THE INFLUENCE OF THE TIME OF FRUIT REMOVAL ON THE GROWTH, COMPOSITION AND BLOSSOMING OF ALTERNATE-BEARING SUGAR PRUNE TREES

by

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INTRODUCTION

Fruit thinning has long been practiced to improve the commercial qualities of fruit, but only within recent years has it been modified so as to cause blossom buds to form in the fruiting year of biennial bearing trees. Magness and Overley (35) and Haller and Magness (20) first indicated that thinning apples heavily, so as to provide a comparatively large leaf area per fruit, would tend to cause annual blossoming. Adopting this practice and introducing earlier times of thinning, Aldrich (1, 2, 3), Harley (23) and Magness (36) and their associates established annual blossoming in field trials with biennial bearing varieties of apples and pears.

In the Sugar prune, also, very early and heavy thinning or removal of the fruit has been found by Dr. L. D. Davis, at the Agricultural Experiment Station, Davis, California, to bring about blossom bud formation in the on year. This work was carried out for two years previous to 1936, when the present investigations were started, although the results have not been published.

These experiments indicate that there is a critical time in the determination of blossom buds which is much in advance of when they can be distinguished microscopically. In the Sugar prune the critical time is about 35 days after full bloom, whereas according to Raglan (45) the floral primordia are first distinguishable at about 90 days after full bloom. If an excessive crop of young fruit remains on the trees after the critical time, even if it is subsequently removed, it prevents the formation of blossom buds.

As the growth and the composition of the tree have been considered previously to be intimately connected with blossom bud formation it was decided to examine these factors in some Sugar prune trees which were defruited before the critical time and others defruited after the critical time. On and off year bearing trees were included in the investigation, for comparison with the defruited trees, because considerable information is available on the growth and composition of such trees.

LITERATURE REVIEW

The relationship of growth to blossom bud formation has been extensively investigated in annual and biennial bearing apple trees (5,16,24, 34,37,46 and 47), it has also been shown in studies on the bearing habits of apple trees (43,49.55). These investigations disclose a positive correlation of blossom bud formation with the length and diameter of the spurs, except when the trees are bearing biennially.

In regular bearing apple trees, whether of annual or biennial varieties, Yeager (55, Roberts (46), Hooker and Bradford (24), Auchter and Schrader (5), Mecartney (34) and others found a marked and positive correlation in the spur classes. Depending on the variety, this correlation was limited to the spurs or extended to the longer shoots also. Thus Roberts (46) found the longer spurs and shoots of several apple varieties to be vegetative and Potter and Putnam (43) found the spur classes of McIntosh and Baldwin to show a positive correlation, but the longer shoots to have a constant relationship in the one and a negative correlation in the other variety.

In biennial trees the heavy crop of the on year prevents blossom bud formation, irrespective of the length of shoot growth. Roberts (46,47) and other workers found that the average growth was less in the on year, which led him to suggest that shoots did not grow enough in length and diameter to form blossom buds in the on year, but the further investigations of Mack (34) and Tucker and Potter (49) indicated that the growth made in the on year may be greater than in the off year, and Mecartney (37) and others pointed out that blossom buds fail to form in the on year on lengths where they would form in the off year. It appears, then, that the correlation of blossom bud formation with spur vigor that exists in regular bearing trees is over-ruled by some factors associated with excessive cropping in biennial trees. Roberts (46), Hooker and Bradford (24) and later workers pointed out that, in regular bearing trees the spurs act as individuals, according to their vigor, but in biennial trees the tree acts as the unit. Thus Hooker and Bradford (24) and Hooker (25) considered that the factors governing blossom bud formation are localised either within the spur or are general in the tree, respectively. The investigations of Hooker (25), Hooker and Bradford (24) and Kraybill and associates (28,29) have established several differences in composition between apple trees in their on and in their off year of bearing. By midsummer of the off year, when blossom buds are formed, the spurs show low percentage moisture, high titrable acidity high percentage of potash and starch, low percentage of nitrogen and free reducing substances.

Hooker (25,26) concluded that carbohydrates were deficient in the on year and nitrogen was deficient in the off year and that these deficiencies robbed the spurs of their individual response and caused the tree to act as the unit. He found that fall applications of sodium nitrate remedied the nitrogen deficiency and caused biennial trees to become annual bearers, when the spurs resumed their individual response. This result from the use of nitrogen has been confirmed only by Crow and Eidt (12), so far as the writer is aware. The other deficiency, that of carbohydrates in the on year, should be made good by heavy and early fruit thinning. However, Potter and Phillip (42) considered that bearing and non-bearing spurs were not directly comparable and analysed only non-bearing spurs. They found that blossom bud formation was constantly associated with insoluble nitrogen, that it showed as close a relationship with the carbohydrate-nitrogen ratio as with insoluble nitrogen, that other factors, such as the accumulation of soluble carbohydrates, have a considerable bearing, that the accumulation of starch prior to July was not an indication of blossom bud formation, that blossom bud formation was particularly associated with high fresh weight and absolute amounts of soluble solids and insoluble solids.

In on and off year Sugar prune trees, Davis (13) found differences in composition similar to the apple, except that the content of nitrogen was the reverse of what had been shown in apple material. In the off year, when blossom buds were formed, the percentage of reducing substances was lower, total nitrogen was higher, and starch, the largest variable, was higher than in the on year. In this material Compton (10) found a higher phosphorus content and Davis (14) a higher percentage of potash and ash in the off than in the on year. Magnesium and calcium were not so clearly affected or consistent in the different fractions examined.

As the factors connected with the determination of blossom buds have been sought in the growth of the tree and the nutritional conditions, it will be of interest to see what growth and nutritional conditions obtain in trees that were defruited before or after the critical time. Research on this problem was directed along the following lines:-

1. The seasonal development of the leaves
2. A morphological analysis of the leaf and length growth of shoots
3. A chemical analysis of the spurs and the wood and bark of laterals
4. The seasonal development of the fruit

MATERIALS AND TREATMENTS

<u>Materials</u>: The Sugar prune trees used in the present study were growing in the University Farm Orchard, Davis, California. A view of them, given in Figure 1, shows the size of these trees in comparison with the ladder, which is 12 feet high. The trees were in the complete alternate cropping condition, except where they were affected by thinning. In the off year there were only a few scattered blossoms on the trees. Some trees in their bearing year and others in their non-bearing year were available in the same block. The trees were irrigated on June 8-10, July 29-30 and September 10, to maintain "available water" (that is, moisture between wilting point and the field capacity of the soils).

<u>Treatments</u>: The trees under investigation were a bearing or fruiting tree in its on year (F), one in its off year (NB), and four other on-year trees (a,B,C,D) which were completely deflorated or defruited by hand, each at a different time.

Each time of fruit removal was selected on previous experience so as to have some trees defruited before, and other trees after, the critical time for blossom bud formation. The details of the treatments and the subsequent blossoming are given in Table I.

TABLE I. Time of fruit removal, location and blossoming responses.

Treatment	Time of Fruit Removal		Location	Percentage Blossom Estimates, 1937
	Date 1936	Days after full bloom (March 12 1936)		
A	Mar. 8		Row 4, Tree 1	100
B	" 28	16 days	" 3 " 1	75 - 100
C	Apr. 11	30 "	" 3 " 2	75 - 100
D	" 28	47 "	" 7 " 3	2 - 5
F	Fruiting tree, on year		" 3 " 5	0
NB	" " off year		" 4 " 2	100

In 1936, A,B,C,D and F produced 100 percent blossoms; NB 0 percent blossoms.

In the present experimental treatment all the fruit was removed to obviate problems in sampling, although in previous experiments Dr. Davis found that heavy thinning had given blossoming responses similar to complete fruit removal. One whole tree was devoted to each treatment so as to provide abundant material for the many samples that were taken, without unduly depleting it of its annual shoot growth. Previous experience on the uniform response of these trees to thinning and defruiting indicated that single tree treatments should afford valid comparisons. The results confirmed this view.

Footnote: The blossom estimates in 1937 were made by Dr. Davis who, in correspondence stated that "a series of counts made in 1936 showed that an estimate of 100 percent bloom really had 70 to 80 percent of all buds as fruit buds. An estimate of 75 percent was one in which the spurs in particular had fewer blossom buds than in the 100 percent group and gave a large enough crop to cause the tree to alternate completely. A 2 to 5 percent bloom represented a very scattered bloom, but not enough to affect the alternating habit. A zero percent bloom was one in which no, or only a very few, blossoms occurred.

FIG. 1 General view of Sugar prune trees

B. first tree on left
C. second tree on left
D. fifth tree on left
A. first tree on right
(few upper limbs only showing)
NB. second tree on right

FIG. 2 Arrangement of the planimeter for measuring leaf areas

SEASONAL DEVELOPMENT OF THE AREA AND NUMBER OF LEAVES PER SPUR LITERATURE

Whether fruit removal at different times after blossoming will influence the growth in length or diameter of the shoots or the growth of the foliage, depends upon whether or not it is done while this growth is taking place. Some estimate on this point could be formed beforehand from previous knowledge of the seasonal growth of trees. Spurs are known to cease growth shortly after blossoming (Roberts (47) and Chandler (8)), and terminals usually within 90 days of full bloom (Barnard and Reed (6) and others). Diametral growth starts with the inception of length growth and continues after its cessation (Proebsting (44)).

However, there was little previous information on the seasonal expansion in leaf area and none on the seasonal increase in leaf numbers. The data were for apple varieties. Kraybill et al. (29) published data which indicated that the leaf area of spurs increased for a period of 34 days after full bloom. Porter and Kraybill (41) showed an expansion of leaf surface for 46 days in a deflorated tree, 40 days in a bearing tree and for 60 days in a 50 percent deflorated tree of Oldenburg apples. Theis (48) showed an increase in leaf area up to the last measurement he made, namely 42 days after full bloom.

As there were no data on the prune or the plum, a study of the seasonal development of leaf number and leaf area of spurs on the same Sugar prune trees which furnished other data for this thesis was undertaken in the Spring 1936.

Footnote: Abstracted from a thesis, entitled "The influence of several times of defruiting on the leaf growth of spurs of the Sugar Prune" by F.T. Bowman, submitted to the University of California in partial fulfilment of the degree of Master of Science, May, 1936 (unpublished).

METHOD

Weekly samples of approximately 100 spurs were collected from the trees. An average number of leaves per spur was calculated from each sample and the increase of this average represented the seasonal increase in the number of leaves per spur.

Thirty spurs of the modal class were taken and their leaf area measured by the planimeter (see Figure 2). It was thought that this would give a measure of the typical spur leaf area at each date, and the succession of these measures an expression of the seasonal expansion in leaf area.

To check the accuracy of this method for obtaining an average seasonal development of leaf area, additional samples were collected from the fruiting tree, F, on March 28 and April 9. The leaves minus petiole were weighed. The leaf area was determined by the planimeter on a known weight of each sample from which an average leaf area per spur was calculated. The results are shown at points X and Y in Figure 3, and demonstrate a close agreement between the values from this weighing method and the planimeter measurements of the modal class.

SEASONAL INCREASE IN THE NUMBER OF LEAVES PER SPUR

When the leaf buds opened in Spring, bud scales and some transitional foliar organs abscissed before the central roll of true leaves appeared. By three days after full bloom generally three leaves had separated from the central roll of leaves; they separated when about 1 inch long by 0.3 inches wide. By 8 days, the central roll of leaves had completely unfolded in what would be finally the four and five leaved spurs. At 27 days, the central roll of leaves had unfolded on almost all spurs, so that new leaves would form on very few other spurs. The internodal growth of the spurs also, apparently, had ceased; the petioles showed a joint at their insertion with the shoot and could be picked from the spur readily, without tearing away some of the spur tissue. At 37 days after full bloom, only spurs with 8 or more leaves were capable of increasing in leaf number as the terminal point was dead and dehiscing from shorter spurs with fewer leaves. The petioles at their insertion were more swollen and axillary buds were appearing. Thus, by this time the units that comprise a spur, leaves and axillary buds were well defined; length growth had ceased but radial thickening took place subsequently.

Spurs with few leaves completed unfolding their leaves early, those with many leaves continued to unfold to a later date and thereby increased the average number of leaves per spur during the season. The seasonal increase in the number of leaves per spur appears in Table 2.

TABLE 2. The seasonal increase in the average number of leaves per spur

Date of sampling	Days after blossoming	A	B	C	F
March 14	2	3.0	3.0	3.0	3.0
March 20	8	4.7	4.1	4.0	4.7
March 27	15				4.8
April 2	21	5.4	5.0	5.6	4.8
April 7	26	6.2	5.3	5.7	5.5
April 14	33	6.1	5.0	5.4	4.8
April 16	35	6.0	4.9	5.6	4.5
April 25	44	6.1	5.1	5.4	4.7
May 8	57	6.0	5.4	6.0	4.9

These data, together with the foregoing notes, would indicate that the number of leaves per spur was determined very early in the season. The average number of leaves per spur of F did not increase after March 20, 8 days after full bloom; of B and C after April 2, 21 days after full bloom; and of A after April 7, 26 days after full bloom. But as B and C carried fruit for 16 and 30 days respectively the average number of leaves of F also, should have increased for a similar period to those treatments.

SEASONAL EXPANSION OF LEAF AREA PER SPUR

The means of measuring the seasonal expansion of the leaf area of spurs was to measure the area of the modal class of spurs, as found in the leaf number classes. On April 7, it appeared that 6 leaves per spur would likely be the mean leaf number per spur, hence spurs with 6 leaves as well as 5 leaves were measured for area. The data are given in Table 3 and Figure 3.

TABLE 3. The seasonal expansion of leaf area in sq. cm. per spur

Date of sampling	No. of leaves of sample	A	B	C	F
March 14	3	4.9			4.6
March 20	5	14.7	12.5	14.7	13.1
March 26	5	26.0	25.9		25.9
April 2	6	44.5	44.6	46.2	42.9
April 7	6	52.2	50.8	49.7	50.9
April 16	6	96.6	93.0	88.0	77.9
	5	58.0	68.0	72.5	60.3
April 25	6	100.7	91.2	90.9	87.1
	5	65.3	73.4	68.8	63.0
May 8	6	107.8	104.2	95.0	78.0
	5	72.1	73.8	73.3	66.2
Aug. 1	6	115.6	105.8	96.0	82.0

Up to April 7, 26 days after full bloom, the leaf area expanded at a uniform rate for all treatments and thus appears as a single line in Figure 3.

At this time, firstly, the rate of leaf growth increased on the earlier rate and secondly, it increased at a different rate in each treatment, so that different leaf areas occurred, by April 16, among the different treatments. The subsequent expansion of leaf areas was comparatively small and gradual, in A, B and C, and negligible in F.

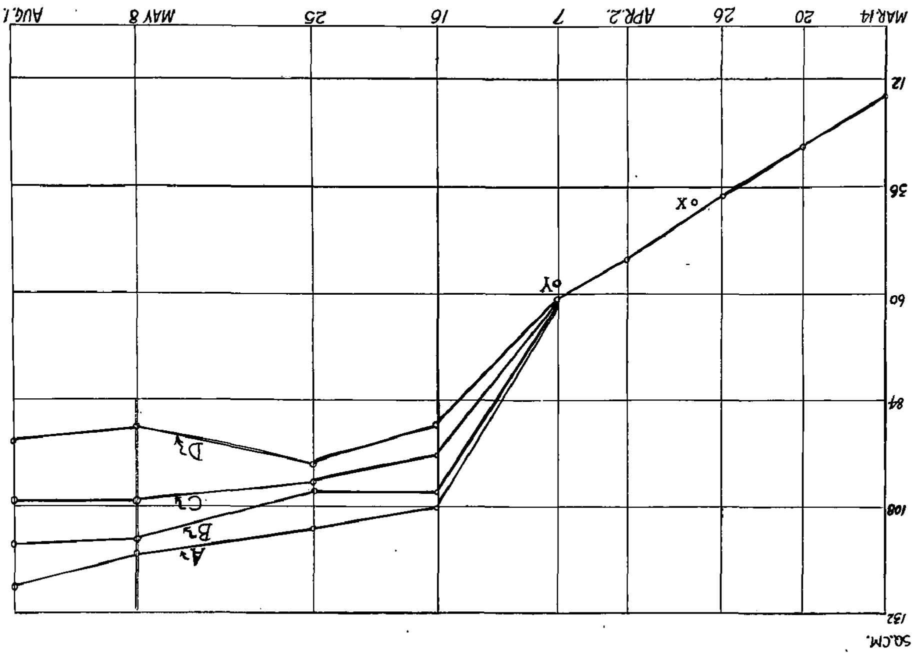

FIG. 3. The seasonal development of the leaf area of six leafed spurs on trees A, B, C and F (marked D in graph).

The data show very clearly that the most important period in the leaf growth of spurs was from 27 to 36 days after full bloom. Differences in leaf area became manifest only during this period, regardless of whether flowers or fruits had been removed from the trees 30 days or 14 days earlier or even 4 days after the onset of this time. Thus by the critical time of 35 days after blossoming, major differences in leaf area of the modal class of spurs had appeared; after this time A, B and C made some leaf growth, but F practically none.

MORPHOLOGICAL ANALYSIS OF SHOOT AND LEAF GROWTH

LITERATURE

Several studies cited in the introduction have demonstrated how the time of thinning affects blossom bud formation but few indicate how much it affects the accompanying leaf and shoot growth of the trees. The information is almost wholly for apple varieties.

Chandler (8) states that "since thinning is done so late that the terminal buds have generally formed (in apples) it cannot influence top growth in the same year, unless it be for the thickening of the trunk and large branches." This has been strikingly confirmed by Palmer and Fisher (38) who recently reported that heavy compared with light thinning for 16 years had increased the diameter of three out of four varieties of apple trees, without materially affecting their height and spread. The differences in leaf area of these trees were reported by Fisher (19) who found small differences in average leaf size, which were not consistent in all four varieties and probably were not significant. Ellenwood (18) also found that thinning apples to 11 inches apart caused no increase in leaf area, although spacing them 13 inches apart gave an increase of 14 percent in area. In the Lombard plum, Waring (53) reported that spurs in one, two and three-year-old wood were increased by one leaf per spur by thinning at the usual time. Spur leaves showed no increase in area but shoot leaves were 30 percent larger. Thinning also increased trunk circumference and the length and diameter of laterals.

Unlike thinning the fruit at the usual time, thinning or removing the blossoms has been shown by Porter et al. (41) and Theis (48) to increase the leaf surface of apple trees and by Chandler (9) to increase the total leaf area of young apple, peach, apricot and pear trees. Roberts (46) found that removing the blossoms of Wealthy apples did not increase the leaf area of the primary bearing spurs (that is, the cluster bases) but it doubled the number and area of the leaves on the secondary spurs arising from the cluster bases.

METHOD

DISCUSSION

A great diversity of methods for recording growth and of the kind of growth recorded, appears in the literature, which not infrequently renders difficult a comparison between the results of different authors. The measures of growth, that have been used, include the following:-

(a) The annual extension in length of the shoots, either the entire range of, or only some of the shoots such as the terminals or the spurs; of the spurs the different kinds of primary or secondary growths may have been examined separately or not;

(b) The leaf numbers and areas, per leaf or per spur;

(c) The diametral growth either of spurs, shoots, branches or of the trunk;

(d) Dry weight measures of the plant parts or of the entire plant.

From the viewpoint of plant physiology the best and final measure of plant growth is the dry weight of the plant. This measure is out of the question in many field experiments, although Chandler (9) used it to obtain the most conclusive data that are available on the influence of fruiting on growth. The dry weight of the annual growths (which are usually measured in fruit trees) would also be considered to be the best measure and could be more widely used; yet separate values for length growth, foliage and diametral growth are desirable, as in the present experiment, because many existing data are expressed in these terms.

Hoblyn (27) and Wilcox (54) discussed the growth measures that may be taken in field experiments; they both pointed out the inadequacy of any single measure, but decided that trunk circumference was probably the most satisfactory single measure.

Vyvyan and Evans (52) drew attention to the diversity of methods, previously used for measuring leaf areas and, as a result of making a morphological analysis of the leaf area of two entire apple trees, proposed a considerable improvement of method for evaluating leaf area. They divided the leaf-bearing shoots into -

1. Primary leaf shoots
2. Primary leaf spurs
3. Primary blossom spurs (cluster bases)
4. Secondary growths (a) spurs and shoots
    (b) axillary spurs and shoots

They found that each group had its own frequency distribution and that each should be measured separately to reach an evaluation of the leaf area of a tree.

In the Sugar prune, however, the measurement of shoots is simplified by the fact that the shoots are all primary whether they blossom or not, there being no secondary shoots arising from primary blossoming spurs, as in the apple. The measurement of shoots is simplified still further by the fact, discovered in the early samples, that the shoots of all lengths form a frequency distribution with a single mode. Spurs and longer shoots thus comprise a single population in the Sugar prune, not two groups as Vyvyan and Evans reported for the apple, and it would be inaccurate to measure separately any part of the population such as the spurs or the laterals.

The frequency distributions of leaf number, shoot length and leaf area are all extremely skewed, those of shoot length being J-shaped.

Although attention has not been directed previously to this type of distribution, several workers have presented either frequency curves or tables which show the extremely skewed kind of distribution. Roberts (46) showed the frequency curve of shoots 1 to 30 centimetres in length of Wealthy apples. It was J-shaped in the on year, but only skewed normal in the off year. Mecartney (37) showed a J-shaped distribution of the spur classes 1 to 10 centimetres long or the Wagener apple in both the on and off year. Dorsey and Knowlton (16) showed frequency distributions of shoots up to 11 inches long of nitrated and non-nitrated trees. The distributions of shoots had two modes in the spur classes which would probably be due to a mixed population of primary and secondary shoots. The nitrated tree tended to form a third mode at the 6 to 7 inch class. Potter and Putnam (43) showed a J-shaped distribution of all lengths of spurs and twigs produced in five years by Baldwin and McIntosh apple trees. These authors used the standard deviation to express variability. The distribution curve of spurs below 1 inch was also J-shaped. Yeager (55) used the standard deviation but did not give any frequency distributions.

The frequency distribution of the prune shoots is of Pearson type 1 (a) (39) and although the standard deviation for this type of curve could be calculated, it could not be used to provide a standard or probably error, as the curve from which it would have been derived was not Gaussian. Hence the means of the leaf and shoot measures were calculated but the significance of difference between means was not estimated. However, the treatments were planned to form a series and they gave a seried growth response, which can be clearly set out in relation to the critical time for blossom bud formation (see figure 8).

The records were taken on more than one limb of most treatments; a comparison of the several means thus affords a measure of the reliability of the general mean. This comparison for the mean shoot lengths of several limbs is shown in Table 4.

TABLE 4 Comparison of the Mean shoot lengths of several limbs

Treat-ment	1st Limb		2nd Limb		3rd Limb		4th Limb		Totals	
	n	m	n	m	n	m	n	m	n	m
A	745	4.74	297	4.69	-	-	-	-	1042	4.71
B	578	3.98	591	4.31	449	3.97	-	-	1619	4.07
C	463	2.14	437	2.75	351	2.22	546	2.51	1797	2.31
D	1115	1.55	-	-	-	-	-	-	1115	1.55
F	512	.808	588	0.697	-	-	-	-	1100	0.75
NB	938	1.225	-	-	-	-	-	-	938	1.22

n - number of shoots m - mean

GROWTH MEASURES RECORDED

Shoot lengths and leaf numbers were recorded in June, 1936, on entire limbs of the trees, on every shoot in turn, so that the leaf number corresponding with each length measurement is known. More than one limb and a total of about 1,000 shoots or more were recorded in this way for each treatment. The measurements include all the shoots on one or more entire limbs.

When the values for length and number were sorted into frequency distributions, they at once showed extremely skewed or J-shaped distributions, with a single mode which was in the spur classes. A further sample of about 200 shoots (more than 10 centimetres in length) was measured on other limbs in most treatments, to ascertain from a larger sample if long shoots formed a second mode and thus gave a bimodal curve for length and leaf number, as Vyvyan and Evans (loc. cit.) had described for leaves. To obtain these additional shoot samples the procedure was to measure all shoots 10 centimetres and longer on limb after limb round the tree, until about 200 measurements were obtained on these several entire limbs. The frequency distributions of these shoots revealed no second mode for shoots and confirmed the expectation that they comprised the tail of a very skewed or J-shaped cruve.

Leaf area per shoot was recorded in each treatment from a random sample of about 200 shoots collected in late July and brought into the laboratory, where the total leaf area on each shoot was measured by a planimeter.

All planimeter measurements were made under a standardized arrangement of the instrument, which is shown in Figure 2. Standard conditions were essential, as area measurements were made throughout the season for one or another part of this study. The instrument was checked periodically against a standard area and an error of 2 percent was found for repeated measurements of a leaf area of 100 square centimetres. The planimeter was set in the same marked position on the board each time. The leaf being measured was held under the glass by a rubber pad, so that the insertion of the petiole with the lamina came directly under an etched hole in the glass, which was the starting point for the area measurements of each and all leaves. When measuring the total leaf area of a shoot the measurements were always taken in order from the proximal to the distal leaves.

An average area per leaf was found from the above sample of 200 shoots.

Diameter measures were taken on a random sample of 100-150 spurs brought into the laboratory and measured by calipers. Two samples were taken -

one in May and the other in June. The June sample was regarded as the one in which the treatments would show their final differences.

PRESENTATION OF DATA

NUMBER OF LEAVES PER SHOOT

Fruit removal at progressively later times in the season caused a progressive decrease in the mean leaf number, as shown in Table 5.

TABLE 5. ... The mean number of leaves per shoot

Treatment	Mean number of leaves
A (blossom buds removed)	7.5
B (fruit removed at 16 days)	7.3
C (fruit removed at 30 days)	6.2
D (fruit removed at 47 days)	5.4
F (on-year fruiting tree)	4.8
NB (off-year bearing tree)	4.7

A and B had a similar high average number of leaves; F and NB both had a low number, from which D probably did not differ significantly; C had an intermediate leaf number.

The frequency distributions are set out by class intervals of 5 leaves in Table 6; those of the first three classes are given in detail in Table 7; and those of additional shoots appear in Table 8. The frequency distributions of leaf numbers per shoot are extremely skewed and have single modes. Shoots of all lengths thus form a single population, but to aid an analysis of the differences between the treatments, the shoots with 10 leaves and less will be called spurs and those with more leaves, laterals. The number of laterals is given as a percentage of the sample in Table 6.

Fruit removal at different times altered the frequency distributions in quite a definite manner. The fruiting tree had a modal class of 5 leaves per shoot and only .05 percent laterals. None of the laterals exceeded 15 leaves per shoot. Fruit removal at 47 days (D) was done too late to affect the distribution in the spur classes, but it increased the number of laterals (3.0 percent). Fruit removal at 30 days (C) gave the same modal class, namely 5 leaves per shoot, as D and F, but this time of fruit removal caused increases in the classes immediately succeeding the modal class, and an appreciable increase in the laterals (5.9 percent). The laterals also extended to higher leaf numbers than D. Fruit removal at 16 days (B) raised the modal class to 6 leaves per shoot and increased still further the frequencies in the classes immediately succeeding the modal class and also raised the number of laterals (8.7 percent). This was effected by increasing the frequencies in the various lateral classes, without increasing the range of the classes, which was similar to C. Blossom removal (A) gave a modal class of 6 leaves like B, but higher frequencies than B in the succeeding classes (up to 20 leaves per shoot) and lower frequencies in the still higher classes. A showed fewer laterals than B (3.3 percent).

The earlier times of fruit removal thus altered the frequency distributions in the following ways:-

1. Shifted the mode to a higher class
2. Increased the frequencies of the classes immediately following the modal class
3. Progressively increased the percentage of laterals
4. Increased the range of classes of laterals, except that A was less than B.

The off year tree (NB) had a characteristic kind of growth. It resembled the fruiting tree in the spur classes but had 2.6 percent laterals

T A B L E 6

Frequency Distributions of Leaf Numbers per shoot

CLASSES	A	B	C	D	F	NB
1 - 5 leaves	377	518	1020	840	818	806
6 - 10 "	530	531	671	240	276	108
11 - 15 "	67	39	21	18	6	7
16 - 20 "	29	22	22	3	-	9
21 - 25 "	21	26	16	6	-	6
26 - 30 "	10	13	17	8	-	-
31 - 35 "	8	9	5	-	-	1
36 - 40 "	-	8	2	-	-	1
41 - 45 "	-	2	4	-	-	-
46 - 50 "	-	2	1	-	-	-
N. =	1042	1170	1797	1115	1100	938
M. =	7.5	7.3	6.2	5.4	4.8	4.7
Laterals %	3.3	8.7	5.9	3.0	0.5	2.6

T A B L E 7

Frequency Distribution of Leaf Numbers per shoot
(Shoots with 1 - 15 leaves)

CLASSES		A	B	C	D	F	NB
2	leaves	9	11	15	18	18	47
3	"	75	84	144	136	141	154
4	"	140	120	304	357	305	287
5	"	153	303	557	329	354	318
6	"	214	337	453	156	174	73
7	"	166	129	125	41	73	20
8	"	79	39	48	22	20	8
9	"	45	16	26	15	6	5
10	"	26	10	19	6	3	2
11	"	16	14	3	7	3	-
12	"	21	12	6	3	2	2
13	"	9	5	6	3	1	2
14	"	11	2	2	4	-	2
15	"	10	6	4	1	-	1
N.	=	974	1088	1712	1098	1100	921

TABLE 8

Frequency Distributions of Leaf Numbers per shoot (of additional shoots with more than 10 leaves per shoot).

CLASSES	A	B	C	NB
11 - 15 leaves	135	50	26	85
16 - 20 leaves	63	48	38	47
21 - 25 "	27	48	16	34
26 - 30 leaves	17	14	12	29
31 - 35 "	12	27	5	12
36 - 40 "	5	11	2	5
41 - 45 "	2	5	1	3
46 - 50 "	1	7	2	6
51 - 55 "	1	4	2	4
56 - 60 "	2	4	-	-
61 - 65 "	0	-	-	-
66 - 70 "	1	-	-	-
N. =	266	218	104	225

similar to D. This tree threw out a number of small spurs on the older wood of spur clusters, which increased its number of growing points by 30 percent over the trees that blossomed.

LENGTH OF SHOOTS

The average length of the shoots produced by the fruit removal treatments is given in Table 9.

TABLE 9 The Mean Length of Shoots

Treatment		Mean Length
A	(blossoms removed)	4.71 cm.
B	(fruit removed at 16 days)	4.07 cm.
C	(fruit removed at 30 days)	2.31 cm.
D	(fruit removed at 47 days)	1.55 cm.
F	(on year fruiting tree)	0.75 cm.
NB	(off year bearing tree)	1.22 cm.

A and B showed a high average shoot length, D, F and NB a low average length, and C an intermediate length. The difference between D, F, and NB is due to the amount of laterals as the average length of the spur is 0.75 centimetres, 0.75 centimetres, and 0.58 centimetres, respectively.

The frequency distributions of the shoot lengths are given in Tables 10, 11, and 12, corresponding respectively with Tables 6, 7, and 8 of leaf number. Table 10 gives the distributions of the entire samples by class intervals of 5 centimetres; Table 11 gives the detailed distribution in 0.1 to 5.0 centimetre classes; Table 12 shows the distribution of lengths in the additional samples of laterals. The frequency distributions are J-shaped, with single modes. The growths 10 centimetre and less are called spurs, those above 10 centimetres are called laterals. The numbers of laterals are expressed as percentages of the entire samples in Table 10; these percentages, being on the basis of length, differ from those based

TABLE 10

Frequency Distributions of Shoot Lengths

CLASSES (cm)	A	B	C	D	F	NB
0.1 - 5.0	876	1046	1706	1077	1094	912
5.1 - 10	52	29	10	15	6	4
10.1 - 15	30	13	11	4	-	1
15.1 - 20	16	9	15	1	-	6
20.1 - 25	10	9	13	-	-	3
25.1 - 30	13	12	5	2	-	3
30.1 - 35	14	8	9	3	-	4
35.1 - 40	4	7	6	1	-	-
40.1 - 45	5	12	4	6	-	3
45.1 - 50	2	5	3	1	-	1
50.1 - 55	6	3	2	2	-	-
55.1 - 60	5	1	3	1	-	--
60.1 - 65	3	5	3	-	-	1
65.1 - 70	1	1	1	1	-	-
70.1 - 75	3	4	1	1	-	-
75.1 - 80	1	1	1	-	-	-
80.1 - 85	1	-	1	-	-	-
85.1 - 90	-	3	1	-	-	-
90.1 - 95	-	-	2	-	-	-
95.1 - 100		-				
100.1 - 105		2				
105.1 - 110						
N. =	1042	1170	1797	1115	1100	938
M. =	4.7	4.1	2.3	1.5	0.7	1.2
Means of spurs (0.1-10 cm				0.75	0.75	0.58
Laterals %	11.0	8.1	4.5	2.0	0.0	2.3

TABLE 11

Frequency Distributions of Shoot Lengths

(Shoots 0.1 - 5.0 cm. long)

CLASSES (cm.)	A	B	C	D	F	NB
0.1 - 0.5	312	447	877	780	776	788
0.5 - 1.0	325	405	548	212	188	74
1.1 - 1.5	97	94	140	36	75	25
1.6 - 2.0	53	48	59	19	25	8
2.1 - 2.5	36	-	28	7	-	-
2.6 - 3.0	17	32	25	9	21	9
3.1 - 3.5	-	-	7	4	-	-
3.6 - 4.0	26	14	11	6	6	4
4.1 - 4.5	-	-	2	-	-	-
4.6 - 5.0	10	6	9	4	3	4
N. =	876	1046	1706	1077	1094	912

TABLE 12

Frequency Distribution of Shoot Lengths of Additional Shoots (more than 10 cm. long).

CLASSES (cm.)	A	B	C	NB
11 - 15	55	21	22	30
16 - 20	38	28	17	31
21 - 25	34	16	7	18
26 - 30	27	19	10	21
31 - 35	15	18	4	15
36 - 40	18	16	7	11
41 - 45	17	11	4	10
46 - 50	6	13	3	5
51 - 55	7	9	0	4
56 - 60	7	14	0	11
61 - 65	1	4	1	8
66 - 70	6	9	1	4
71 - 75	2	3	2	3
76 - 80	3	2	2	1
81 - 85	0	2	1	0
86 - 90	1	3	1	
91 - 95	-	2	-	
96 - 100	-	2	-	
101 - 105	-	3	1	
106 - 110	-	1	-	
111 - 115	-	-	-	
116 - 120	-	1	-	
121 - 125	-	-	1	
126 - 130	-	-	-	
131 - 135	-	1	-	
136 - 140	-	1	-	
N. =	237	199	84	172

on leaf number shown in the previous section.

Fruit removal had a similar effect on the frequency distributions of shoot lengths to that shown on leaf numbers.

Blossom removal (A) and fruit removal at 16 days (B) increased the mode over the fruiting tree. Both A and B gave much increased lateral growth. Treatment A produced a higher percentage of laterals than B (11.0 percent and 8.1 percent, respectively) but B produced more longer shoots (Tables 10 and 11). Fruit removal at 30 days (C) gave a reduced mode compared with A or B and gave a range of laterals less than B and more comparable with A, but the frequencies in these lateral classes were lower than A and B and thus the percentage of laterals was less (4.5 per cent). Treatment C showed an increase of vigor over the fruiting tree, holding intermediate position between A or B and D or F. Defruiting at 46 days (D) was too late to affect the vigor of the spur classes which were thus similar to the fruiting tree. But some laterals developed which in range and frequencies were less than treatments A, B, and C. The laterals in D were similar to the non-bearing tree (2.0 percent and 2.3 percent respectively).

The off-year tree made a characteristic kind of growth as already mentioned, because of the breaking into growth of many dormant buds. It thus had a lower mode than a fruiting tree (with a high frequency in the modal class) and shoots that in range and vigor were similar to tree D and much less than the trees A, B or C.

LEAF AREA OF SHOOTS AND MEAN LEAF AREA

The average leaf areas of about 200 shoots produced by the various fruit removal treatments are given in Table 13.

As a basis for using these samples, it is first necessary to compare their average number of leaves with those from the large samples previously recorded in Table 5, the numbers in which are given in Table 4. The differences resulting from this comparison, which are shown in column five of Table 13, are small except that D and NB are high to the extent of about 10 percent. These differences will be referred to again, when generalising the growth data in the discussion.

Treatments A and B show a distinctly greater leaf area of shoots than other treatments; treatments F and NB have low areas; C has an intermediate area between these extremes; D shows an increase in average area over F, but, as it will be shown later (relation of the number to the area of leaves) that the leaf areas of similar leafed spurs in D and F were similar, D is rather to be grouped with F and NB in the lower leaf area group. The increased area of D is almost solely due to laterals.

The frequency distributions of the leaf areas are given in Table 14. They are much skewed towards the low leaf area classes and have a single mode. Compared in the order A, B, C, D, F they show, like length and leaf number, that the mode moved progressively to a higher class with the earlier times of fruit removal.

The differences in the mean leaf area of shoots are brought about by two factors, namely -

1. The differences in leaf number per shoot
2. Differences in the mean leaf area of shoots with the same number of leaves.

If the former factor along were operative the frequency distributions would resemble the leaf number distributions, but as they do not the second factor, which will be discussed in a later section dealing with the relation

TABLE 13

Leaf Area of Shoots and Mean Leaf Area

Treat- ment	No. of shoots in sample	No. of leaves measured	Av. No. of leaves	Difference from Mean No. of leaves given in Table 5	Leaf area per shoot	Mean Leaf area
					sq. cm.	sq. cm.
A	200	1523	7.6	+0.1	133.9	17.7
B	193	1370	7.1	-0.2	120.2	17.4
C	192	1250	6.5	+0.3	104.2	16.0
D	198	1181	6.0	+0.6	85.8	14.4
F	200	936	4.7	-0.1	52.1	11.2
NB	200	1067	5.3	+0.6	64.9	12.2

T A B L E 14

Frequency Distribution of Leaf Areas of Shoots

CLASSES (sq. cm.)	A	B	C	CLASSES (sq. cm.)	D	F	NB
				10 - 29	33	54	49
				30 - 49	28	50	52
20 - 50	19	29	40	50 - 69	53	51	44
51 - 80	30	69	64	70 - 89	18	23	14
81 - 110	45	45	40	90 - 109	31	8	13
111 - 140	43	17	18	110 - 129	3	9	8
141 - 170	25	8	7	130 - 149	11	-	7
171 - 200	9	-	2	150 - 169	4	3	1
201 - 230	5	3	6	170 - 189	1	-	1
231 - 260	3	10	2	190 - 209	3	2	1
261 - 290	3	4	5	210 - 229	3	-	1
291 - 320	3	1	3	230 - 249	2	-	3
321 - 350	7	3	3	250 - 269	1	-	1
351 - 380	2	1	-	270 - 289	3	-	1
381 - 410	2	-	1	290 - 309	-	-	2
411 - 440	-	1	-	310 - 329	2	-	1
441 - 470	2	1	-	330 - 349	-	-	1
471 - 500	1	1	-	350 - 369	-		
501 - 530	1	-	1	370 - 389	-		
				390 - 409	-		
				410 - 429	1		
				430 - 449	1		
N. =	200	193	192	N. =	198	200	200
M. =	133.9	120.2	104.2	M. =	85.8	52.1	64.9

of leaf number to area, is important.

How these differences are brought about by the time of fruit removal is explained by data already presented on the seasonal development of the foliage of the spurs. The number of leaves per spur was decided soon after blossoming so that only trees A, B and C were defruited early enough to be influenced by the treatment (Table 2). Treatment D, being carried out at 47 days, thus gave a similar distribution in the spur classes to F (Table 6 and 7) although the development of more laterals, which amount to 3.0 percent raised the mean leaf number slightly. The leaf area also was decided early in the season (figure 3), although later than leaf numbers. The highest rate of leaf growth occurred between 26 and 35 days after blossoming; later than this the rate of increase was much less. The trees A, B and C were defruited early enough to affect appreciably the leaf area of spurs, whereas fruit removal at 47 days (D) was so late as to affect the leaf area of only the longer spurs and of the laterals.

The mean leaf areas, also given in Table 13, show that A, B and C, gave high values, F and NB low values, and D an intermediate value.

DIAMETRAL GROWTH OF SPURS

The average diameters, together with the frequency distributions, in which there were, at most, only five classes, and often only three classes, are given in Table 15. The diameters of the spurs of treatments A, B, C and D were probably significantly larger than F in May, but on July 30 when diametral growth was completed were scarcely so. This similarity is more apparent than real, as the spurs sampled from F were predominately short spurs which were relatively stout. Longer spurs from F were thin.

The four treatments A, B, C and D showed no distinct differences amongst themselves in average diameter of the spurs and appeared rather similar in the thickness of their laterals. This similarity is of interest since, as A, B and C formed blossom buds and D did not, it does not support the suggestion that has been made, particularly by Roberts (47), that diametral growth is an external criterion of the fruitful condition. In the light of these time-of-thinning trials it is considered that diametral growth and blossom bud formation are coincident phenomena only when other conditions, governed by the load of fruit, are suitable at the critical period of ripeness to blossom.

The relationship that exists between length and the average diameter of spurs is shown in figure 4. With increases in length, the diameter increased up to 0.75 centimetres in May and 1.25 centimetres in July, and then decreased. This relationship arises from the fact that in external appearance the sub-axillary wedges coalesced in the shorter spurs, whereas they did not in the longer spurs. In long shoots of A, B, C, D and NB the axillary wedges coalesced but not in F.

A graphic idea of the seasonal change in diameter of the spurs, according to the several length classes, is afforded by a comparison of the two graphs in figure 4. The seasonal change in the diameters of one year old laterals is represented for trees A and F in figure 5. The laterals on these trees were in the prominent axillary wedge stage in late April, six weeks after blossoming, and were similar in appearance. By July 27th A had developed sufficient secondary thickening to almost obliterate the wedges, but F showed only slight secondary thickening so that the wedges remained prominent.

Fruiting inhibited diametral growth, as has been previously indicated for the apple by Roberts (47), Hoblyn (27) and Wilcox (54), and fruit removal up to 47 days (D) increased diametral growth, because the main increases in diameter were made after April 27th and after the critical time, when also were made the gross demands of the crop on the food materials of the fruiting tree.

TABLE 15 Frequency Table of Spur Diameters

MAY 22

Class Value	A	B	C	D	F	NB
0.2 cm.					78	-
0.3 cm.	83	59	43	70	38	-
0.4 cm.	89	109	74	67	5	-
0.5 cm.	8	15	21	26	-	-
0.6 cm.	-	-	-	-	-	-
Mean (cm.)	0.36	0.38	0.38	0.37	0.24	
JULY 30						
0.2 cm.	-	-	-	11	3	-
0.3 cm.	-	6	10	36	120	68
0.4 cm.	73	59	43	63	53	110
0.5 cm.	76	55	55	54	11	45
0.6 cm.	-	7	13	6	-	7
Mean (cm.)	0.45	0.43	0.46	0.40	0.36	0.40

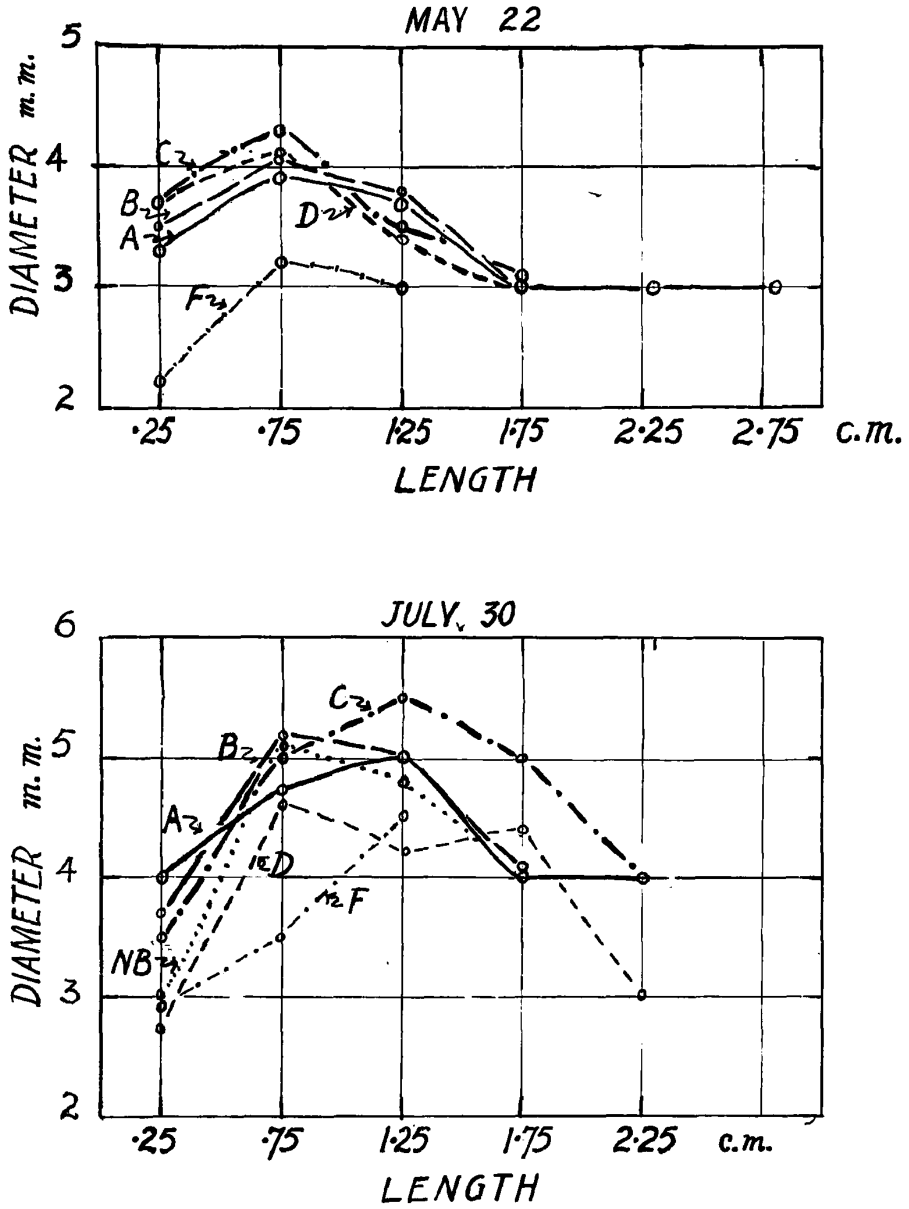

FIG. 4. Relation of diameter to length of spurs on May 22 (above) and July 30 (below).

DERIVED DATA

The records of growth were taken in such a way, as indicated in the section on method, that leaf number of the shoots could be related to shoot length in one series of records and to leaf areas in another. Thus, data could be derived on the relationship of leaf number to shoot length or to leaf area, in each treatment. By this procedure, the discrete measure, leaf number, will be related to the infinite type of measures, leaf area and shoot length. From this examination it will also be seen how it happened that the frequency distributions of leaf area were less J-shaped than those of leaf number, which, in turn, were less J-shaped than those of shoot length.

RELATION OF THE NUMBER TO THE AREA OF LEAVES PER SHOOT

The average leaf area, per leaf number class of each treatment, was calculated and plotted. Freehand curves drawn to them appear in figure 6. The relationship was not entirely a straight line in any treatment except F. The relationship appeared to be a compound curve, such as will appear also in the relationship of leaf number to shoot length.

In each treatment it was a straight line increase up to a certain leaf number class, when it became less and then later resumed the former type of increase in some treatments (A, B, C) but not in others. The leaf number classes at which these changes occurred have been assembled in Table 16.

FIG. 5. Diametral Growth of one year old laterals from April 27 to July 27 of trees A and F. (axillary spurs removed)

1. A showing axillary wedges April 27
2. F showing axillary wedges April 27
3. A showing diametral growth from the axillary wedge stage, (compare with 1.) Photo taken July 27.
4. F showing slight diametral growth from the axillary wedge stage (compare with 2.) Photo taken July 27.

TABLE 16 Leaf Number classes at which occur changes in the relation of number to area of leaves per shoot

	Inflection from straight line increase of area with number	Resumption of regular increase of area with number
A	15 leafed class	21 leafed class (by interpolation)
B	12 leafed class	15 leafed class
C	" "	16 " "
D	straight line	...
F	9 leafed class	...
NB	7 " "	straight line

The high initial relationship of area to number was maintained to the highest leaf number class (15) in A, to a lower class (12) in B and C, lower still (9) in the fruiting tree and lowest (7) in the off-year tree. The values for D gave only a straight line increase.

The inflection from the regular relationship might have been due to cyclic growth. This was observed in the trees but not particularly noted in the samples.

The differences of average area per leaf number class among A, B, C and D were small up to the 11-leafed class, although according to previous work, Bowman (7), were significant at the 7-leaf class. Treatments B and C were decidedly lower than A from the 12 to 16-leaf classes and were high again in the 17 to 20-leaf classes. The few highest values for B were higher than for A.

The off-year tree showed a distinctly lower relation of area to number than the other treatments and, coupled with the data already given on leaf number and shoot length, indicate that it had a different growth status to either bearing or defruited trees.

In all treatments there was an unequal rate of increase of area with number. This indicated that leaf area distributions would differ from leaf number distributions and that the frequency distribution of leaf area will be less J-shaped than leaf number. This would follow from the following consideration:

1. Within the straight line relationship, doubling the leaf number more than doubles the area. Hence the area distributions are spread more to the right than leaf number distributions, particularly in those treatments (A, B, C) having the greatest effect on leaf area.
2. The small difference of area between the first and second leaf number classes, lead to their inclusion in the first area class. Although this grouping does not much affect A, B and C, as the frequencies in these number classes are small, it piles up the frequencies in the first area class in D, F and NB where these number classes are more populous. This and the third factor skews the distribution very much to the left in D, F and NB.
3. In the period of inflection the area increases only slightly with number. As this period occurs at a leaf number class successively lower in the order A, B and C (similar) F, NB, it follows that the area distributions will be crowded towards the left increasingly in that order.

RELATION OF THE NUMBER OF LEAVES TO THE LENGTH OF SHOOTS

The average shoot length of each leaf number class was calculated for the different treatments and free-hand curves fitted to the results, which appear in figure 7a and b; a shows actual data; b shows freehand curves for the data.

The relationship is of the nature of a compound sigmoid curve, in which the rate of increase of length with leaf number changed, as follows:

1. First came a practically flat part of the curve in the region including 3 to 7 leaf classes.

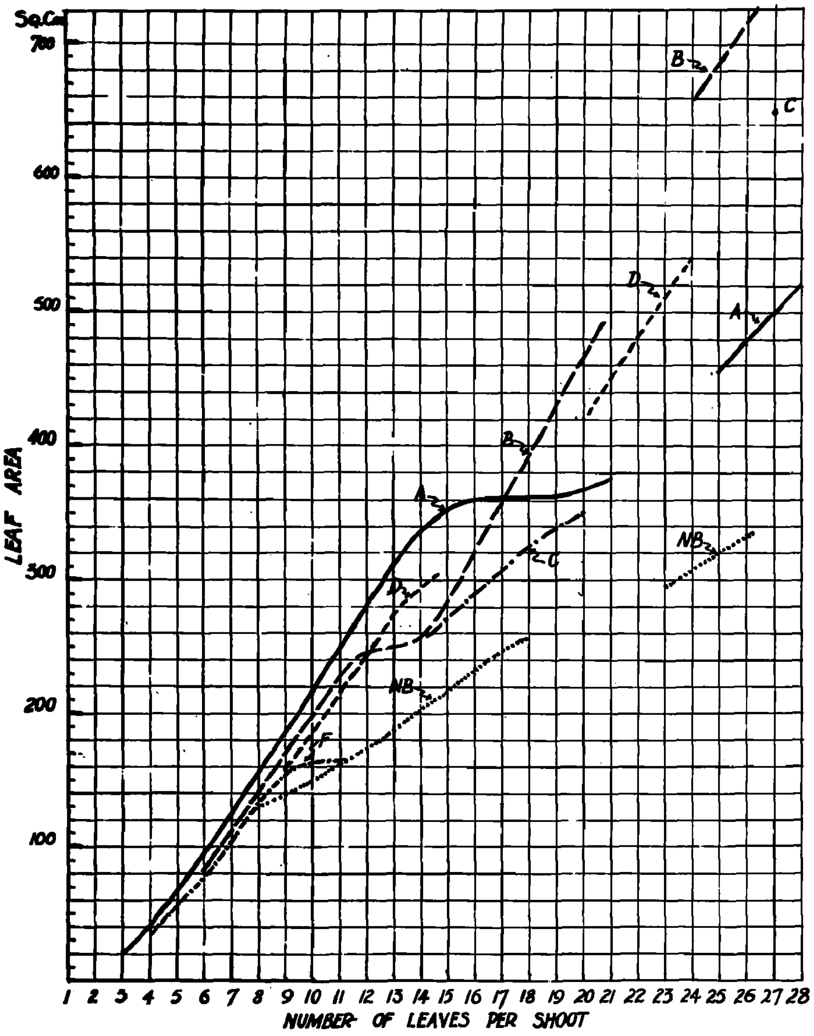

FIG. 6. Relationship of Leaf number to the leaf area of shoots.

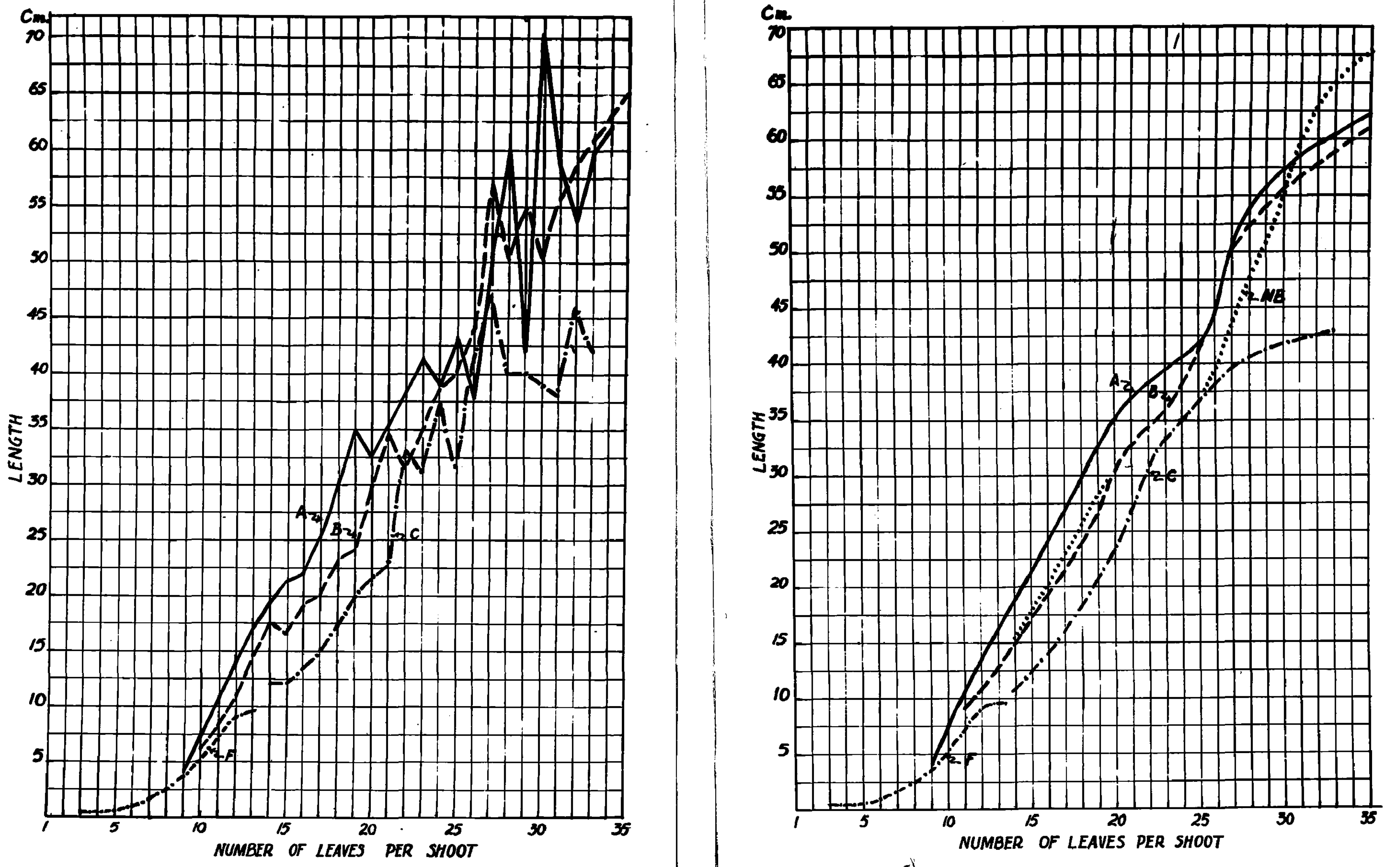

FIG. 7. Relation of leaf number to length of shoots; (a) left, actual data (D and NB omitted);(b) right freehand curves for data of (a), (D omitted and NB included).

2. Next, the slope of the curve changed abruptly and rose steeply. In part 1 increases in leaf number up to 7 leaves were associated with very small increments in length, but beyond 7 leaves, with large increases in length. Moreover, these increases with extra leaves were rather constant and gave practically a straight line.
3. Beyond 20 leaves per shoot the averages became less reliable because of the smaller numbers in each leaf number class, but the straight line increase declined at about 20 to 25 leaves per shoot. The average increase in length became much less and the curve flattened off.
4. At about the 28-leafed class, a second rise in the rate of increase of length with leaf number commenced, but the data were not sufficient to tell when this rate fell off.

Parts 1, 2 and 3 resemble a growth curve and the resumption of a higher rate of increase (part 4) may be an indication that cyclic growth occurred in the long laterals. As with the parts of a usual growth curve, part 1 indicates that conditions for growth were poor, probably due to the great competition for nutriment between growing points. Part 2 corresponds with the usual "grand period" of growth; fewer shoots were making growth and the growth rate was higher than at other times. At the 28-leaf class, the conditions for active growth became less favourable and the rate of increase fell off.

The influence of fruit removal on this relationship is shown in the leaf numbers above 6 or 7 (that is, parts 2, 3 and 4 of the curve) where the early removal of fruit clearly increased the length per leaf number class.

The general relationship of leaf number to shoot length at once indicated that the frequency distributions of length would be more J-shaped than leaf number, because several leaf number classes (3, 4 and 5) which are themselves populous, largely fell within one length class. The 3 to 6-leaved spurs comprised the bulk of the leaf number distribution, and, since these classes fell within the 1 centimetre length class, it is apparent that the frequency distributions of shoot lengths would be distinctly J-shaped.

DISCUSSION

THE RELATIVE AMOUNTS OF LEAF AND SHOOT GROWTH

Since all the measures of growth that have been taken are physiologically inter-dependent, it is of interest to see how fruit removal affects the relative amounts of them. To show this, the mean values given previously have been converted to relative figures on the basis of the fruiting tree as 100, and are shown in Table 17.

TABLE 17 The Relative Amounts of Leaf and Shoot Growth

	Leaf No. per shoot	Leaf area per shoot	Length per shoot	Diameter of spurs	area per leaf
NB	98	125	162	111	109
F	100	100	100	100	100
D	112	164	206	108	129
C	129	210	308	122	143
B	151	230	543	116	156
A	155	257	629	120	159

All measures of growth showed progressive increases according to the earlier time of fruit removal. Apart from the increases of diameter, which were slight, the progressive increases were least in the leaf number per shoot and in area per leaf, greater in leaf area per shoot, and greatest in length per shoot. The data thus show a disproportionate increase in shoot length area per shoot and of leaf area per shoot to leaf number per shoot. The result is that the earlier times of fruit removal gave a much greater leaf area per shoot and especially length per shoot than would be expected from the increase in leaf number. This striking result is shown graphically in figure 8.

The comparative effects illustrate the physiological dependence of shoot length upon the leaf area of the shoots and of the leaf area upon leaf number. It is possible that diametral measures also would have shown large relative differences had they been expressive of the entire shoots instead of only the spurs.

THE RELATION OF LEAF AND SHOOT GROWTH TO THE CRITICAL TIME FOR BLOSSOM BUD FORMATION.

It remains to show the relationship of the leaf and shoot growth to the critical time for blossom bud formation. This relationship is shown in figure 8, where the relative values just mentioned are plotted against the time when the fruit was removed.

These curves epitomise the growth data of this study and although data from additional trees, to give more points on the curve, would be desirable, they clearly indicate the manner in which growth responds to the time when fruit is removed and how this growth is related to the critical time for blossom bud formation.

For the leaf number and the length of shoots, the curve fitted to the measurements is reversely sigmoid. The measurements in trees A and B form part I, those of C indicate part II, and D the start of part III of the reverse sigmoid curve. A tree thinned at 9 weeks would have been required to complete the data, but the indications from interpolation are that the growth response from fruit removal at and after 9 weeks would be similar to a fruiting tree.

In leaf area per shoot and per leaf the curves indicate a more or less uniform reduction of leaf area with the time the fruit remained on the tree, but, as was pointed out in Table 13, the values for B were slightly low and C and D about 10 percent high, compared with larger samples. So probably the values for leaf area of shoots and mean leaf area with these adjustments would also have been sigmoid.

The critical period for blossom bud formation at about 35 days after full bloom, falls low in part II of the sigmoid curves for the length and the leaf number of shoots and in the lower half of the curves for leaf area. At this time the growth responses to fruit removal have fallen from the high values of earlier defruitings and approach those of a fruiting tree.

Yet it is apparent that this relationship, as it appears in Figure 8, is not critical. The significance of the greater growth made by trees A, B and C probably lies in the fact that it would have been taking place still actively at 35 days after full bloom, whereas trees D and F would have been making comparatively little growth by that time. The relationship does clearly show that, to bring about blossom bud formation again in the same year in on-year trees, it is necessary to cause considerably greater growth than a fruiting tree. Fruit removal at six weeks (D), which did not cause blossom bud formation, had little influence on leaf and shoot growth.

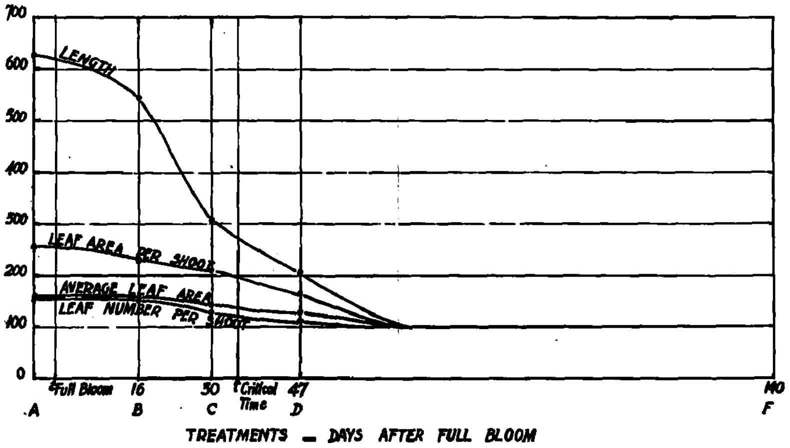

FIG. 8. Relation of growth to the critical period for blossom bud formation.

CHEMICAL COMPOSITION

LITERATURE

There is little previous information on what might be the effect on the composition of removing or thinning the fruit at different times. Aldrich (1) showed that thinned apple trees which produced blossom buds increased in carbohydrate content within three weeks of thinning. Waring (53) found thinning to give very inconsistent effects on the composition of the Lombard plum. The one year old bark and wood of thinned trees had a higher percentage of total sugars and starch, but lower acid hydrolyzable material and lower ash, than unthinned trees. There was a similar content of nitrogen and phosphorus. The current season's wood of thinned trees had a lower percentage of nitrogen, phosphorus and ash. The two year old wood and bark of thinned trees showed a lower content of total sugars, slightly lower starch and higher acid hydrolyzable material. Moisture content was higher with greater fruit production.

Potter et al. (41) examined the effect on the composition of deflorating Oldenburg apple trees to the extent of 100 percent and 50 percent compared with a bearing tree. The complete defloration showed distinctly higher accumulations of starch, lower nitrogen, higher phosphorus and ash than the bearing tree. Due to fluctuations in reducing sugars and sucrose, no constant differences were found in these constituents, although the data show lower reducing sugars in the deflorated tree late in the season. Davis (13) found that a completely deflorated Sugar prune tree gave values for reducing sugars intermediate between a bearing and a non-bearing tree; it rather resembled a bearing tree in starch content, a non-bearing tree in nitrogen content of the bark, but a bearing tree in nitrogen content of the wood and spurs.

MATERIAL AND METHODS

1. Material

Spur and lateral material shown in figure 9, was collected for analysis during May, June and July, thus amply covering the period of blossom bud formation. Sufficient spurs were collected also between blossoming time and the beginning of May to enable moisture determinations. The spurs consisted of the current season's growth from old spur systems, until June 26 and July 27, when older spur wood was included. Laterals were ample in supply, the trees, except NB, having been in the off-year in 1935. Usually six one year old laterals were collected, stripped of their current season's terminal and axillary growth and divided into wood and bark and their dry weight determined. The axillary spurs provided sufficient material for moisture determinations. As these operations took several hours, the laterals were placed in cold storage at 32° F. after collection and were brought out in rotation for preparation.

The times of collecting the material used for analysis were as follows:

Spurs	One year old laterals	Days from full bloom
1.	1. April 28	48 days
2. May 20	2. May 20	70 "
3. June 3	3. June 2	84 "
4. June 26	4. June 27	108 "
5. July 27	5. July 28	139 "

2. Methods

Drying. The early spur samples were cut up finely by pruning shears and dried in a vacuum oven at 55° to 60° C. The later spur samples and the wood and bark material was dried in a large evaporator at 55° with air circulation, when the material was cut less finely and placed in baskets partly lined with paper. Dry weight was obtained after drying for 24 hours.

Grinding. The samples were ground in a Wiley mill to pass a 90-mesh-to-the-inch sieve.

Extraction and Clarification. Duplicate two gram samples of the dry material were extracted in a Soxhlet apparatus with 80 percent alcohol for at least 4 hours. The filtrate was used for determining reducing substances and total sugars, the residue for determining starch and hemicellulose. The filtrate was evaporated almost to dryness, then taken up with water, clarified by neutral lead acetate without adding excess. This material was filtered, with several washings, into 250 millilitre Erlenmeyer flasks, deleaded with dry powdered potassium oxalate. This material was then filtered into 250 volume flasks, neutralised and made up to volume.

Free reducing substances were determined, usually immediately after clarification, on a 1/5th aliquot, using the Quisumbing and Thomas method of reduction and the sodium thiosulphate method of determining the copper. The free reducing substances were calculated as invert sugar from Quisumbing and Thomas Sugar Tables.

Sucrose was considered as the difference between free reducing sugars and total sugars.

Total sugars were determined on an inverted 1/5th aliquot of the above cleared solution. The solution was inverted by adding 10 millilitres of hydrochloric acid (specific gravity 1.109) and, after shaking, standing overnight. This solution was neutralised with sodium hydroxide solution, turned faintly acid, made up to volume (100 millilitres). Total sugars were determined by the same procedure as free reducing sugars.

Starch. (See footnote 1) The dry residue was washed into 250 millilitre beakers, water added and boiled for exactly 3 minutes to gelatinise the starch. After cooling the solution was incubated at 37° C for 12 hours with 5 millilitres of an 0.1 percent diastase solution (See footnote 2). The filtrate was used for starch determinations, the residue for hemicelluloses. After incubation the solution was filtered under suction, washed several times. The filtrate was transferred to a 250 millilitre volume flask, neutralised and made to volume. The reducing power was determined on a 1/5th aliquot by the same procedure as free reducing substances. Starch was expressed as glucose from the Quisumbing-Thomas Sugar Tables, multiplied by the factor 0.95.

Hemicellulose. The residue of the above filtration was washed into 500 millilitre Erlenmeyer flasks with a 2.5 percent sulphuric acid solution and hydroyzed by boiling for two and a half hours with a reflux condensation. This material was filtered, washed and the filtrate neutralised

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Footnote 1. Starch determination has been the subject of much investigation recently. Following the publications of Hanes (21,22) it was decided to use malt diastase for starch digestion.

Footnote 2. Diastase was prepared as follows: Barley seeds were soaked overnight, then sterilized the next day with 1 percent formaldehyde solution for 10 minutes. After washing in running water the seeds were germinated. When the radicles had appeared to the extent of one quarter of an inch, the seeds were air-dried under a fan and then oven dried at 40° C. The seeds were then finely ground, soaked in distilled water for two hours with occasional shaking at a temperature below 20° C. The material was allowed to settle and the supernatant liquid filtered under suction. Sufficient 95 percent ethyl alcohol was added to make the solution 50 percent in strength. After shaking, the solution was allowed to settle. The supernatant solution was filtered under suction to a clear liquid, the temperature being kept under 20° C. This solution was then made 70 percent alcoholic with 95 percent ethyl alcohol. The solution was filtered under suction using a hard filter paper and finally the precipitate caught on the filter paper. The precipitate on the filter paper was air dried under suction at a temperature below 20° C, and then held in a desiccator over sulphuric acid. The diastase preparation kept its activity for weeks in the dry state and when made up to 0.1 percent solution was held in an ice box at 10° C. with a few drops of added Toluol.

1 2 3

FIG. 9 Materials used for chemical analyses.

1 and 2. Two year old laterals April 27 with axillary spurs (leaves removed) after removal of the axillary spurs these laterals provided wood and bark samples. Moisture determinations were made on axillary spurs.

3. Spur clusters (leaves removed), which, after removal, at the arrows, from the branch, provided spur material, in June and July. Earlier spur material consisted of only the current year's growth on these clusters.

with sodium hydroide solution, using phenophthalein as an indicator. The solution was then turned slightly acid and brought to volume. A 1/5th aliquot was used for determining the reducing power, by the same procedure as free reducing substances.

This routine analysis of the hemicelluloses was considered unsatisfactory because of the too frequent failure of replicate samples to check satisfactorily, and the results are omitted in the presentation of the data.

The analyses of total ash, soluble and total nitrogen, phosphorus and potash, were carried out by courtesy of Michigan Agricultural Experiment Station, using official methods.

Expression of results. The data were calculated to a dry weight and a fresh weight basis. Following the usual practice the data are presented on a dry weight basis. The differences between the fruiting tree and the defruited trees appear less on the dry than on the fresh weight basis, as the dry weight basis eliminates the effect of the significant differences in moisture content of these trees after April 14.

PRESENTATION OF DATA

MOISTURE

The time of fruit removal caused several distinct changes in the moisture content, especially of the spurs. The data appear in figure 10. In this material, blossom removal (A) caused a considerable but temporary reduction in moisture content which returned again to that of a normal fruiting tree within 20 days of full bloom. Fruit removal at 16 days (B) also caused a marked, temporary reduction in moisture. The moisture conent was not reduced as much nor for as long a period as by blossom removal. Fruit removal at 30 days (C) and 47 days (D) did not affect

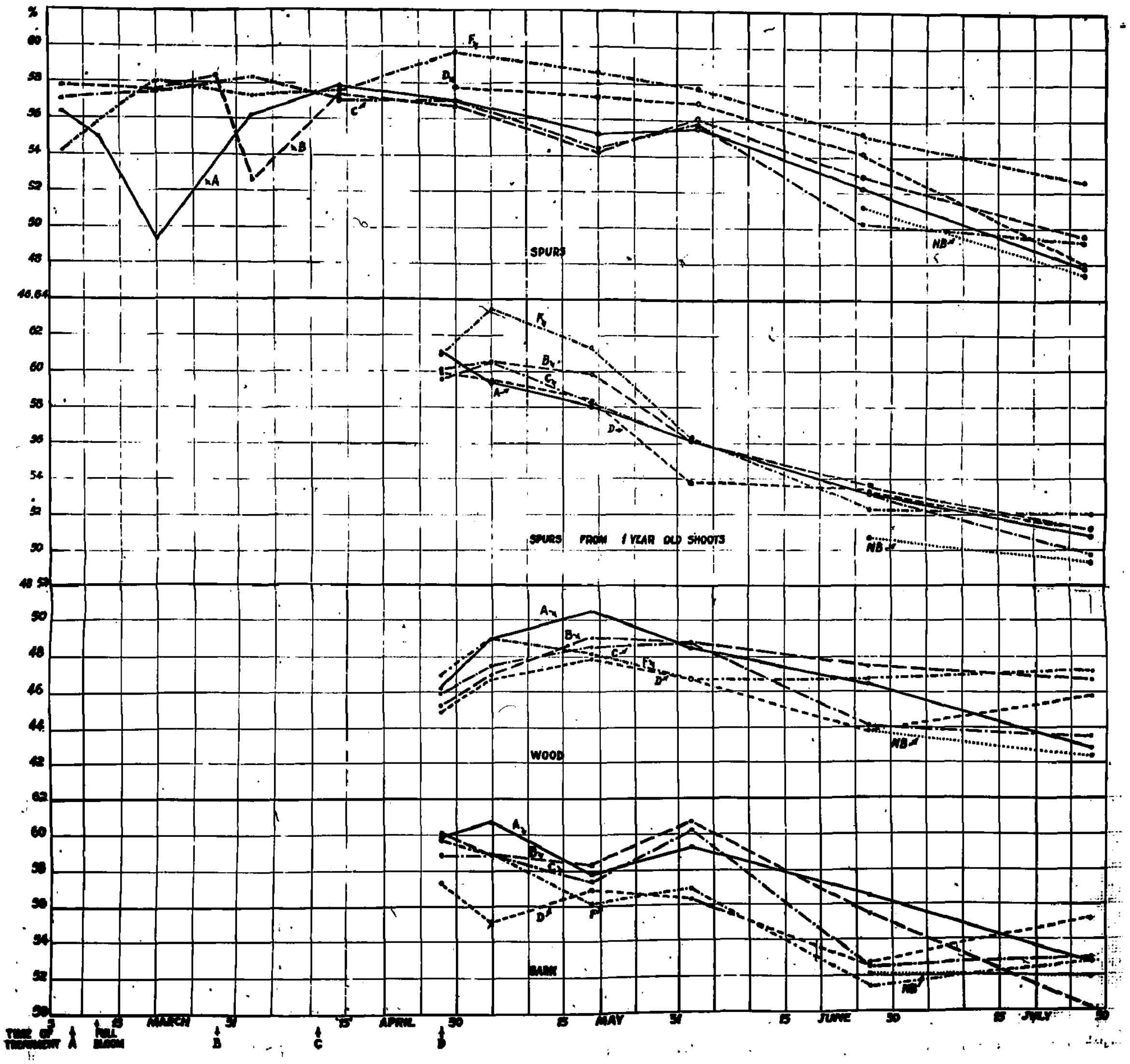

FIG. 10. Moisture, as percentages of fresh weight in spurs, spurs from one year old shoots (i.e. laterals) and the wood and bark of laterals.

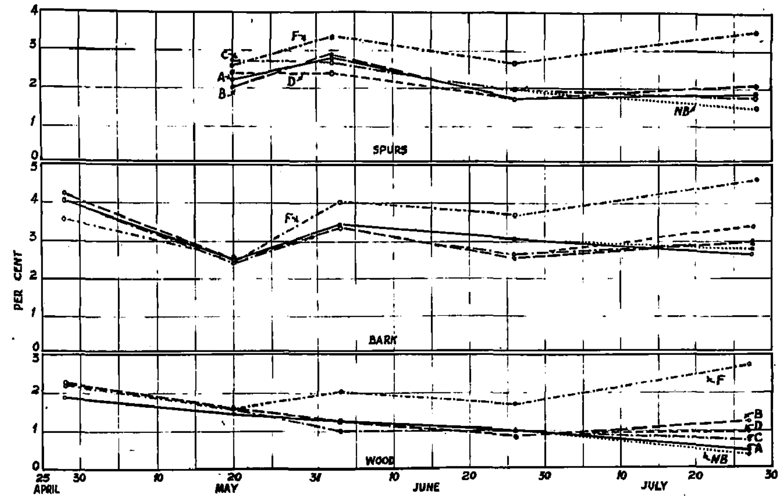

FIG. 11. Reducing substances, as percentages of dry weight in spurs and the bark and wood of laterals.

the moisture content immediately after it was done.

After the temporary reduction in moisture content of A and B, these trees and also C and F had a similar moisture content to the fruiting tree on April 14.

The fruiting tree then gained in moisture content over the defruited trees and showed a higher moisture content for the rest of the season.

The defruited trees A, B and C had similar moisture percentages until late June and July, when they showed more scattered values. Fruit removal at 47 days gave intermediate values between the fruiting and the defruited trees.

The seasonal trend in moisture content of the fruiting tree was level for the first month (up to April 14), after which the defruited trees steadily declined in moisture content. The fruiting tree continued to increase for another 15 days before it started to decline in a similar way to the defruited trees. For this reason the fruiting tree showed a higher moisture content for the rest of the season.

These results differ from the fewer data of Davis (13), who found that the moisture content increased up to the last of April or the first of May, in all fractions (bark, wood and spurs) of both bearing and non-bearing trees.

In the fractions from the bearing trees the amounts of water remained reasonably constant for the remainder of the season, in those from the non-bearing trees they began to drop about May 1.

The clear effect of fruit removal on the moisture content of the spurs was not shown in the wood and bark of laterals and only during May in the axillary spurs from laterals.

It is apparent that the effect of fruit removal on moisture content is one that is localised in the spurs, thereby differing from other constituents to be discussed later.

REDUCING SUBSTANCES

Fruit removal produced a distinct change in the content of reducing substances. The data appear in figure 11. The change appeared in the spurs and in the wood and bark of laterals. In the trees from which fruit was removed the reducing substances were similar to or higher than the fruiting tree until May 20th, when they became less and remained so for the rest of the season. All fractions showed a similar change. The content of reducing substances was similar in all the defruited trees, irrespective of the time at which the fruit had been removed, and the content of defruited trees was similar to that of an off-year tree in June and July.

It appears, then, that the seasonal changes in reducing substances of the defruited trees resemble those of an off-year tree as described by Davis (13). Davis found, however, that debudded material (that is, corresponding with treatment A of the present study) had a content of reducing substances intermediate between an off and on year tree.

SUCROSE

The trees from which fruit was removed tended to have an increase in sucrose content after May 20, whereas the fruiting tree showed a low sucrose content. The data are given in Table 18.

STARCH

The trees from which fruit was removed all showed a uniformly higher starch content than the fruiting tree. The data appear in figure 12. In the fruiting tree, starch was low until June 3, when it showed some

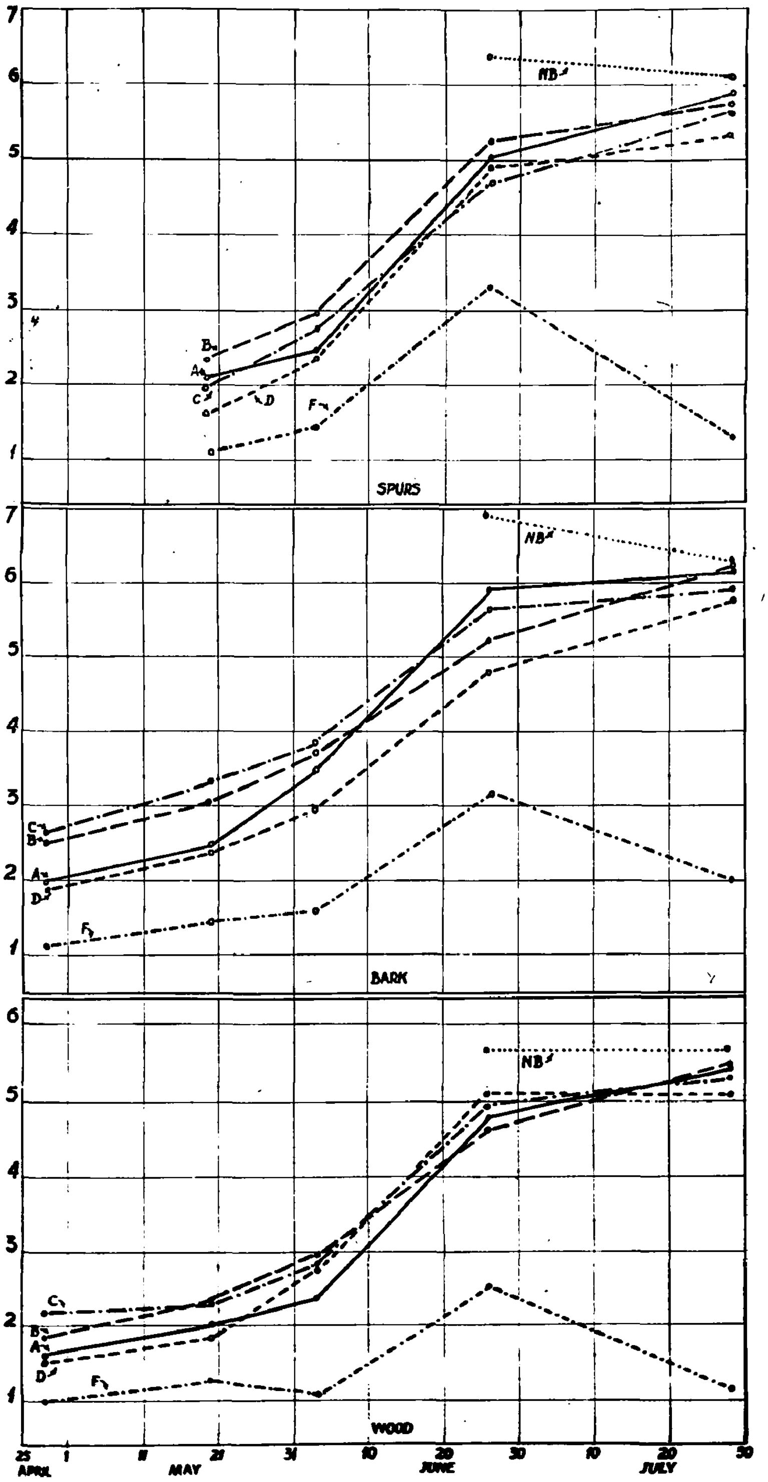

FIG. 12. Starch, as percentages of dry weight in spurs, and the bark and wood of laterals.

TABLE 18 Sucrose in percentage of dry weight

Material	Treatment	April 28	May 20	June 3	June 26	July 28
Spurs	A	-	0.1	1.4	1.3	1.8
	B	-	0.1	1.2	1.4	1.2
	C	-	0.1	0.1	0.7	1.2
	D	-	0.1	0.2	1.0	2.1
	F	-	0.1	0.1	0.5	1.0
	NB	-	-	-	0.8	1.4
Bark	A	2.1	2.3	2.0	1.0	2.3
	B	1.8	2.1	1.6	2.1	2.1
	C	2.1	2.5	2.5	1.5	2.0
	D	2.0	2.2	1.8	1.0	2.0
	F	2.1	2.2	1.5	1.0	1.5
	NB	-	-	-	1.2	1.3
Wood	A	0.4	0.4	0.4	0.4	0.1
	B	0.3	0.4	0.4	0.5	0.2
	C	0.2	0.4	0.4	0.3	0.1
	D	0.2	0.4	0.4	0.4	0.1
	F	0.3	0.3	0.2	0.2	0.1
	NB	-	-	-	0.3	0.4

accumulation. All the defruited trees, however, despite differences in fruit removal time, showed a comparatively high starch content which increased during the season and in June and July was only somewhat lower than the off-year tree.

NITROGEN

Total Nitrogen. During the season the defruited trees showed a level to slightly increasing content of total nitrogen, whereas the fruiting tree, although it started with the highest content, steadily declined in total nitrogen. The defruited trees had a distinctly higher percentage of total nitrogen than the fruiting tree after May 20. All trees from which fruit was removed had rather similar amounts of total nitrogen. These amounts in the June and July samples, were not quite as high as the off-year tree.

The data confirm Davis's finding that the non-bearing spurs of the Sugar prune are lower in nitrogen than the bearing spurs, a condition which is contrary to that in apple spurs as established by Kraybill and associates (28, 29) and Hooker (25).

The separation of total nitrogen into the soluble and insoluble fractions is of particular interest, as it shows that they are affected differently by fruit removal. The soluble fraction is more variable in content. The data appear in figure 13.

Soluble Nitrogen. The defruited trees differed from the fruiting tree in seasonal trend; at the end of April the defruited trees, except C, started with a low content of soluble nitrogen and showed an increasing content until the end of July. The fruiting tree started with the highest content in April, showed a steeply declining content in May and June and ended on July 26 with the lowest content of soluble nitrogen. The defruited trees were lower than the fruiting tree in early May, similar to it in late May and early June and higher in late June and July. At the latter times, the defruited trees gave lower values than the off-year tree.

Insoluble Nitrogen. At the end of April, the fruiting and the defruited trees had rather a similar content of insoluble nitrogen with A B and C at a higher level than D and F. Thereafter all the defruited trees showed a comparatively constant content of insoluble nitrogen, but the fruiting tree steadily declined in this constituent. Tree D was similar to a fruiting tree on April 28, but by May 20 was similar to other defruited trees.

TOTAL ASH

Contrary to expectations, the fruting tree did not differ from other

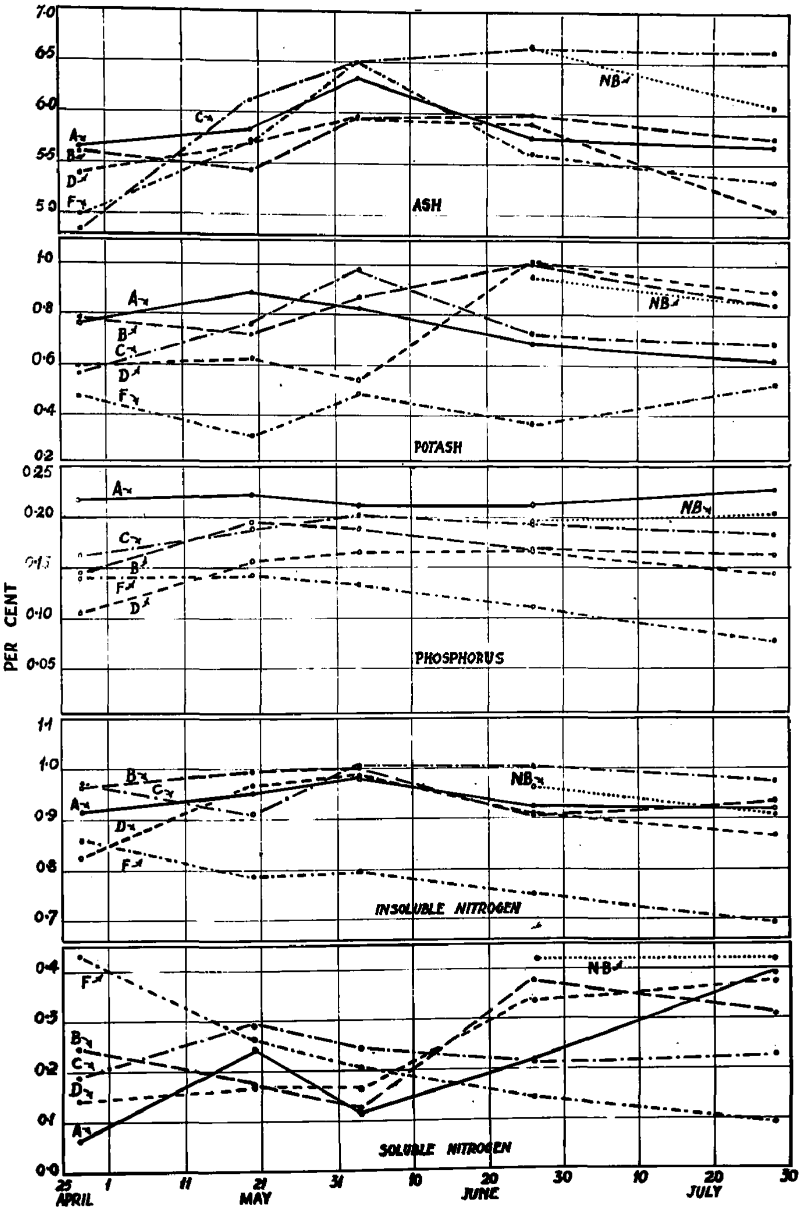

FIG. 13. Ash, potash, phosphorus, insoluble nitrogen and soluble nitrogen, as percentages of dry weight, in the bark of laterals.

trees in ash content until late July. At this time F and D showed a lower ash content than the defruited trees and the off-year tree. Tree C was outstanding for high ash content in June and July. The data are given in figure 13.

POTASH

Fruit removal had a distinct effect on the potash content. The data, as percentages of K_2O, appear in figure 13. At the end of April trees A and B (early times of fruit removal) already showed a higher content of potash than the fruiting tree and trees C and D (fruit removal at 30 and 46 days, respectively) had intermediate amounts of potash. Within a month tree C had a similar content of potash to other defruited trees and after two months D showed a similar level of potash. With these exceptions the defruited trees maintained a distinctly higher level of potash than the fruiting tree from the end of April to the end of July. At this time the fruiting tree increased in potash content, probably due to migration from the leaves, such as has been shown by Lilleland and Brown (33) to take place from the leaves of the d'agen prune in California after July.

PHOSPHORUS

During the period of analysis, all the trees from which the fruit was removed, showed a level or slightly increasing content of phosphorus. The fruiting tree, however, showed a slight decrease during the season with the result that defruited trees had a greater content of phosphorus than the fruiting tree after May 20. Among the defruited trees, blossom removal (A) gave the highest value of phosphorus and fruit removal at 45 days (D) gave the lowest content of phosphorus. In tree A the seasonal trend was level; trees B and C started with lower amounts but increased to higher levels by May 20; tree D started with the lowest content of phosphorus and increased to a level inferior only to other defruited trees by June 3. At the time of the June and July sampling the phosphorus content of the defruited trees was similar to the off-year tree.

The data expressed as the percentage of P_2O_5 appear in figure 11.

DISCUSSION

1. Influence of fruit removal on composition. Fruit removal altered the composition from that of a fruiting tree and caused it to approach that of an off-year tree, as indicated by the late June and July samples, when sample values for an off-year tree were also available. It also caused a difference from the fruiting tree, similar to what occurs in off-year trees, in reducing substances, starch, nitrogen and potash in the previous work of Davis (13, 14) and phosphorus (Compton (10)). The early times of fruit removal, A and B, caused early marked and temporary reductions in moisture and all times of fruit removal altered the moisture content after April 14 from a fruiting tree.

The effect of the latest time (D) of fruit removal did not become apparent until some time after it was done. It thus gave intermediate values for potash, phosphorus and insoluble nitrogen in May. This tree showed a prolonged effect of fruit development on composition. It carried fruit for a period of 47 days but did not reach a high level of potash and phosphorus till 108 days after full bloom, or of nitrogen till 70 days after full bloom.

2. Relation of Composition to blossom bud formation. Apart from the intermediate values for phosphorus, potash and insoluble nitrogen of tree D just mentioned, which occurred in May and early June, the composition

of the four defruited trees, particularly during June and July, when blossom primordia were most likely appearing, does not indicate any constituent which was critically associated with the blossom bud formation of A, B and C or the absence of blossom bud formation in D.

These results do not support the view that the general composition of the spurs, or the tissues adjacent to the spurs, such as the bark or wood of one-year old laterals which bear spurs, is the determining factor for blossom bud formation. The results would, therefore, direct attention to the alternative view that small amounts of a blossom-forming substance, acting in a strictly localised manner are responsible for blossom bud formation. The interest in the critical time is that probably a change in development within the buds is initiated at that time, which permits of later blossom bud formation. Such a change in development would be likely to result from the action of a growth regulating substance, which would be likely to be produced by such trees as A, B and C, which made good leaf and shoot growth, extending over the critical time but not produced sufficiently by such trees as D, which made much poorer leaf and shoot growth and rather resembled a fruiting tree in these particulars.

GROWTH OF THE FRUIT

LITERATURE

Where fruit removal or thinning determines the critical time for blossom bud formation, the development of the fruit needs to be known with exactness for the conditions that obtain in that season. A study was, therefore, made of the blossom production, fruit setting and the development of the fruit. The growth of the Sugar prune has not been presented previously, although Davis (13) studied the change in content of moisture, sugars and nitrogen during the season 1928. The investigations of Conners (11), Dorsey and McMunn (17) Tukey (50, 51) and Lilliland (30, 31) and others indicate that stone fruits make growth in three phases. I is a period of increase up to the start of pit hardening; II is a period of slower increase in size while the pit is hardening, and III is the final period of increase including the final swell.

Among plums, d'agen, Robe and Tragedy were found by Lilliland to show pronounced cyclic growth and Climax to show only slight cyclic growth. The development of the flesh, endocarp and kernel was presented separately as dry weight increases. As in other stone fruits, the endocarp in these plum varieties grew mostly during phase II of fruit growth; the flesh increased mostly in phase III, when the stone made little growth. The kernel also increased in dry weight during phase III. Tukey (50) studied particularly the growth of the embryo relative to that of the fruit. He found that the embryo was suppressed in phase I, while the nucellus and integuments increased rapidly. The embryo grew rapidly during phase II. Tukey (51) later examined the development of the seed of several varieties of peaches that ripened at different seasons. He found that the nucellus and integuments increased in size (millimetres) for a similar period during phase I in all varieties. The embryo then increased rapidly with the inception of phase II and grew for a similar period in all except early ripening varieties, in which the embryo aborted. The embryo was still growing in early and midseason varieties but had completed growth in late varieties when the fruit entered phase III of its growth.

METHOD

Flowering and Setting. The original number of blossoms was recorded and the set of fruit was counted periodically on five representative branches selected at random around trees B, C and F. The fruit that would drop at each time of record was shaken from the trees and thus omitted from the records of set fruit. The fruit that had dropped at any particular time could thus be calculated from a previous number of fruits or of blossoms. The number of leaf buds on these branches was also recorded so that the setting could be expressed on the basis of all spurs that bore leaves.

Development of the fruit. Samples of fruit were taken from the fruiting tree (F) to find the seasonal increases in fresh and dry weights and volume. The numbers of fruit in each sample are given in Table 19. The samples were taken into the laboratory, the fresh weights recorded and volumes ascertained by displacement of water. On three occasions volumes were not found on the same samples as were used for fresh and dry weights. The samples were then cut into small pieces and dried in a forced draught oven at 55-60°C. The pericarp and the kernel or seed were recorded separately after April 16, 35 days after full bloom.

Samples of the drop fruits were taken periodically; they consisted of fruits which were about to drop, that is, which fell when the limbs were gently shaken. The drop fruit was recorded for fresh and dry weight and volume. Notes were made on the macroscopic appearance of the stone and embryo in the set and drop fruit, as well as on the waves of shedding.

PRESENTATION OF DATA

FLOWERING

The main fact that emerged from an examination of flowering of the on-year trees B, C and F in the Spring of 1936, was the proportion of blossoming shoots which were without leaves to those with leaves and to the leaf or non-bearing shoots. An analysis of this condition on representative limbs gave the results shown in Table 19.

Between 15 and 24 percent of the shoots produced flowers without leaves and consequently made no extension growth in the on-year. The excessive blossom bud formation and flowering thus inhibited the start of vegetative growth to that extent. Off-year trees, however, produced some 30 percent of the shoots, practically all being small spurs, from dormant buds on the old spur clusters. By this means, then, the number of spurs was maintained. Yet the 15 to 24 percent bearing spurs that were without leaves depended upon the leafed spurs and thus the set per spur described later is expressed on the basis of leafed shoots.

A similar condition was found by Dr. Davis again in 1938, the next on-year. He used a classification of blossom production, similar to that mentioned, for shoots (that is spurs and longer shoots together) and for spurs separately. The results appear in Table 19 and the condition is shown in figure 14 _a_ and _b_. Of the trees examined in 1938, tree 3/5 was

TABLE 19

The percentages of leaf and flower-producing shoots

	On representative limbs,1936			On representative limbs,1938			On spur clusters only,1938		
	B	C	F	tree 3/5	tree 7/1	Row 15/16	tree 3/5	tree 7/1	row 15/16
Blossoming shoots - (a) without leaves	23.7	21.0	14.8	25.4	35.5	27.5	28.0	42.0	29.2
(b) with leaves	49.8	63.0	61.1	66.8	49.7	60.7	69.5	56.8	69.8
Leaf shoots - without blossoms	26.5	16.0	24.1	7.9	14.8	11.8	2.5	1.3	0.9
Leaf shoots, with and without blossoms	76.3	79.0	85.2	74.7	64.5	72.5	72.0	58.1	70.7
Number of shoots examined	533	481	643	694	1020	752	515	737	564

FIG. 14. Flowering of Sugar prune, 1938, on long shoots (left) and on spurs (right) showing flowering shoots without leaves at X.

was the fruiting tree of the present investigations; tree 7/1 was one of the smaller and more precocious trees in the Sugar prune block, and the group marked rows 15 to 16 was a composite of two trees from each row. Tree 7/1 and group 15/16 had not been used in the present investigation. These trees had not been subject to any fruit thinning treatment and were therefore deeply entrenched in the alternating habit; other trees that had been defruited early enough to cause annual blossom bud differentiation seemed to have more spurs with leaves.

The differences between the 1938 and 1936 data would indicate that these prune trees were increasing in fruitfulness in succeeding on-years. There were relatively fewer leaf shoots and more leafless bearing spurs in 1938 than in 1936. Dr. Davis stated in correspondence that the fewer leaf buds were characteristic of the trees in the on-year of 1938. The trees were bearing about as full a crop of blossoms as possible.

SETTING. In the fruit-setting process the majority of the blossoms and young fruit fall in a series or waves of drop fruit. Dorsey (15) found the pistils of plums to fall in three distinct stages, namely (a) immediately after bloom, (b) two to four weeks after bloom, and (c) later, following considerable enlargement of the pistil. In the first drop the flowers bore abortive pistils. The period of abscission of the 2nd drop was 17-30 days after bloom. The third drop was characterised by the fruit abscissing from the pedicel; embryo development had started but was arrested in an early stage; endosperm was partly formed, but often overtaken by the embryo to the extent of being found naked in the nucellus; the seed could enlarge to nearly full size with only slight growth of the embryo. As the fruit may set so heavily that it can only grow to a small size, Dorsey thought that competition was not the primary reason for the drops. He attributed the third drop directly to the arrest of embryo development.

In the Sugar prune, the number of flowers, the extent of the three drops and the final setting on the fruiting tree (F) are given in Table 20. The first shedding was smaller than the second and the third or June drop was comparatively small. The remaining set of 21.2 percent was heavy and resulted in small fruit.

TABLE 20. Summary of Fruit Setting, Fruiting tree (F)

	No. of fruits at the start and end of each drop	Fruits remaining after each drop	Fruits falling in each drop
		percent	percent
Number of - Flowers	1682	100.00	...
1st drop - ended Apr. 2	1682 - 1242	73.85	26.15
2nd drop - ended Apr.24	1242 - 563	33.5	40.35
3rd drop - ended June 18	563 - 356	21.2	12.3
Number of set fruit	356		21.2
			100.00

Shortly before ripening a slight shedding of maturing fruit took place, which amounted to 2.7 percent of the final set of fruit.

SEASONAL DEVELOPMENT OF THE FRUIT AND SEED

FRUIT.

The fresh and dry weight increases of the pericarp (flesh and stone) and the seed (kernel) are given in Table 21 and figure 15. The upper graph shows the seasonal development of the entire fruit and of the seed separately; the lower graph the percentage dry weight of the fruit and seed, which thus may be directly compared with the phases of growth of the fruit and seed above. The seasonal increase in volume, fresh and dry weight of the fruit agreed closely with one another and showed the three

TABLE 21

The Seasonal Increase in Fresh and Dry Weight and Volume of Sugar Prune Fruits and Seeds

Date	Days after full bloom	No. of fruit in sample	Av. Vol.	Av. Fresh Wt.		Av. Dry Wt.		Per Cent Dry Wt.	
				Set Fruit	Seed	Set Fruit	Seed	Set Fruit	Seed
			c.c.	G.	G	G	G		
March 17	5	100		0.10	-	0.20	-	19.5	-
March 24	12	200		0.10	-	0.016	-	16.2	-
April 2	21	100		0.27	-	0.04	-	15.4	-
April 8	27	80		0.75	-	0.09	-	12.0	-
April 16	35	20	2.3	2.53	0.18	0.24	.0136	9.6	7.4
April 23	42	20	3.6	3.48	0.28	0.38	.0203	10.7	7.3
April 30	49	20	4.1	5.00	0.34	0.60	.0238	11.9	7.1
May 7	56	20	5.2	5.28	0.25	0.73	.0172	13.8	6.9
May 18	67	15	6.7	6.88	0.27	1.16	.0355	16.7	13.3
June 3	83	15	7.2	7.64	0.32	1.41	.0660	18.4	21.0
June 9	89	15	7.7	9.10	0.34	1.62	.0886	17.8	26.9
June 18	98	15	-	12.35	0.35	1.90	.1455	15.3	41.7
June 26	106	15	11.7	12.80	0.33	2.20	.1630	16.4	49.7
July 25	135	15	12.7	13.25	0.30	2.75	.1870	20.8	62.0

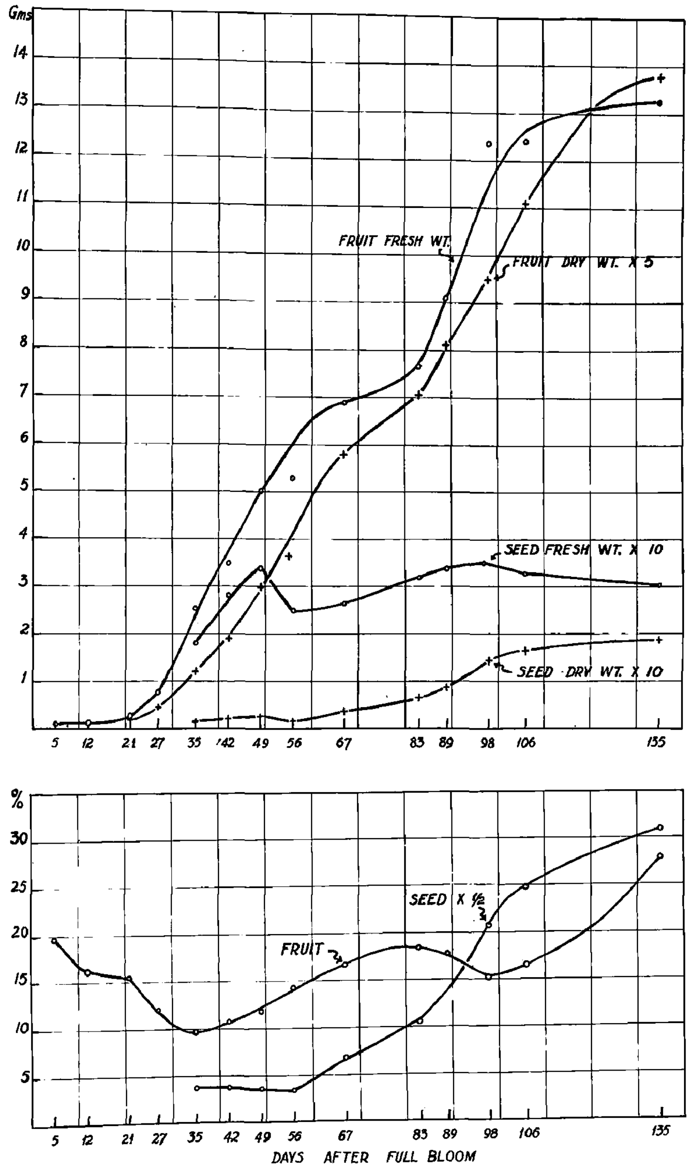

FIG. 15. Fresh and dry weight increases of the fruit and the seed (above) and the changes in the percentage dry weight of the fruit and the seed (below).

typical phases of growth. This growth may be considered a double growth curve, in which the parts were as follows:

Phase I.	(1st growth curve part	a	March 12 - April 2	21 days
	(" " " "	b	April 2 - May 7	35 days
" II.	(" " " "	c	May 7 - May 18	11 days
	(2nd " " "	a	May 18 - June 1	14 days
" III.	(" " " "	b	June 1 - June 26	25 days
	(" " " "	c	June 26 July 25	29 days
	Total number of days of fruit growth			135

The progress of the hardening of the endocarp was observed in relation to the stages of fruit growth. The first traces of hardening became evident during phase I, but the rapid hardening took place during phase II of fruit growth. On April 24, 42 days after full bloom, about 50 percent of the setting fruit showed a slight hardening at the distal end of the endocarp. The tissue of the endocarp was identifiable, in other fruit, by a lighter colour than the rest of the pericarp. By April 30, the pits were rapidly hardening along the ventral suture; by May 7, they were hardened throughout but were still capable of being cut with a knife. By May 18, the pits were hard enough to turn the edge of the pruning shears used to cut the fruit.

Parts a and c of each growth curve have a slower rate of growth than part b of each curve. These different rates of growth affected the percentage dry weight as shown in the lower graph of figure 15. The percentage dry weight was high at blossom time and during part a of the first growth curve. The percentage fell during part b, but rose with the inception of pit hardening on April 24 and continued to rise in part c of the 1st growth curve and part a of the 2nd growth curve (that is Phase II). The percentage fell again in part b of the 2nd growth curve, and rose to the highest level during ripening in part <u>c</u> of the second growth curve. The prune differs from the stone fruits used for dessert in part <u>c</u> of the second growth curve, as the fruit is allowed to hang until it drops. In this period, although the fresh weight remained constant, there was a considerable gain in dry weight.

SEED

The development of the seed of the Sugar prune, like that of other PRUNUS species, took place in several distinct stages. First was a growth of the integuments and nucellus, coinciding with phase I of the fruit growth. Then followed a development of the endosperm which appeared macrospically the size of a pin's head on April 28, 47 days after full bloom, thus coinciding with the rpaid phase of pit hardening. By May 18, the endosperm had grown to the extent of occupying half the nucellus. The embryo also appeared at this time, the cotyledons of the embryo occupying half the endosperm. By June 3, the embryo was fully grown and filled the seed coats. After this time the cotyledons increased in firmness and dry matter.

The increases in fresh and dry weight and the percentages dry weight of the seed, the records of which commenced on April 16, are given in Table 21 and figure 15. The fresh weight increased until April 30, that is while only the integuments and nucellus comprised the kernel. It then fell sharply between April 30 and May 7, coincident with the earliest macroscopic appearance of the endosperm. After this time fresh weight increased with the growth of the endosperm and embryo until June 18, after which it declined slightly. In dry weight, the seed showed only slight gains in the nucellar stage, that is till April 30 and a continuous increase during the remainder of the period, more rapid till June 18 and less rapid after this time, when the fresh weight actually decreased. The percentage dry weight also showed distinct changes before and after the appearance of the embryo. The percentage dry weight declined slightly but constantly till May 7 when the nucellus was noted to be becoming more fluid. The percentage dry weight increased rapidly from 6.9 percent on May 7 to 62.0 percent on July 25.

THE RELATION OF THE WAVES OF FRUIT DROPPING TO THE GROWTH OF THE FRUIT

The time that the waves of fruit dropping occurred, relative to the phases of fruit growth, and also the time when, in the growth of the fruit, these drops were initiated are indicated by available data, and are presented in figure 16.

The first drop which was completed within 30 days of full bloom occurred within part a of the first growth curve. The second drop, which occurred during the next three weeks and was practically complete by the end of the second week, occurred in part b of the second growth curve. The third drop, which included two phases (3a and 3b), both identified by the abscission of the fruit from the pedicel as the June drop, was spread over some 50 days and occurred mainly during parts a and b of the second growth curve.

The factors which determine the drop of fruit operate before the fruit actually drops. The factors themselves and the time when they operate are very uncertain. If the time were known with some certainty the factors would be better defined.

A means of tracing back to the time when the drop was initiated should be provided by the dry weight records. This assumes that once the fruit ceased to grow, it would not increase in weight while on the tree. It would tend to lose weight, but as it was collected when about to drop, the loss would have been negligible. Fresh weight would be variable because of moisture withdrawal. The dry weight of the drop fruit traced back to the set fruit, is shown in figure 14 and other data are given in Table 22.

The second drop fruits recorded on April 8, 16 and 24 were similar in weight and traced back to April 3. On April 24 the fruit previously recorded as drop had turned yellow and shed off.

The remaining fruits at that time showed differences in size, the smaller ones having turned yellow at the stalk end identifying them as the June drop. This fruit was the start of the next drop, 3a, which was sampled again on April 30 and May 7. It traced back to April 12, when the set fruit was showing the increased rate of growth in phase I of fruit growth. The set fruit also showed traces of pit hardening, but drop fruit showed no pit hardening.

Some "to-drop" fruits were noted and their dry weight recorded on May 7. This fruit was so similar to the drop fruit of April 24 and 30 and May 7 that probably it was a later phase of the same drop. It would trace back to the 15th of April instead of the 12th, and thus comes within the same phase of fruit growth.

The drop fruit called 3b was more advanced in development than 3a; on June 3 it had partly developed pits and on June 18 had imperfectly hardened pits or very thin entire pits. Embryos had aborted when 2 to 3 millimetres long or after slight growth of the cotyledons in about one quarter of the drop fruit. Both samples traced back to April 30, 48 days after full bloom, which immediately followed the first record of endosperm development and pit hardening in the set fruit.

The dry weight of the set fruit on May 7 is lower than the interpolated curve. This is probably due to having sampled a mixture of set and "to-drop" fruits, which as both were green although of different sizes, were not distinguished between on this date. This accords with deductions that

TABLE 22

Weights and Records of Dropping Fruit

Date	Days after full bloom	Average fresh weight (G)	Average dry weight (G)	Remarks on drop fruit	Remarks on set fruit
March 17	5			Shedding of flowers	
March 24	12			f. has dried husks; considerable variation in development	
April 2	21			Husks fallen; large fruit double the size of the others.	
April 8	27	(a). 306	.037		
April 16	35	(a). 365	.039	Set and to-drop f. very distinct	Endocarp defined by lighter colour
April 23	42	(a). 314	.04	f. previously recorded as drop f. have turned yellow and shed. Remaining f. show differences in size, the smaller showing yellow at stalk end. These sampled at (b)	Pit hardening, size of pin's head in 50% of set fruit.
		(b)1. 100	.13		
April 28	47			This drop (3a) is light. Pedicel retained on tree, hence "June drop".	Endosperm showing as big as pin's head in nucellar tissue
April 30	49	(b)1. 400	.118	This drop fruit is without stalk. Fruit still hanging on tree is green.	Stone hardening rapidly along ventral suture; embryo pin's head size; nucellus watery.

(continued)

Date	Days after full bloom	Average fresh weight (G)	Average dry weight (G)	Remarks on drop fruit	Remarks on set fruit
May 7	56	(b)1. 310 (c)2. 100	.1580 .190	(b) drop almost complete (c) is f. which will soon drop	Stone hard throughout but cuttable
May 18	67			May 16-17 North Wind	Stone turns edge of pruning shears Endosperm occupies half nucellus; embryo half the endosperm.
June 3	83	(c)3. 856	.606	f. of this drop have partially developed stones	Embryo occupy all seed; cotyledons soft.
June 9	89				Cotyledons firm
June 18	98	(c)3. 610	.530 Shrivelled	Drop f. has imperfectly hardened pits or thin entire pits Embryos aborted after slight cotyledonary development. End of final drop.	
June 27	107				Fruit sweet, separates from stone. Seed coats turning brown. f. has slight blush.
July 25	135				Fruit ripe and dropping

Note: Weight of dropped flowers not recorded; a = 2nd. drop; b = 3a drop; c = 3b drop. f = fruit.

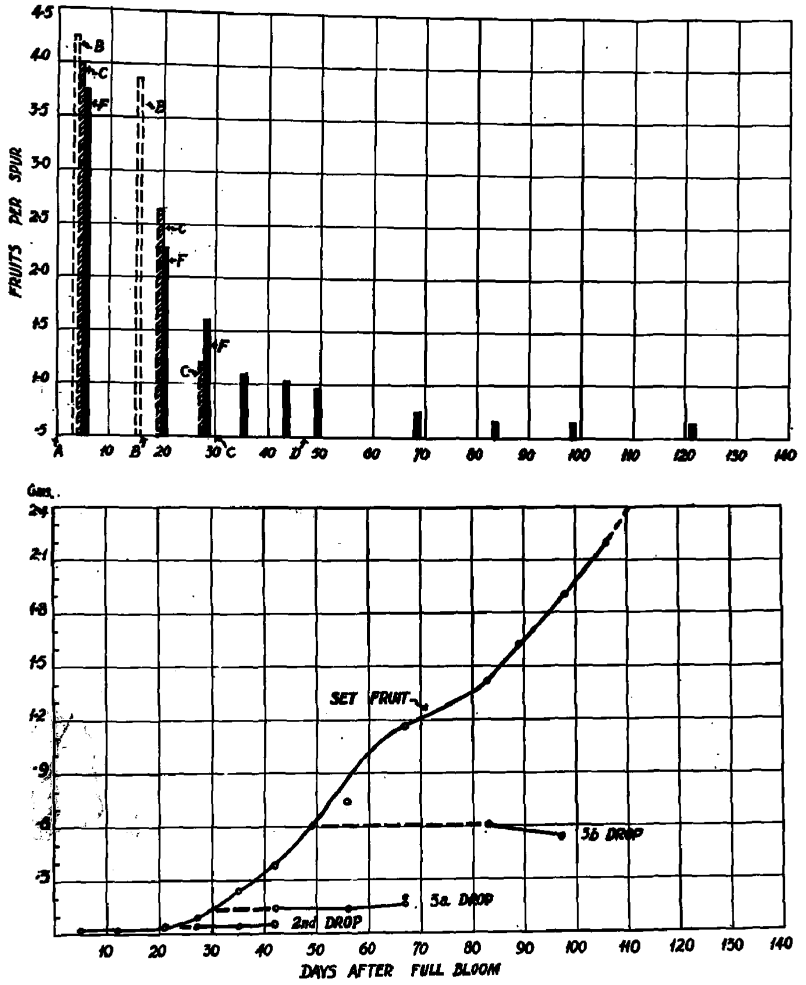

FIG. 16. Number of fruits per spur during the season (above) and the dry weights of the drop fruit in relation to the set fruit (below).

the 3b drop was in process of initiation at this time.

The time when the dropping of fruit is initiated being thus arrived at, enables a closer examination of the possible casual factors. The second drop is initiated at the inception of part b of the first growth curve, and evidently indicates a lack of the growth stimulant that activates the setting fruit into the rapid increases in size of the first growth curve. The 3a drop is initiated in part b of the first growth curve and may occur because of the competition for nutrients during this active growth. The cause must be of a particular kind, as, the three separate records of this drop trace back to the one period, April 12. The 3b drop is initiated with early endosperm and embryo development. The failure of this tissue to grow from cytological and genetic causes, removes this stimulation to the growth of the fruit which thus fails to compete and survive. Moreover, competition should be stronger at this time because of the inception of pit hardening.

It is of particular interest to this study that, according to these deductions, the first, second and 3a drops were initiated before the critical time of 35 days after full bloom.

DISCUSSION

The influence of fruit growth on leaf and shoot growth . The growth of fruits at the same time as shoots and leaves is a factor that inhibits growth, in addition to such other factors as water and nutrients, temperature and length-of-day which determine the seasonal growth of trees. When that factor was reduced or removed within 35 days after full bloom (treatments A, B and C) growth was considerably increased and blossom buds were subsequently differentiated.

The development of the fruit in the first growth curve appears to decide quantitatively the leaf and shoot growth made by trees that have blossomed. It was shown (Figure 8) that the leaf number, the length and the leaf area of shoots was increased most by treatments A and B (blossom removal and fruit removal at 16 days); a good deal less by C (30 days) and comparatively little by D (47 days). Interpolation between D and F indicates that fruit removal at nine weeks after full bloom would probably not increase growth. The results for shoot length and leaf number formed a reversely sigmoid curve, and those of leaf area showed a uniform reduction with the time that the fruit was borne. When these data were compared with fruit growth (figure 15), it was found that they coincided with the first sigmoid curve of fruit growth. Treatments A and B fell in part a, C early in part b, and D late in part b of the first growth curve; defruiting at 9 weeks, later than which growth would not be improved by fruit removal, coincided with the limit of part b of the curve. These comparisons show that there is a reciprocal and quantitative relationship of vegetative growth with fruit development.

The development of the fruit in the first growth curve appears also to affect the frequency distributions of the different growth measures. In A, B, C, D and F, these were altered with the progressively longer periods of fruiting in the following manner.

1. Heightening the mode, apparently due to
2. Reduction of the frequencies immediately following the mode
3. Reduction of the longer shoots (laterals) in number (that is, percentage of the sample) and in length (that is, range of classes).

As the shoots longer than the mode grew later than shorter shoots, it is apparent that these latter will be inhibited by the longer periods of fruiting of C, D and F. This inhibition added to the frequency of the mode and caused a heightening of this class.

The singular development of the leaf area of six-leafed spurs presented in figure 3 is also related to the development of the fruit. The seasonal development of leaf area of trees A, B, C and F was similar for 26 days after full bloom, irrespective of the fact that the fruit was removed from A 30 days before, from B 11 days before, and C 3 days after this time. After 26 days the rates of leaf growth differed in the different treatments so that differences in area were brought about by April 16, 35 days after full bloom. When these results are referred to the growth of the fruit, it is seen that 26 days after full bloom was the start of part b, or the rapid growth of the fruit in the first growth durve and that only after the fruit started to grow rapidly did it reduce the leaf area of the spurs of trees F and C. The reduced leaf growth of B compared with A was due to growth of the fruit for 16 days in part a of the first curve of fruit growth.

At first sight, the death and dehiscence of the terminal point of the spurs, which was observed April 14 to 16, would appear to be related to part b of the first growth curve, but as the defruited tree (A) and the off-year tree (NB) also showed the dehiscence, it apparently was caused by some factor that ran parallel with this phase of the development of the fruit.

An off-year tree shows a seasonal growth of leaves and shoots essentially similar to a fruiting tree, indicating that fruit development is but one additional factor along with others that limit growth. When this factor was removed or reduced, especially in part a of the first curve, vegetative growth increased considerably from either a fruiting or an off-year tree. These increases probably derived from the high reserves of carbohydrates and other nutrients with which, as shown by Davis (13) a bearing prune tree entered the on-year. Mack (34) also observed that if anything prevented the set in the on-year of biennial apple trees the growth was considerably more than that of the off-year tree.

During the time that growth can be influenced, the dry weight production of fruit per spur was small. The dry weight production of fruit per spur was calculated to include both the set and the drop fruit. It was about three times that of the single fruit during phase I of fruit growth and about two-thirds that of the single fruit for the remainder of the time the fruit grows. Thus, the seasonal dry weight production per spur was greater in the early critical period and less during pit hardening and ripening than would appear from the seasonal increases of single fruits. The dry weight production of flowers per spur in A was 0.2 grams; of fruit in B was 0.3 grams, in C 0.4 grams and in D on the basis of other trees it was 0.6 grams. The fruiting tree produced 9.0 grams of fruit per spur.

The small differences in the dry matter production of fruit between C and D greatly influenced growth and determined at the critical time whether blossom buds would form later or not. This was probably due to the nutritional conditions being at a minimum in the period between blossoming and the critical period. Fruiting after 35 days was an additional drain upon the nutrition sufficient to limit the growth of the great majority of the shoots and leaves abruptly and, it is believed, before a necessary change in development within the buds could be brought about which would lead later to blossom bud formation.

The Influence of Fruit Growth on Composition. The influence of fruiting on composition was to cause clear departures from the defruited trees in the content of moisture, reducing substances, sucrose, starch, nitrogen, potash and phosphorus. The departure in moisture of the spurs began after

April 14, that in insoluble nitrogen, potash and phosphorus, after April 28, that of reducing substances and sucrose after May 20, that of soluble nitrogen after June 3.

After the above mentioned dates, the fruiting tree showed a higher content of moisture and of reducing substances and a lower content of sucrose, starch, potash, nitrogen and phosphorus. Moisture was first affected, then the ash elements and finally the carbohydrates.

Of the carbohydrates, the bearing tree, after May 20, showed a combination of high reducing substances, low sucrose and low starch. If it may be assumed that reducing substances were reducing sugars, it appears that the bearing tree was unable to form the higher carbohydrates and that the lower carbohydrate storage of a fruiting tree is initiated by the failure of reducing sugars to condense to sucrose. Reducing sugars thus accumulate in bearing trees to a higher level of nutrition than in trees without fruit.

Considerable interest attaches to the order in which these changes appeared and whether they derive from one another, in view of the need for balance among the nutrients. It is a point for consideration, therefore, whether the changes in carbohydrate metabolism derive from the effect of fruiting on the mineral constituents. The investigations of Phillips, Smith and Dearborn (40) indicate that a disorganization of carbohydrate metabolism is characteristic of the early stages of a deficiency of potash. In the prune material, insoluble nitrogen and phosphorus were affected as well as the potash, although the potash content, being affected earlier and more by fruiting, has priority as a cause for the different carbohydrate metabolism of a fruiting tree.

Such changes are the fundamental and complex effect of fruiting on nutrition, for which the causes are to be sought in the growth of the fruit. The moisture change (on April 14 or 33 days after full bloom) occurred when the fruit entered part b (rapid growth) of the first growth curve; the change in phosphorus, potash and insoluble nitrogen (after April 28 - 48 days after full bloom) at the latter end of this period of growth and at pit hardening; the changes in reducing sugar and sucrose (after May 20 or 70 days from full bloom) occurred after the fruit had entered the second growth curve.

As all these times at which fruit was removed were during the first growth curve and caused the departures alluded to, it is clear that the early stages alone of fruit development did not have a permanent effect on composition. Fruit removal at 47 days (D), however, was late enough to cause intermediate values in moisture, potash and phosphorus in May and in insoluble nitrogen at the end of April. In other words it is the continued growth of the fruit in the second growth curve that influences composition. This is distinct from the effect of fruiting on leaf and shoot growth and the critical time for blossom bud formation, which is caused by the growth of fruit in the first growth curve.

Having noted this clear and orderly change in composition of the bearing tree, a re-examination of the literature was made. The chief literature to yield information, since it afforded some material with which to compare the bearing tree, was that showing the composition of bearing and non-bearing trees.

The extensive data, provided by Davis (13) (14) and Compton (10) on alternate bearing Sugar prunes, show quite clearly a similar departure of the bearing trees from the non-bearing trees in reducing sugars, nitrogen, ash, potash and phosphorus to that reported herein. In general, this change occurred in the bark and wood and in spur material on April 30 to May 15, more often on the later date in the wood than the bark. In addition the content of calcium and magnesium became lower in the off-year tree at about the same time. Lilleland (32) presented the content of potash and phosphorus, calcium and magnesium, as milligrams per leaf in the leaves of bearing and defruited French prune trees. The latter had a distinctly lower content of potash and phosphorus and a similar content of calcium and magnesium.

In the apple the evidence for the effect of fruiting on the different constituents and the time of change is not so consistent.

Hooker's (25) data indicate a clear influence of fruiting on the content of reducing sugars, potash, phosphorus and nitrogen, beginning early in June. Potter and Kraybill (41) also showed an influence on reducing sugars, nitrogen and phosphorus, which appeared in July. In this instance, the seasonal increases in dry matter of the fruit being presented, the influence could be traced to the period of most rapid increase of dry matter in the fruit. Kraybill (28, 29) showed some influence on the content of moisture, nitrogen, phosphorus, and ash, the differences appearing early in the season. All analyses showed a strong effect on starch content.

Much more definite information on the influence of fruiting on composition should be a valuable guide to some horticultural practices such as ordinary fruit thinning and manuring, although, since the effect is caused by the late growth of the fruit, it cannot be expected to affect the alternate cropping question, since growth and blossom bud formation are affected by the early growth of the fruit.

SUMMARY

1. The material for the investigation consisted of 4 on-year alternate bearing Sugar prune trees which were deflorated or defruited, each at a different time. Blossoms were removed from one tree (A) and fruit was removed from the others at 16 days after full bloom (B), one at 30 (C) and one at 47 days (D). An on-year fruiting tree (F) and an off-year tree (NB) were included for comparison.

2. Blossom or fruit removal induced blossom buds to form again in trees A, B and C, but not in D. These results agree with previous experience that there is a critical period at about 35 days for blossom bud formation in such trees.

3. These trees were used to examine the influence of the time of fruit removal on growth, composition and the relationship of these factors to blossom bud formation.

4. A review of the literature indicates the conditions of growth and composition that prevail in alternate cropping apple and plum trees and the little information available on the effect of thinning on growth and composition.

5. The average number of leaves of spurs was increased by fruit removal through the growth of the spurs later into the season. The average leaf number was determined at 10 days in F; 22 days in B and C and 27 days in A.

6. The seasonal expansion of the leaf surface of selected spurs was similar in all treatments for 26 days after full bloom, when it became greater in the earlier defruited treatments. This increase established greater average areas of leaves within 35 days of full bloom in the defruited trees in the order A, B, C and F.

7. The frequency distributions of the lengths or leaf numbers of shoots (all being primary) of the Sugar prune showed an extremely skewed or J-shaped curve, with a single mode which is in the spur classes. Such a distribution precludes the use of probable error.

8. The average number of leaves of shoots, the average length of shoots, the average leaf area of shoots and the average area of leaves were increased from those of a fruiting tree in the order D, C, B, A. The off-year tree gave values rather similar to the fruiting tree.

9. The relationship of the number to the area of leaves per shoot was examined in detail. As well as indicating the influence of fruit removal, the relationship indicated reasons why the leaf number distributions were more J-shaped than those of leaf area.

10. Relationship of the number of leaves to the length of shoots was sigmoid. This relationship indicates why distributions of shoot length are more J-shaped than shoot leaf number.

11. Expressed on a relative basis, length growth was increased relatively more than leaf area and leaf area relatively more than leaf number, by fruit removal.

12. When expressed in relation to the time when the fruit was removed, the values for the above measures clearly indicate a sigmoid reduction of growth with time after blossoming that fruit remains on the tree. This generalisation of the data indicates that fruit removal after nine weeks would not improve the growth over a fruiting tree.

The critical period at 35 days after full bloom fell in part II of this curve, when the responses of growth to fruit removal were rapidly falling off.

13. Treatments A and B caused marked and temporary reductions in moisture

content of spurs. By April 14 all defruited and fruiting trees had a similar moisture content, but after this date the fruiting tree assumed a higher water content for the rest of the season than the defruited trees. Treatment D showed a content of moisture intermediate between the earlier defruited trees and the fruiting trees. The effect on moisture was localised in the spurs.

14. All the defruited trees showed lower content of reducing substances than the fruiting tree after May 20 and a higher content of sucrose and starch.

15. Insoluble nitrogen, phosphorus and potash were higher in the defruited trees after April 28, soluble nitrogen after June 3 and ash in late June and July.

16. Fruit removal at these four different times caused the composition to closely approximate that of an off-year tree in May, June and July. Tree D, however, showed intermediate values in May for insoluble nitrogen, potash and phosphorus.

Apart from these differences, no constituent could be found that was critically associated with the blossom bud initiation of A, B, C and the absence of blossom bud formation of D.

17. Flowering was found to inhibit completely the vegetative growth of 15-24 percent of the shoots of on-year trees. Off-year trees produced some 30 percent of shoots from dormant buds, which thus maintained the number of shoots in the tree.

18. The seasonal development of the entire fruit and of the seed is presented in detail. The Sugar prune showed the double growth curve in fresh or dry weight that is characteristic of other stone fruits. The rate of growth in the different parts of the growth curves clearly affected the percentage of dry weight of the fruit. The growth of the seed showed distinct

growth phases, that of the nucellus corresponding with the first growth curve of the fruit, that of the embryo with the second growth curve. The progress of the pit hardening process was observed relative to the growth of the fruit and seed.

19. The different times of fruit dropping were referred to the growth curve of the fruit. By tracing back the dry weights of the sheddings to the dry weight growth curve of the set fruit, the initiation of the sheddings was allocated to definite parts of the first growth curve of the fruit.

20. The leaf and shoot growth recorded from the defruited trees was referred to the growth curve of the fruit. The amount of leaf and shoot growth made seemed to be quantitatively determined by the stage of development reached by the fruit in the first growth curve. Considerable increases in growth were obtained only by removing the fruit in part I of the first growth curve, although the dry matter production of the fruit up to this stage was very small.

21. The alteration of the frequency distributions caused by fruit removal and the seasonal expansion in leaf area of selected spurs was explained by the growth of the fruit in the first growth curve.

22. Fruiting caused clear departures in composition from the defruited trees in moisture, reducing substances, sucrose and starch, nitrogen, potash and phosphorus. Moisture was affected first, nitrogen and the ash elements later and the carbohydrates last. The distinctive carbohydrate metabolism of the fruiting tree and its relation to the earlier changes in nitrogen, phosphorus and potash is discussed.

23. The times of departure in composition are referred to the growth curve of the fruit. It is shown that the earlier stages alone of fruit growth

did not have a permanent effect on composition, although fruit production for 47 days (tree D) showed an effect on composition for a period of 30 to 50 days after fruit removal.

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