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CARBOHYDRATE BALANCE AS A MAJOR FACTOR
AFFECTING YIELD OF THE COFFEE TREE ^{1/}

By

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The greatest demand the developing fruit imposes upon the coffee tree (*Coffea arabica* L.) is for carbohydrate material originating in photosynthesis. How great is this demand relative to the capacity of the tree for carbohydrate production? Is the rate of current production of sugar and starch sufficient to support vegetative growth and fruit development simultaneously, or must previously accumulated storage carbohydrate be depleted? The relation between supply and demand may be determined by following an appropriate carbohydrate index without necessary reference to absolute rates of photosynthesis or rates of utilization. Such an index should show increases during periods when photosynthesis exceeds utilization and decreases when utilization is in excess. Moreover, changes in the index should bear a direct relation to the over-all balance of supply and utilization in the tree.

Carbohydrate fractions in various parts of the coffee tree were reported by Dean and Beaumont (6). Total sugars, starch, and acid-hydrolyzable materials were determined in roots, bark of vertical branches, fruiting lateral branches, new lateral branches, leaves, and fruit of fertilized and unfertilized trees. On examination of their data the fraction most sensitive to fertilization appears to be the starch in the leaves and young lateral branches. In fertilized trees these authors reported 13.56 percent starch in the leaves and 8.16 percent in the lateral branches; whereas, the total sugar concentrations in these parts were 5.63 percent and 3.70 percent, respectively. In many plants, starch is a reserve form of carbohydrate which can be utilized readily for growth processes. Hence, the starch content of coffee leaves or young lateral branches might satisfy the requirements of a carbohydrate index.

In choosing between the leaves and the lateral branches as the most appropriate plant part to be used in the index, it is evident that the leaves have a practical advantage in that successive samples may be removed from a tree with relatively little damage to the tree.

Diurnal Variations in Starch Concentration of Coffee Leaves

If values for leaf starch are to serve as a carbohydrate index for the coffee tree, they must reflect seasonal trends in the carbohydrate balance of the tree as a whole. Large variations in leaf starch during a day might miti-

^{1/} Credit is due Mr. Edward Fukunaga and his staff at the Kona Branch Station who supplied the growth measurements and collected leaf samples used in this study.

gate its value as an index. In many herbaceous plants the starch content of the leaves varies greatly in the course of a single day. In studying the hourly variations of carbohydrates in leaves of sunflower, Clements (2) found in one case that the starch concentration when expressed on a fresh weight basis, dropped from 1.6 percent to 0.2 percent in 1 hour between 6:00 p.m. and 7:00 p.m. This loss in starch represented a decrease of about 9 percent of the total dry weight of the leaf. Denny (7) determined the changes in starch content of leaves during the night for a number of plant species. In tobacco and sunflower leaves, losses as great as 90 percent of the starch were observed during the night. In leaves of woody plants such as grape, hawthorne, and peach, nocturnal losses of starch were significant, but not as great as in the herbaceous plants studied. From the studies of Clements and Denny it is evident that in many plants much or most of the starch found in the leaves functions as a transitory storage form and might not prove useful as an index of carbohydrate status for the plant as a whole.

Diurnal changes in the starch content of coffee leaves were determined at the Kona Branch Station on May 20 and 21, 1952. The trees sampled were in experimental plots receiving complete fertilization. The samples taken were fully mature leaves, which had been produced in the spring months of the same year. At each sampling time, four replicate samples of 12 leaves each were obtained. Each sample consisted of three leaves from different sides of each of four trees. Thus, a total of 48 leaves from 16 trees was obtained at each sampling. The same 16 trees were used at each time of sampling. The fresh weight of each sample was determined, the leaves were cut into thin strips and quickly dried in a forced draft at 70° to 74° C. Six to 10 minutes were required for collection of the samples. The total time elapsed between the beginning of sampling and the beginning of drying did not exceed 30 minutes. The results of this experiment are shown in table 1.

In contrast with the leaves of other plants as reported by Denny, the coffee leaves showed no significant loss of starch during the night. There was a statistically significant increase in starch between 12:05 p.m. on May 20 and 11:00 a.m. on May 21. This increase was not great, but may indicate that the over-all rate of synthesis was currently exceeding the rate of utilization of starch at the time these samples were taken. In any event, it is apparent from these results that the starch of coffee leaves is not subject to large fluctuations of the type found in sunflower by Clements. It is reasonable, then, to suppose that in the coffee leaf starch is stored and utilized over periods of days or months rather than minutes or hours, as is the case with some other plants.

Seasonal Variations in Carbohydrates of Coffee Leaves

Between 1947 and 1951 a study of the seasonal variations in nutrient element composition of coffee leaves was conducted at the Kona Branch Station. The trees used for this purpose were made available by the Department of Horticulture. From the earlier results of these studies (4, 5) it became apparent that more knowledge was needed of the seasonal variations of carbohydrates in the coffee tree. For the purpose of obtaining such information, 18 trees were selected for detailed study. These trees were spaced 12 feet apart. Each of the trees had three vertical branches. These verticals were 1, 3, and 5 years of age in December 1949 and 2, 4, and 6 years old at the end of the following year. Leaf samples were obtained during the first week of each month during the period between May 1949 and March 1951. One sample of 10 mature leaves was obtained from

Table 1. Diurnal variations in the starch concentration (expressed as percentage of the dry weight) of coffee leaves.

Time of sampling	Starch
May 20 - 12:05 p.m.	10.63
2:00 p.m.	11.54
4:00 p.m.	11.92
6:00 p.m.	11.69
8:00 p.m.	11.94
May 21 - 5:10 a.m.	11.57
7:00 a.m.	12.28
9:03 a.m.	12.17
11:00 a.m.	12.25
Least significant difference	
5 percent	1.285
1 percent	1.742

the current year's growth on each of the older two vertical branches of each tree. During a portion of the study similar samples were obtained from the previous season's growth (i.e., the portion of the branches currently producing fruit). During the 1950 season, samples were also obtained from the 2-year-old vertical branch.

At frequent intervals during each season as the crop developed on the trees, samples of fruits were taken from each vertical branch. For each sampling date the cumulative production of fruit was calculated from the weight of a known number of fruits in the sample and the recorded weight of any fruit harvested.

Five lateral branches on each vertical were tagged and measured at regular intervals to provide an index of vegetative growth.

The results of these determinations on two vertical branches from each of 18 trees were plotted for detailed study. Since these data are too voluminous to be reported here in their entirety, illustrative examples have been chosen for detailed description.

An additional 24 trees were studied less intensively throughout the same period. From these trees leaf samples were obtained and analyzed, usually at monthly intervals. Determinations of yield and stem growth were made annually.

Carbohydrate fractions in the young mature leaves of one tree are shown in table 2. It may be seen that leaves from each vertical branch showed marked variations in starch content during the period of observation. In comparison with these variations in starch, the changes in concentrations of reducing sugars

Table 2. Seasonal variations in carbohydrates (expressed as percentage of the dry weight) of coffee leaves borne on vertical branches of different ages.

Date	Age of vertical branch								
	2 years			3 and 4 years			5 and 6 years		
	Starch	Reducing sugar	Total sugars	Starch	Reducing sugar	Total sugars	Starch	Reducing sugar	Total sugars
<u>1949</u>									
May				4.61	4.36	7.61	10.60	2.81	5.93
June				12.52			7.69	3.00	5.10
July				5.81			6.84	2.76	6.74
Aug.				4.03			5.32	2.56	6.26
Sept.				7.05			5.49	2.49	6.16
Oct.				6.34			3.62	2.65	5.88
Nov.				5.11	2.48	5.55	4.01	3.00	6.41
<u>1950</u>									
Jan.	6.91	1.90	6.34	10.77	1.88	6.32	8.69	2.07	6.17
Feb.	10.40	1.68	5.65	13.43	1.78	4.67	12.58	1.51	5.87
Mar.	11.42	1.51	6.63	9.64	1.99	6.53	13.01	2.11	6.55
Apr.	20.86	1.78	6.28	15.89	2.12	5.00	18.73	1.87	6.32
May	22.38	2.51	6.16	16.57	2.06	6.40	19.92	1.51	6.41
June	15.10	2.66	5.80	12.02			13.52	3.23	5.10
July	5.60	2.13	6.33	5.08			6.45	2.58	6.16
Aug.	6.55	2.40	5.89	2.70	2.42	4.39	4.24	1.98	5.56
Sept.	3.63	2.14	6.43	1.25	2.23	5.48	1.05	1.99	5.16
Oct.	2.06	2.01	5.34	1.06	2.21	4.98	0.68	1.72	3.60
Nov.	1.80	2.07	5.14	0.47	2.77	4.46	0.80	2.11	4.75
Dec.	3.11	2.22	5.54	0.73	4.58	6.55	2.33	2.32	6.19
<u>1951</u>									
Jan.	1.54	3.56	6.61	5.03	2.34	4.98	2.04	2.45	5.59
Feb.	3.94	2.99	7.16	5.35	2.41	6.58	3.60	3.19	6.56
Mar.	5.76	2.68	6.84	6.22	3.48	6.87	8.45	2.58	6.14

and total sugars in the leaves were essentially negligible. Leaves from the 2-year vertical showed variations from 22.38 percent starch in May 1950 to 1.54 percent in January 1951. Starch in leaves of the 4-year-old vertical varied from 16.57 percent in May 1950 to 0.47 percent in November 1950. For the 6-year-old vertical the variation was from 19.92 percent in May to 0.68 percent in October.

The period of rapid decrease in starch, as shown in table 2, corresponds with the period of rapid fruit growth. The intimacy of this correspondence is illustrated in figure 1. In this figure are plotted records of leaf starch, fruit pro-

2/ Explanation of figure 1. Plots for leaf starch are designated by the years during which the leaves were formed: 1948 leaves, — —; 1949 leaves — —; 1950 leaves x—x. Fruit produced during 1949 was borne on the stem segment bearing the 1948 leaves and is designated — —. Fruit produced in 1950 is designated — —. Designations for lateral branch growth during 1949 and 1950 are the same as for the leaves formed during those years.

duction, and growth of lateral branches from one vertical in its third and fourth years of age. Records are shown for starch concentrations in both younger and older mature leaves. Each curve is designated by the year during which the leaves were produced. For example, the 1948 leaves were those attached to the segment of stem on which were borne the 1949 fruits.

During May, June, and July of 1949 the starch content of the 1948 leaves dropped very rapidly. The 1949 leaves showed an increase in May which was followed by losses in June and July. Thus, during the early growth of the fruits, the starch content decreased first in the older leaves. As fruit growth continued, the starch content of the younger leaves also decreased. The moderate crop produced by this vertical branch in 1949 would not be expected to impose an excessive demand for carbohydrate reserves. Relevant to this observation, it is noted that the starch content of the 1949 leaves reached a minimum value in August. For the remainder of the period of fruit development, it appears that the photosynthetic production by these leaves was sufficient to compensate for any carbohydrate moved to the fruit. Starch accumulated during November, December, and January, a period when both vegetative and fruit growth were nil. In 1950 a much larger crop was produced by this branch. Rapid depletion of starch from both 1949 leaves and 1950 leaves was evident during May, June, and July, when this crop was developing. Starch values remained low for several months thereafter as production of the crop continued.

Records for 5- and 6-year vertical branches from two trees are plotted in figure 2. Starch values are for leaves produced in the same year they were sampled, except for the period between January and May when only leaves of the previous season were mature. In these two examples the relationship of fruit production to leaf starch depletion is further illustrated. The vertical of tree 115 produced only a negligible amount of fruit in 1949, and correspondingly, there was no decrease in leaf starch for this branch during the period between May and August. This result illustrates the fact that the decreases in leaf starch which may occur during the summer season are not entirely dependent upon climatic factors peculiar to that season but are a response to demand of the developing fruit. Furthermore, such decreases are related to the quantity of fruit produced. During the same period the branch from tree 255 which produced a good crop in 1949 lost starch from its leaves quite rapidly. In 1950 both branches had a good crop of fruit, and both lost most of the starch from their leaves during the period of rapid fruit growth.

From the above illustrations it may be seen that the starch concentration of the coffee leaf has attributes of a good carbohydrate index in that periods of rapid decreases in the starch values correspond to periods of rapid fruit growth when the demand for carbohydrate is known to be high. Moreover, at the end of the period of fruit development, the leaf starch values may increase rapidly.

Influence of Carbohydrate Reserves upon Growth and Yield

During years when climatic and physiological factors are favorable to fruit production, the quantity of fruit produced by a tree is dependent upon factors of tree capacity. Indexes of tree capacity are the cross-sectional area of the vertical branches and the amount of bearing wood produced by growth of lateral branches during the previous season (1, 5).

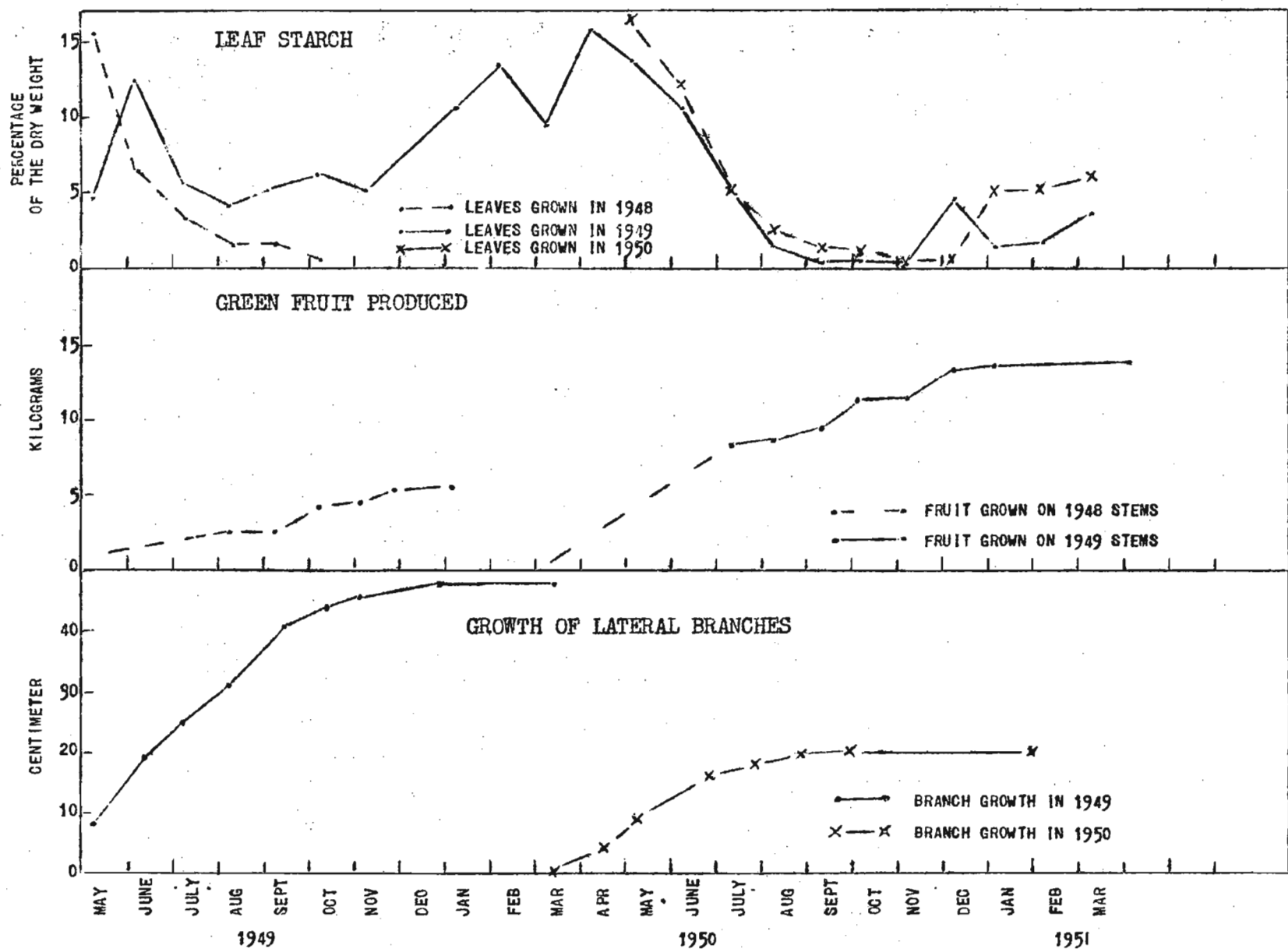


Figure 1. Seasonal records of leaf starch, fruit production, and growth of lateral branches from one vertical in its third and fourth years of age 2/

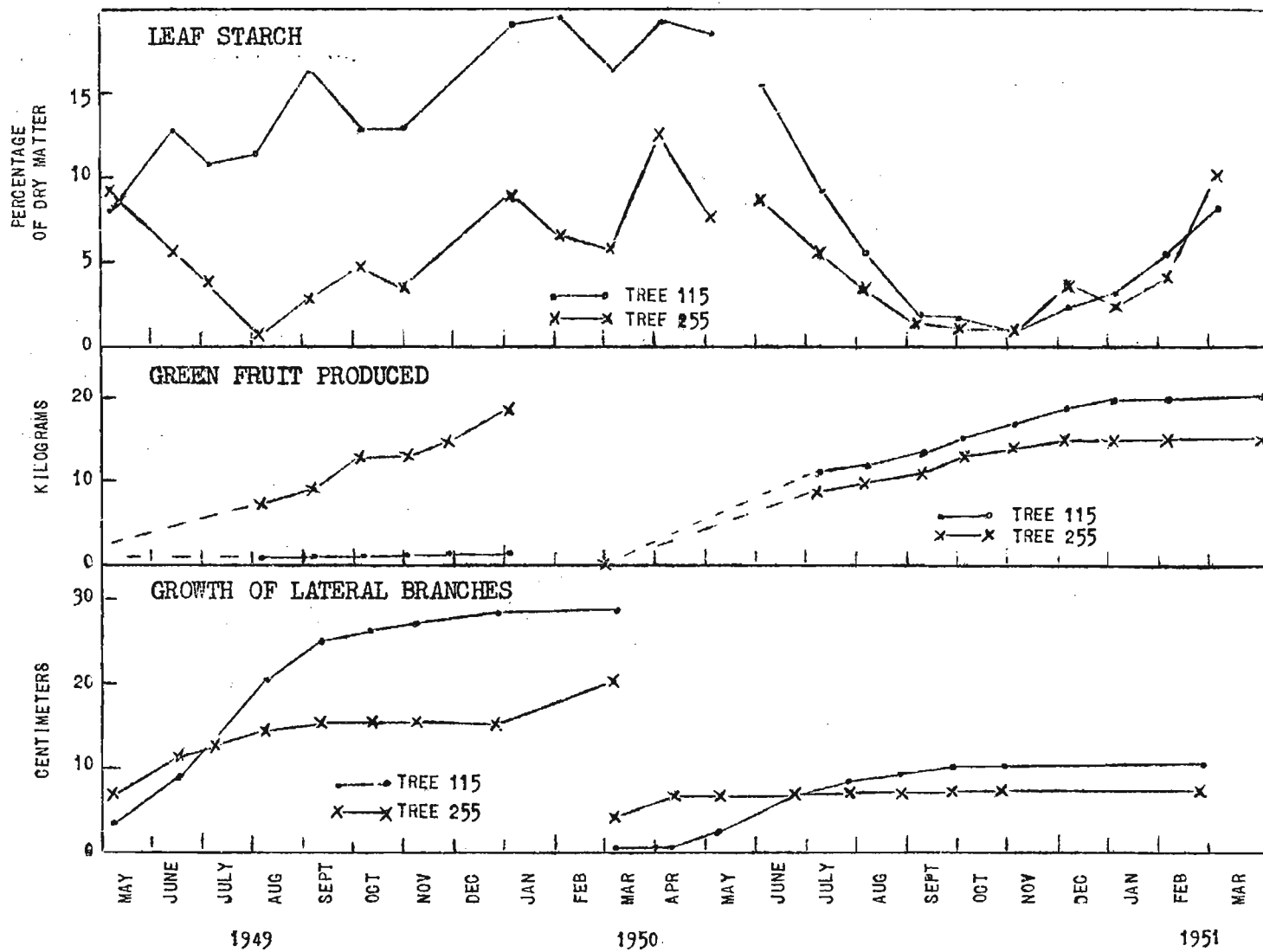


Figure 2. Seasonal records of leaf starch, fruit production, and growth of lateral branches from verticals in their fifth and sixth years of age. Starch values are for leaves produced during the same year as sampled, except for the period between January and May, when only leaves of the previous season were mature.

For a given tree, a year of heavy bearing may be followed by a year of light bearing. This may be attributed in part to insufficient production of new bearing surface (i.e., growth of lateral branches) while a heavy crop is being produced (1). That curtailed growth of lateral branches can be associated with an excessive depletion of starch from the young mature leaves during the growth of the fruit crop can be illustrated in the examples of figures 1 and 2. The records of figure 1 show that for this tree, growth of the lateral branches in 1949 proceeded at a generally rapid rate until September. The decreased growth rate in September may be associated with the lower rainfall in that month (figure 3). Final cessation in growth in November and December coincided in time with low minimum temperatures. In 1950 the growth rate had been decreased as early as July, corresponding in time with nearly complete depletion of starch from the young mature leaves. Tree 115 (figure 2) showed rapid growth in 1949 until September. Starch remained high throughout the growing period in this case. In 1950 there was only a brief period of rapid growth followed by near cessation in July, a month in which starch was being depleted from the leaves rapidly. Tree 255 showed a reduced growth rate as early as July in 1949, which corresponded in time with rapid depletion of starch from the leaves of this tree. This tree grew only briefly in 1950, its period of growth corresponding to a brief period of moderately high leaf starch. In brief, each of these trees for which detailed records have been presented showed curtailment of lateral growth early in the season to be associated with depletion of starch from the leaves. Where the concentration of starch in the leaves remained high, or at a moderate level throughout the growing season, the growth rate remained high throughout the summer months. In the latter cases, cessation of growth was during months of lower rainfall and lower minimum temperatures. This relationship between depletion of starch and early curtailment of lateral branch growth is found in the other trees studied as well as in the examples presented here.

From the results reported thus far it is clear that depletion of starch from the young mature leaves during the growing season is associated with curtailment of lateral stem elongation. Thus, insufficient carbohydrate supply during the growing season limits the bearing surface for the crop of the following year. In addition to this influence upon growth which may be considered an effect upon the bearing potential of the tree, an accumulation of carbohydrates in the newly produced branches following growth cessation appears essential to high yield. The degree to which this accumulation may occur is indicated by the increase in concentration of starch in the young mature leaves during the period of flowering and early fruit growth (December to May for trees grown in the locality of the Kona Branch Station). Most of the trees of this study showed increases in leaf starch between December 1949, and May 1950. The starch curve of figure 1 is typical of most of the trees. The curves for trees 115 and 255 (figure 2) represent the extremes encountered among the trees studied for this period.

To determine whether there is a relationship between starch accumulation during early fruit development and the yield later in the same year, it is necessary to relate yield to tree size. A "yield index" was calculated by dividing the total yield of each tree by the total cross-sectional area of the bearing vertical branches. Such a yield index should give a measure of the relative efficiency of a tree for production during a particular year, if it is assumed that tree capacity is faithfully represented by the cross-sectional area of the verticals. The latter assumption appears to be essentially valid since in a year of high production the yield per tree was found to be correlated with the cross-section area in a relationship which was nearly linear (5) (table 61).

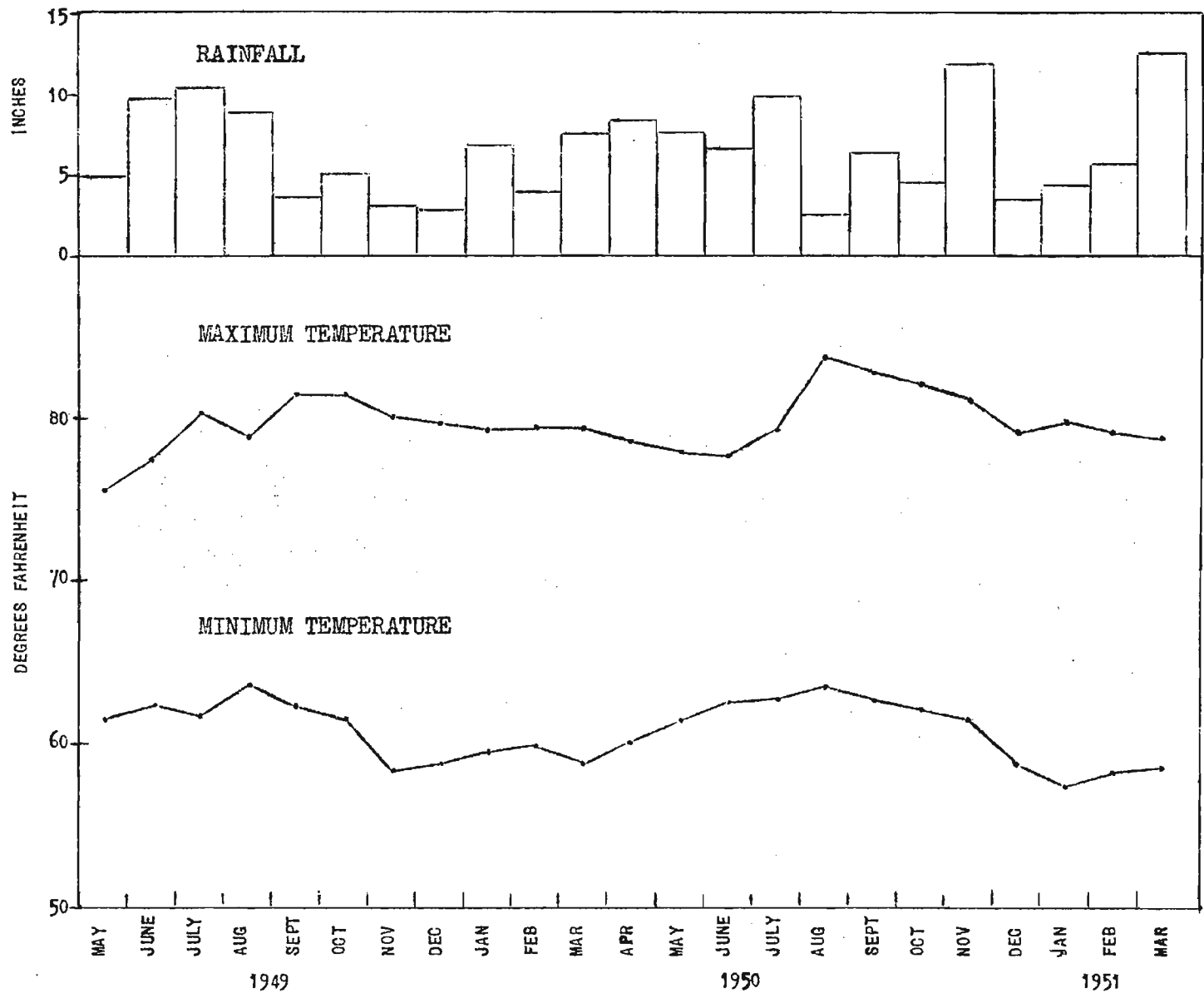


Figure 3. Monthly rainfall, mean monthly maximum temperatures, and mean monthly minimum temperatures at Kainaliu, Kona, Hawaii.

The yield index is correlated with the content of starch in the young mature leaves in April and May, as shown in figure 4. This relationship is based on all the data available to date. It represents the data obtained from 42 trees in 1950 (dots) and those obtained from 18 trees in 1949 (points marked x). The correlation coefficient is 0.8406. The concentration to which the starch in the leaves rises during early growth of the fruit appears to be, therefore, one of the important factors determining to what extent a tree will bear to its full capacity.

Inspection of the records from the 18 trees from which extensive data were obtained suggests another relationship which has not yet been subjected to detailed statistical analysis. This relationship has to do with the period of time during which the fruit continues to mature. During the 1950-51 season a number of the trees studied produced a large proportion of their mature crop in February, March, and April of 1951. This behavior can be traced back to a relatively high proportion of late flowering. Although the flowering behavior was not studied in detail, it is known in general that the major flowering occurs when a heavy rain follows a relatively dry period, usually February or March. November and December of 1949 were relatively dry months, but some heavy rain occurred in January 1950 (figure 3). In general, it appears that trees which had not accumulated a relatively high content of leaf starch by January 1950 had a high proportion of late fruiting. From these observations, the level of leaf starch at the time of flowering may be a major factor in determining the extent to which flowering will occur at one time. In other words, if the tree has accumulated insufficient reserves at the time when climatic conditions are suitable to initiate flowering, then the flowering may be sporadic, occurring over a period of several months. However, this possible relationship requires more detailed study.

Relationship of Leaf Starch to Total Leaf Dry Matter

It may be noted from the data which have been presented that the starch content of coffee leaves may vary from less than 0.5 percent of the dry matter to over 25 percent. The percentage of dry matter in a leaf, therefore, may be greatly affected by the amount of starch present. To determine how closely variations in starch are reflected in the total dry matter of the leaves, 107 samples of young mature leaves collected in May, June, and July of 1950 were subjected to statistical study. The correlation coefficient was found to be 0.9554. The regression line is the solid line of figure 5. The dotted lines in the figure represent the limits within which the starch content of any particular sample could be estimated with odds of 19 to 1. The regression equation for estimating starch as percentage of fresh weight from total dry matter, as percentage of fresh weight, is $Y = 0.5389 X - 16.1102$. This relationship is suitable for rough estimation of leaf starch in young mature leaves (at least for the months investigated) by merely determining the percentage dry matter of the leaves. Inasmuch as the accurate determination of starch requires considerable time and care, this relation may prove of value for diagnostic purposes when high accuracy is not required.

Factors Regulating Leaf Starch

From the relationships shown in figures 1 and 2, it is to be expected that, in a tree bearing anywhere near its capacity of fruit, starch will be depleted from the leaves during fruit growth, since the demand of the growing fruit apparently exceeds any possible rate of photosynthetic production which may take place concurrently. However, any factor which would aid photosynthesis during this period should have the tendency of alleviating and delaying this depletion, with the final effect of allowing vegetative growth to proceed for a longer period of

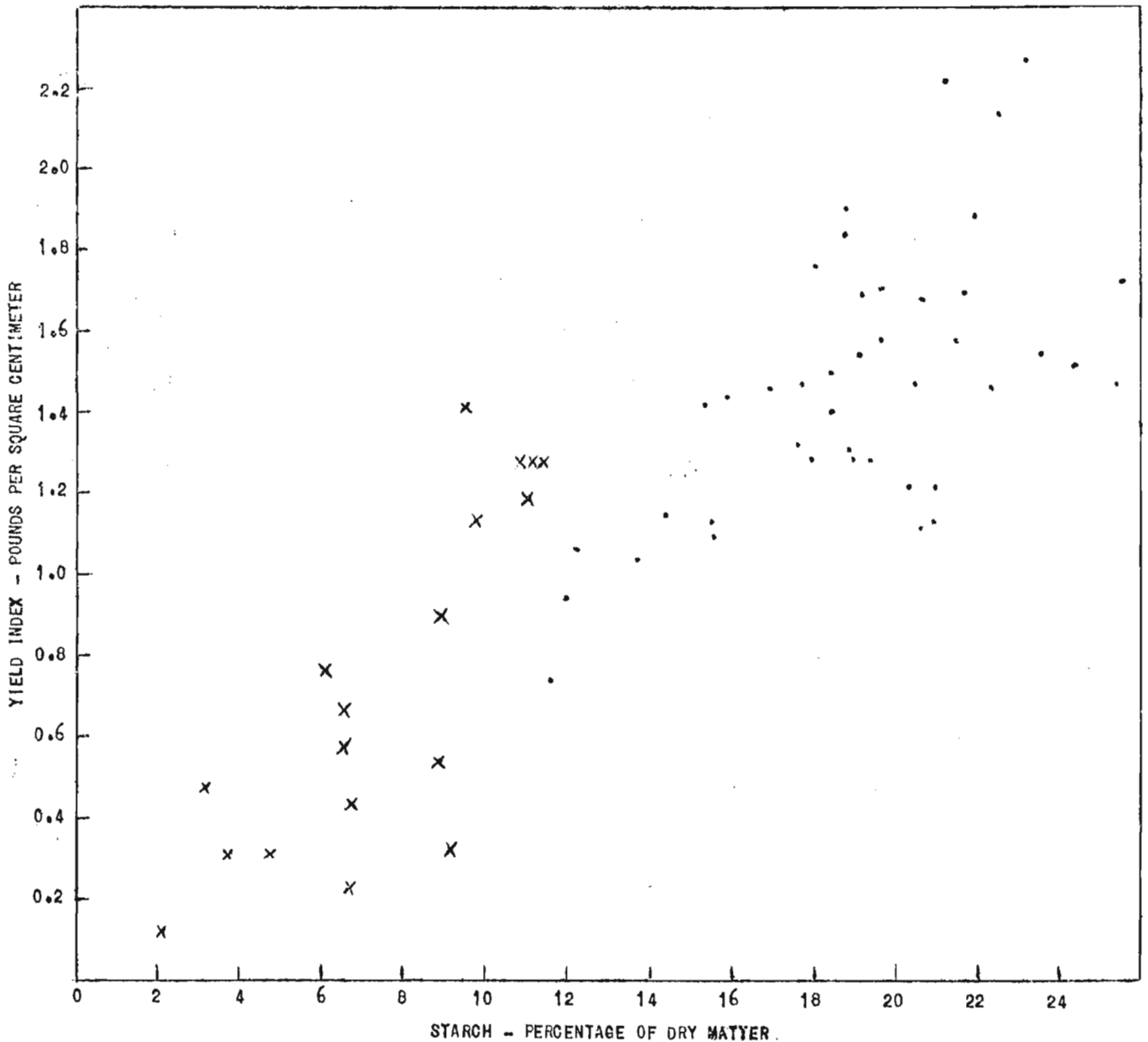


Figure 4. The relationship between leaf starch in April and May and the yield index (yield in pounds per unit of cross sectional stem area of bearing verticals in square centimeters). The data are from 42 trees during 1950 (dots), and from 18 trees in 1949 (crosses). See text for further details.

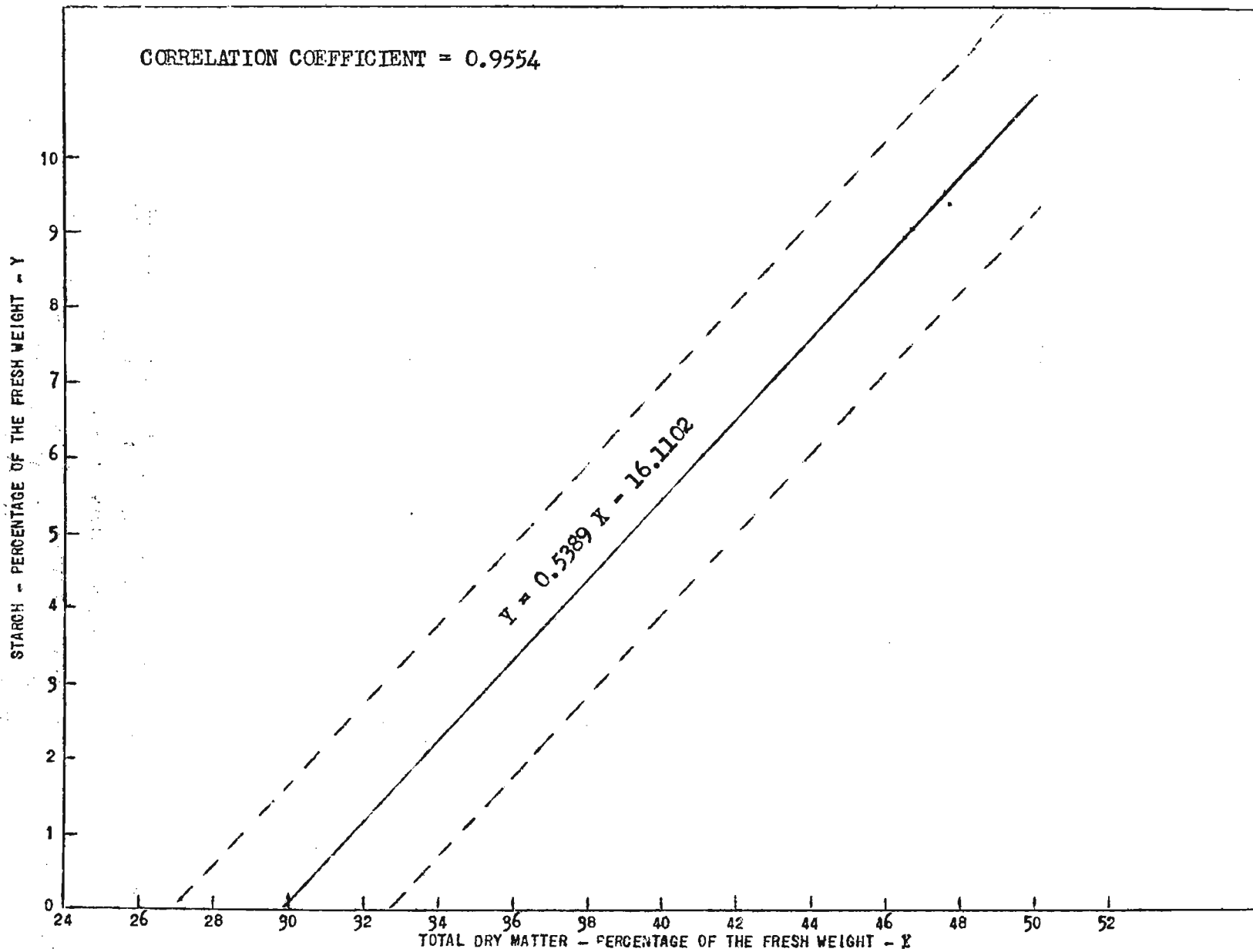


Figure 5. The relationship between total dry matter and starch. The solid line is the regression obtained from 107 samples of young mature leaves collected in May, June, and July of 1950. Dotted lines represent limits within which starch may be estimated from the dry matter of a sample with odds of 19 to 1.

time. This vegetative growth of lateral branches is essential in two respects. In the first place, it produces the bearing surface for next year's crop. And, of equal or greater importance, it provides new leaf area and hence photosynthetic production for both the current crop and that of the following year.

After the grand period of fruit growth, carbohydrates may be expected to accumulate as evidenced by the increases in leaf starch during this period (figures 1 and 2). The extent to which this rise occurs in the newly produced lateral branches has an important bearing upon the yield index of the next crop, as shown in figure 4. To control the bearing efficiency, it therefore appears necessary to promote this accumulation of carbohydrate reserve. One factor which may limit this accumulation is a deficiency of potassium.

In various plant species potassium deficiency is known to impair accumulation of polysaccharide reserves such as starch (3, 8). Sufficient potassium should be present in the trees at all seasons if yield is not to be limited. However, from results which have been reported in part (4, 5), and from further results to be reported elsewhere, it is evident that the most critical period with respect to the potassium concentration in the leaves is during the harvest season. The low concentration in the leaves at this time is related to a considerable accumulation of this element in the fruit. In trees bearing heavily, the potassium concentration of the leaves in December was found to be highly correlated with the percentage of dry matter in the leaves 2 months later (5). In view of the close relationship between the percentage of dry matter and percentage of starch in coffee leaves (figure 5), these results reported earlier indicate that the lack of sufficient potassium at the end of the harvest season may prevent the rapid accumulation of starch necessary for a high bearing efficiency. Attempts to offset this depletion of potassium by supplying potassium fertilizer at frequent intervals between March and July were not very effective, but it may be possible to increase the potassium concentration in the leaves by fertilization later in the summer.

A considerable amount of nitrogen is also moved from the leaves as the fruits develop. This depletion may be sufficiently severe to result in yellowing and early dropping of the older leaves, thus impairing the photosynthetic capacity of the tree. A small scale experiment conducted by Mr. Edward Fukunaga at the Kona Branch Station indicates that early leaf drop can be prevented by supplementary application of nitrogen during the summer months. A more comprehensive experiment on this question is now in progress.

Any factor which will increase photosynthetic rate would appear to contribute to yield of coffee. One factor which may be of considerable importance in some localities of the Kona district is light intensity. Although the benefits of shading have been stressed by some workers [see references in (9)], Tanada (9) found no ill effects of strong sunlight on coffee trees grown in nutrient solutions at Honolulu. Moreover, his results show that plants grown without shade had 3.71 percent starch in their leaves, but plants grown in one-half shade had only 0.32 percent starch. The relations of sunlight to yield in the coffee orchards in Kona still require investigation. General observations indicate that the lower elevations have more sunlight than the higher elevations of the Kona district, since the presence of blanketing clouds is more frequent at the higher elevations. In general, the times of flowering and fruit maturation are both earlier at the lower elevations. At lower elevations, flowering is more uniform, yields are high, and the fruit matures during a short period of time. Undoubtedly, temperature differences also play a part in some of these responses associated with difference in elevation. The need for further information on the interplay of

light and temperature factors in the physiology of coffee in the Kona district was illustrated recently by the increased incidence of "black bean," a disorder in which the cotyledons fail to mature, but shrivel and turn black. A survey conducted by Mr. Edward Fukunaga in May 1953 showed certain relationships which, at the least, are very suggestive. In the Kona district, black bean occurs in the late season harvest only at relatively high elevations. Several orchards in this area were investigated. The only orchards in which black bean was found were those in which the spacing distance between trees was narrow and pruning had been light. These orchards had very dense growth of foliage. Further, the black beans occurred on the lower branches of the older verticals, where the shade was most dense. Samples of young mature leaves were taken from three orchards at elevations of 1,500 to 1,800 feet. The percentages of dry matter in these leaves, the approximate starch contents as estimated from the relation of figure 5, and the actual starch percentages as determined by analysis are shown in table 3. The estimated starch percentages of the samples fall well within the range of deviation to be expected from the relation of figure 5. This illustration confirms the utility of the estimated starch values for purposes of approximation.

Table 3. Observations relevant to the incidence of black bean in three orchards at elevations of 1,500 to 1,800 feet in Kona, Hawaii as observed in May, 1953.

Orchard	Approximate spacing feet	Incidence of black bean	Leaf composition (fresh basis)		
			Dry matter percent	Estimated starch percent	Actual starch percent
A	9 x 9	none	39.69	5.28	4.17
B	7 x 6	occasional	32.50	1.41	1.47
C	7 x 6	high	28.46	0.00	0.82

The leaves collected from the orchard high in the incidence of black bean had the lowest starch percentage. In light of the relations of starch to growth and yield, as illustrated in earlier sections of this paper, it is suggested that black bean develops as a result of insufficient carbohydrate for the normal development of the fruit and that lack of sunlight is an important factor. If this is the case, cultural practices which should aid in preventing recurrence of this disorder are wider spacing and more heavy pruning. In any event, it is evident from these observations that more detailed studies of the relations of light and temperature to carbohydrate status of coffee trees grown at different elevations would be of value.

Summary and Conclusions

The concentration of starch in the leaves of the coffee tree represents a suitable carbohydrate index, as evidenced by the following:

1. Starch accumulates in higher concentrations in the leaves than in other parts which have been analyzed.

2. The concentration of starch in the leaves has a very wide range of variation (i.e., from less than 0.5 percent to over 25.0 percent).
3. Leaf starch in coffee does not vary greatly during a 24-hour period, showing that its accumulation does not represent transitory storage as is the case in some other plants.
4. Seasonal variations in the leaf starch concentration may be great. Concurrent variations in soluble sugar concentrations are relatively slight or insignificant.

Seasonal changes in the starch concentration of the leaves reflect changes in the balance between carbohydrate production and utilization. During the grand period of growth of the fruit, the leaf starch concentrations decrease rapidly. The rate and extent of this decrease is related to the amount of fruit developing. As fruit growth approaches completion, leaf starch concentration increases if nutritional or environmental factors are not limiting.

By following detailed records or logs of the starch concentration throughout a season for a number of trees, it is possible to detect several seasonal periods where the carbohydrate balance (as evidenced by the starch concentration) may become limiting and profoundly affect the yield of the tree:

1. During the grand period of fruit growth, if the depletion of carbohydrates is too rapid and too severe, vegetative growth may be limited. This has the twofold effect of limiting the bearing surface for the crop of the following year, and of limiting the leaf area and hence the capacity of the tree for photosynthesis for the current crop and for the following crop as well.
2. The productive efficiency during the current year may be limited if insufficient carbohydrate reserve has accumulated at the time of flowering and early fruit growth.
3. The extent of carbohydrate accumulation at the time when climatic conditions are favorable for flowering may affect the extent of flowering at that time, and hence the extent of early and late bearing.

Results to date indicate that some control over carbohydrate production and accumulation may be exercised through fertilization, spacing, and pruning. Further studies are needed to determine the effectiveness of these practices with reference to the relationships reported here.

Seasonal changes in the total dry matter of coffee leaves are closely correlated and are largely the result of changes in starch concentration. From this relationship an approximation of the starch level in leaves of specified maturity may be obtained by simply determining the percentage dry matter in the leaves.

Observations are described which, in light of the experimental results reported here, indicate black bean of coffee may be caused by lack of sufficient carbohydrate to permit normal development of the fruit under conditions of low light intensity.

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