantiated. The figures for the diseased trees, though not quite significantly different, strongly reinforce the significance of those for the healthy trees.

As neither the nuts nor the kernels from the two types of trees were weighed separately, it is of course possible that the total mean weight of copra produced by the left-spiralled trees was no greater than that from the right-spiralled. Nor is it claimed that all races of coconut, in all soils and climates, behave in this way. The biological fact here presented is however, I believe, novel. Many explanations can be suggested for it, of which I hope to discuss some elsewhere.

.....

DAVIS, T.A. (1962) The non-inheritance of asymmetry in Cocos nucifera.
J. Genet. (under publication).

T. A. Davis

Asymmetrie und Ertrag bei Kokospalmen

Zusammenfassung

Die Blätter der Kokospalme (Cocos nucifera L.) sind in links oder rechtsdrehenden Spiralen angeordnet; Zahlungen an 3,028 indischen Palmen und an 13,842 Bäumen in andern Gebieten ergaben, dass die Palmen mit linksdrehenden Spiralen etwas überwiegen (52,05% in Indien, 52,90% in den übrigen Verbreitungsgebieten). Kreuzungsversuche zeigten, dass wider Erwarten der Drehsinn der Blattspirale nicht genetisch fixiert ist.

In einem Feldversuch, der sich über die Periode 1955-1960 erstreckte, lieferten die Palmen mit linksdrehenden Blattspiralen eine grossere Zahl von Nüssen (Tab. 1).

Die Zahlen für gesunde Bäume, geben $t = 2,721$. (126, Freiheitsgraden). Als die Wahrscheinlichkeit dass die Unterschied, die ebensoviel oder noch mehr beträgt, klein ist, die Annahme dass, die linksdrehende Bäume eine höhere Ertrag haben, ist stark gestützt.