

VOL. 5

JANUARY, 1931

NO. 6

# HILGARDIA

*A Journal of Agricultural Science*

PUBLISHED BY THE

*California Agricultural Experiment Station*

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Alternate-Bearing Sugar Prunes Associated with  
Fruit Bud Formation

LUTHER D. DAVIS

UNIVERSITY OF CALIFORNIA PRINTING OFFICE  
BERKELEY, CALIFORNIA



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## SOME CARBOHYDRATE AND NITROGEN CONSTITUENTS OF ALTERNATE-BEARING SUGAR PRUNES ASSOCIATED WITH FRUIT BUD FORMATION<sup>1</sup>

LUTHER D. DAVIS<sup>2</sup>

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### INTRODUCTION

The horticulturist uses the term "alternate-bearing habit" to designate the tendency of certain fruit trees to produce a heavy crop in one year, followed the next year, by a much lighter crop. Although this condition of alternate bearing is perhaps more marked in some varieties of apples than in other fruits, a tendency toward alternate bearing does exist in fruits other than the apple, and the degree of the alternating habit may be determined by the degree to which a given internal condition exists.

Practically all of the investigations concerned with alternate bearing have been made with apple trees. Although a number of conditions have been described to account for this habit in the apple, very little work has been done with other fruits which have a pronounced alternating habit. The Sugar prune, under the conditions existing at Davis, California, is a very pronounced biennial bearer. Yield records and observations at blooming time show that a tree which produces a heavy crop in one year will produce almost no crop the following year—possibly only a dozen or so blossoms. The climatic conditions at Davis are such that they rarely interfere with the normal bearing habit. The Sugar prune (*P. domestica*), under these conditions, would seem to be an especially fit subject for the investigation of any chemical differences which might be associated with the alternate-bearing habit and fruit-bud formation.

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<sup>1</sup> Also presented to the Faculty of the Graduate Council of the University of California in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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## REVIEW OF LITERATURE

Nutritional conditions within the fruit spur have long been considered responsible for the production of flowers or for vegetative growth. Loew,<sup>(28)</sup> publishing in 1905, believed that a certain concentration of sugars became available to the growing point. Fischer<sup>(16)</sup> was the first to advocate the idea of the carbohydrate-nitrogen relationship, which he believed to be the one controlling flower-bud formation. In 1918 Kraus and Kraybill,<sup>(24)</sup> working with the tomato, enlarged upon the two classes of carbohydrate-nitrogen relationships postulated by Fischer. They described the relationships in four classes which they thought were responsible for vegetative growth or for reproduction.

Any conditions which would affect the formation of fruit-buds would necessarily have to exist before the time at which fruit buds can be recognized under the microscope. Although no work has been done on the time of fruit bud differentiation in the Sugar prune, some varieties of plum and of the French prune have been investigated. Goff<sup>(17)</sup> found the first evidence of differentiation in the Rollingsstone plum (*P. americana*) in Wisconsin to be on July 8. Drinkard,<sup>(14)</sup> working in Virginia, found differentiation in the Whitaker plum (*P. munsoniana*), the first week in September. Japanese plum fruit buds were differentiated much earlier, about the second week in July. This investigator found slight development going on throughout the winter following. Tufts and Morrow<sup>(48)</sup> found that at Davis, California, the French prune (*P. domestica*) showed differentiation in late July or early August. Ball,<sup>(4)</sup> working with three varieties, Victoria, Monarch, and Pond's Seedling (all *P. domestica*), under the conditions existing in England, in the two seasons 1924 and 1925, found the earliest signs of differentiation in the period mid-July to early August. The last-named investigator found all three varieties to have reached the same stage by November 1. The ovules and pollen grains were not usually formed until January or February.

The literature dealing with the factors affecting the formation of fruit buds is extensive. Wiggans<sup>(49)</sup> has prepared an extensive bibliography dealing with the factors favoring or opposing fruit bud formation. Summers<sup>(42)</sup> more recently has reviewed the factors in bud formation. The review of literature in this paper will be confined to studies indicating the time at which the factors may be operating and to the literature dealing with the chemical composition of bearing and non-bearing plants.



The methods employed in an effort to cause fruit bud formation have been largely of an external nature. Among them are pruning, soil management, disbudding, deflorating, and thinning. Crow and Eidt<sup>(11)</sup> found that disbudding as early as possible before full bloom was most effective in causing annual bearing in apples. Thinning experiments on apples by Beach<sup>(5)</sup> in New York and by Auchter<sup>(3)</sup> in West Virginia seemed to cause no increase in fruit bud formation. At the New Hampshire station<sup>(25)</sup> when half the flowers were removed at blooming time an appreciable increase in fruit bud formation was found.

Drinkard,<sup>(13)</sup> working in Virginia with dwarf apple trees, found that summer pruning of the branches in the latter part of June greatly stimulated fruit bud formation. Fall pruning did not materially influence the crop of fruit buds. Ringing at the time the foliage was fully developed gave better results than earlier ringing. Root pruning at the time the foliage was fully developed produced a marked stimulation in fruit bud formation, but root pruning on April 23 gave a much smaller increase. Shaw<sup>(41)</sup> found that whereas ringing apple trees on May 1 or June 15 increased fruit bud formation, ringing on July 15 or August 1 had no effect. The above data tend to show that any operation which would cause fruit bud formation must take place reasonably early in the season.

Magness<sup>(29)</sup> found that the removal of the subtending leaves from a spur bud generally prevented its becoming a fruit bud even though leaves were left on adjacent spurs. Harvey and Murneek<sup>(20)</sup> found that the defoliation of apple spurs in Oregon on June 15 greatly reduced the number of fruit buds formed. Roberts,<sup>(38)</sup> working with plum seedlings, found that the removal of a leaf inhibited the formation of a fruit bud at that node and decreased the amount of adjacent storage tissue. Removing alternate leaves slightly reduced the formation of fruit buds at undefoliated nodes.

The work on defoliation indicates that the formation of fruit buds is dependent upon the carbohydrates elaborated by the subtending leaves or upon a rather localized condition created by them. The carbohydrate supply does not, however, seem to be the only factor. Remy<sup>(39)</sup> found that in the leaves of pears and apples a nitrogen content of 1.25 per cent dry weight was necessary if fruit bud formation was to take place. Aldermann,<sup>(1)</sup> in West Virginia, found the percentage of fruit buds formed very much increased in peach trees that had been fertilized with nitrogen. Drinkard<sup>(15)</sup> found that a very low soil moisture greatly reduced fruit bud formation in dwarf apple trees.

Roberts<sup>(37)</sup> considers that a proper balance between carbohydrates and nitrogen must be attained before fruit bud formation can occur. He believes that the conditions which cause an excessive formation of fruit buds in any one year are largely responsible for alternate bearing. Swarbrick,<sup>(43)</sup> from the results of an analysis of length growth and the formation of fruit buds in apples at Long Ashton, England, showed a positive correlation between the time when the length growth ceased, and the number of fruit buds formed. The trees on rootstocks which were noted for their precocity of fruit bud formation were those that ceased growth early. He believes that early cessation of growth permits the accumulation of a higher concentration of carbohydrates, which is favorable to fruit bud formation. He suggests that the deposition of easily detectable reserve materials and the formation of fruit buds are complementary, and that the relation of soluble carbohydrates to nitrogen is a deciding factor.

Hooker and Bradford,<sup>(22)</sup> in a study of the localization of the factors determining fruit bud formation, found that conditions back of the spur might be decisive in their performance. They found that the starch in the region back of the spurs of bearing and non-bearing apple trees varied in the same direction as the starch of the spurs. They suggested that the fruit might utilize the carbohydrates as rapidly as manufactured and that when the crop is sufficiently heavy the whole tree may behave as a unit. They suggested that the inverse correlation between a high starch and a low nitrogen content accompanying fruit bud formation in the apple were not of fundamental importance but were more or less accidental. This opinion agrees very well with the findings of Hartig<sup>(19)</sup> that the seed year in the beech is accompanied by eight or nine years' starch accumulation. During the seed year the starch accumulation is swept out. Murneek<sup>(31, 32, 33, 34)</sup> has shown that flowering and fruiting exert a dominating effect on the metabolic activities of the plant and that the flowers, fruit, and leaves draw especially heavily on the carbohydrate and nitrogen supply.

Butler, Smith, and Curry,<sup>(7)</sup> analyzing different parts of two apple trees, found that the reserve foods were stored chiefly as starch and sucrose. The roots and branches contained relatively more starch than the trunk.

Mitra<sup>(30)</sup> analyzed apple spurs at frequent intervals throughout the year. A marked increase in total carbohydrates and starch occurred during August and September. The starch and sugars disappeared rapidly in the spring at the time new growth was taking place. Kray-

bill, Potter *et al.*<sup>(25)</sup><sup>3</sup> analyzed bearing and non-bearing apple spurs from trees growing in a sod plot receiving no fertilizer and from a cultivated plot receiving a complete fertilizer which was relatively high in nitrogen. They checked their judgment of bearing and non-bearing spurs by a record of the performance of tagged spurs the following season. They observed a wide variation in the performance of individual trees, so that the spurs were well removed from ideal conditions for bearing and non-bearing spurs. They suggested that the data should be considered from the viewpoint of conditions favorable or unfavorable to fruit bud formation. These investigators failed to find the conditions of starch storage which were considered by Hooker<sup>(21)</sup> as being indicative of conditions favorable to fruit bud formation. They suggested that a localization of conditions leading to a condition of dominance may have masked the results of the gross analysis. They did find agreement with the carbohydrate-nitrogen relationships postulated by Kraus and Kraybill.

☞ Harvey and Murneek,<sup>(20)</sup> in an analysis of defoliated apple spurs in which the fruit bud formation was greatly reduced, say: "The defoliated spurs are shown to contain more water, reducing sugars, total sugars, nitrate nitrogen, soluble nitrogen, and total nitrogen, but less soluble solids, insoluble solids, total solids and hydrolyzable polysaccharides, than spurs supplied with their own leaves."

Kraybill<sup>(26)</sup> studied the effects of shading and ringing upon fruit bud formation and upon the chemical composition of the apple and peach. Shading trees for two seasons reduced fruit bud formation to nearly zero, whereas the unshaded trees formed 65 per cent fruit buds. The starch content of unshaded trees was higher and the nitrogen content lower than that of shaded trees. Gourley,<sup>(18)</sup> working in New Hampshire, found that the spurs which were forming fruit buds were larger and had much more starch packed in the cells than did those not forming fruit buds. He found the same conditions in two years, 1913 and 1914; the trees, however, alternated.

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<sup>3</sup> Since the preparation of this manuscript the following publications have appeared:

Potter, G. F., H. R. Kraybill, *et al.*

1930. Some effects of defoliation on fruit spur composition and fruit bud formation in the Oldenburg apple. New Hampshire Agr. Exp. Sta. Tech. Bul. 41:1-26

Potter, G. F., and T. G. Phillips.

1930. Composition and fruit bud formation in non-bearing spurs of the Baldwin apple. New Hampshire Agr. Exp. Sta. Tech. Bul. 42:1-41.



## MATERIALS AND METHODS

The Sugar prune was produced by Burbank. One of its parents seems to be the French prune; the other is unknown. The trees furnishing the material for this study are from a block growing in the University orchard. They are about nine years old and have already attained a decided alternating habit. There are forty trees in the block, nearly equally divided between bearing and non-bearing.

The fruit of the Sugar prune is borne very largely on spurs two years old or older. For the analytical materials, branches were selected that had approximately twenty-five spurs a piece (fig. 1). A branch of this kind would be about two and one-half feet long and half an inch in diameter at the base.

Disbudding previous to blooming has been found to cause apple spurs to set fruit buds for the following year.<sup>(11)</sup> In the latter part of February, 1927, the fruit buds were removed from a large number of branches of the kind described in the previous paragraph. These branches were on trees that seemed to have a heavy crop of fruit buds. Observations at blooming time established the fact that the trees did have a heavy crop of blossoms. It was hoped that these branches would form fruit buds again and that some of the changes could be followed by chemical analyses. Disbudding was not done in the winter of 1928.

In 1927, three types of material were taken for analyses: "bearing," "non-bearing," and "disbudded." In 1928, instead of the sample from disbudded branches, an additional type of sample was taken. Bearing and non-bearing spurs were selected from the main scaffold limbs. These, although larger than the spurs from the regular sampling limbs, were of a spur nature and were expected to reflect some of the conditions farther back in the tree.

During the summer of 1928, it seemed advisable to take samples still farther removed from the bearing areas. Samples of roots and borings from the trunk were taken. The root samples were dug at a depth of about two feet and at a distance of about three feet from the tree. Roots about one-half inch in diameter were used. Holes one inch deep were bored into the tree trunk about six inches above the ground level, and the borings were made into a composite sample.

*Sampling.*—Six to eight branches of the kind described above were used for each sample. Only one branch was chosen from a tree. Samples were taken each time before 8:30 A.M. and brought into the laboratory, where the buds, flowers or fruit, and leaves, as the case

might be, were immediately removed. The spurs were broken off at their base; then the bark and wood of the branches were separated and analyzed separately. The separated and unseparated portions of the bark and wood were kept under moist toweling except at the time



Fig. 1. Terminal portion of branch of Sugar prune showing fruit buds and distribution of spurs along the branch.

the separation was being made. The wood fraction was cut into small pieces as soon as the separation was completed. The buds, spurs, flowers or fruit, and leaves were counted at each sampling. Each sample, as soon as completed, was weighed and placed in a ventilated oven kept at

70° C. At the end of forty-eight hours it was weighed again. The fruit buds and flowers were treated in a similar manner up to petal fall. After petal fall the fruit was divided into two lots. One lot, having been dried as above, was used for the determination of total nitrogen. The second lot was dropped into boiling 95 per cent alcohol to which a little calcium carbonate had been added, and was then used for the carbohydrate determinations. The lot that was dried for the total nitrogen determinations included the flesh and pit. The lot preserved in alcohol included both flesh and pit until the time when the pit hardened, that is, by May 28; after that date the samples put up in alcohol include only the flesh. In the later samples the fruits were too large for more than fifteen of them to be put in a sample. In these cases samples were put up in triplicate, and the average carbohydrate content of the three was found. The dried material was ground to pass through a 40 to 50-mesh screen.

*Moisture Determinations.*—At the end of forty-eight hours the dried material was removed from the oven and weighed. The loss of moisture was calculated as per cent moisture on a fresh weight basis.

*Reducing Substances.*—One to four grams of dried material, except in the case of the fruit preserved in alcohol, was weighed into alundum thimbles and extracted in a Soxhlet extraction apparatus for five hours with 95 per cent alcohol. The alcohol was removed from this extract under reduced pressure at 60° to 65° C. The dry residue was taken up in water. The water solution was cleared with neutral lead acetate (specific gravity 1.24), the precipitate centrifuged off, and the excess lead removed from the supernatant liquid with potassium oxalate. The lead oxalate was filtered off and the filtrate made up to volume.

Since a large number of determinations were involved in this investigation, as short a method as possible for determining the reducing power seemed desirable. The picric acid method of Willaman and Davison<sup>(50)</sup> was used. Thomas and Dutcher<sup>(47)</sup> found that a determination of the reducing substances on a lead acetate cleared sample gave too high results by the picric acid method when compared to a copper method. In an investigation of this nature the direction of the curves representing bearing and non-bearing trees would seem to be just as important as agreement with a value such as a copper method might give on isolated samples.

At least two distinct fractions in the cleared extract produce color with picric acid. One fraction produces color at room temperature; the other upon heating. The reaction at room temperature reaches a very definite end point by the end of two hours and remains stable for



at least five hours. Table 1 shows the time in which this color reaches a maximum. To prevent variations in room temperature the color was produced in a water bath kept at 18° to 20° C.

TABLE 1  
TIME IN WHICH THE MAXIMUM COLOR IS PRODUCED BY ALKALINE PICRIC ACID AT  
18° TO 20° C

Time in hours.....	1	2	3	4	5
Colorimeter reading.....	15.0	13.9	14.0	13.7	14.0

The term "color produced by heat" has been taken to be the value found when the color value obtained at room temperature is subtracted from the color value after the heating period. All color values were compared with the color produced by a standard solution of pure glucose. The color produced by heat is the one compared with the values obtained by the copper method. In the copper method the cuprous oxide was filtered off and then determined volumetrically. Figure 2 shows the relationship between the two values. These curves are representative of those for other fractions. Table 2 shows these data for bearing and non-bearing bark for 1928, which is typical of the other fractions. The nature and significance of this fraction which produces color at room temperature are not known.

*Sucrose*.—Sucrose was hydrolyzed with invertase.

TABLE 2  
PERCENTAGE OF REDUCING SUBSTANCES OBTAINED BY THE PICRIC ACID METHOD FOR  
BEARING AND NON-BEARING BARK ON A DRY-WEIGHT BASIS, 1928

Date of sampling	Bearing bark			Non-bearing bark		
	Total	18°-20° C	By heat	Total	18°-20° C	By heat
Jan. 5.....	7.3	3.3	4.0	8.1	3.8	4.3
28.....	7.3	3.5	3.8	8.6	4.0	4.6
Feb. 19.....	6.9	3.7	3.2	7.2	3.2	4.0
March 4.....	6.7	3.2	3.5	6.7	2.6	4.1
17.....	7.2	3.5	3.7	6.3	3.2	3.1
31.....	7.5	4.0	3.5	6.6	3.6	3.0
April 14.....	7.6	4.1	3.5	8.6	3.9	4.7
30.....	7.2	4.1	3.1	7.8	4.2	3.6
May 5.....	7.4	4.2	3.2	7.8	4.3	3.5
12.....	7.6	4.5	3.1	7.5	4.3	3.2
19.....	7.5	4.7	2.8	6.9	4.3	2.6
28.....	7.7	5.0	2.7	6.6	4.6	2.0
June 15.....	7.8	4.7	3.1	6.9	4.1	2.8
July 4.....	7.0	4.2	2.8	6.1	3.4	2.7
31.....	6.7	2.6	4.1	5.2	2.0	3.2

*Starch*.—Starch was determined on the residue after the alcoholic extraction. As a combination of the methods of Cameron<sup>(8)</sup> and of Collins<sup>(10)</sup> was used, the method will be described in detail. The material was ground sufficiently fine for the easy removal of all the soluble sugars, but not fine enough for starch digestion. After extraction and drying the residue was transferred to a ball mill and ground for 4 to 12 hours. Bark and spurs were ground for 4 hours, but it was necessary to grind the wood samples for 12 hours. At the end of the grinding period the jars were removed from the mill and about 40 cc of water were added to each one. Next, all were placed in a closed steam bath, heated for half an hour at 100° C, and then removed and cooled to about 35° C. Ten cc of a 2.0 per cent taka-diastrase solution, 10 cc of an acetate buffer, pH 5.0 and 1 cc. of toluene were added.

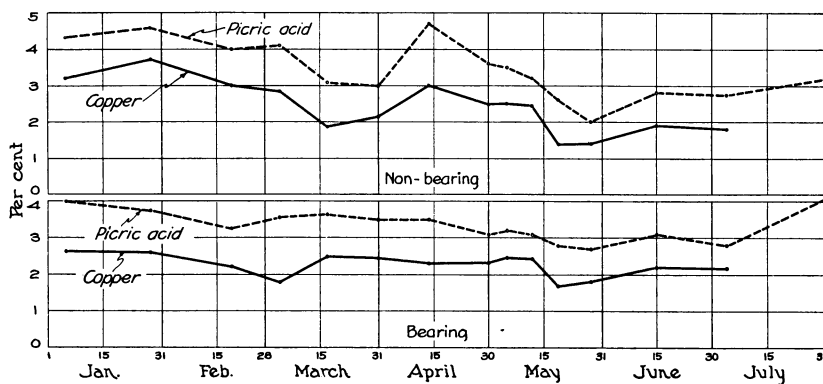


Fig. 2. Comparison of the values for reducing substances in bearing and non-bearing bark obtained by the picric acid and copper reduction methods.

The jars were then stoppered and put back on the mill, which was mounted in an incubator kept at 38° C. The mill was run for a short time at intervals to keep the digestion mixture well mixed. The digestion was allowed to continue for 36 hours. At the end of this time the material was washed into centrifuge bottles, 3 cc of neutral lead acetate (sp. gr. 1.24) was added to cause flocculation, and the whole mass was centrifuged. After the supernatant liquid was poured off, the excess lead was removed by potassium oxalate, filtered, and made up to volume. The reducing power of the filtrate was determined by the picric acid method. A taka-diastrase blank was carried along with each set of determinations.

Acid hydrolyses on the filtrate of starch digestions are objectionable in plant materials because of the danger of releasing reducing sub-

stances other than the products of the starch hydrolysis. To see whether the taka-diastase hydrolysis had reached an end point in the plant material as it had in the pure starch, a 50 cc. aliquot of the filtrate from the starch digestion was hydrolyzed with 5 cc of HCl (sp. gr. 1.125) on a steam bath for  $2\frac{1}{2}$  hours. At the end of this time the solution was cooled, neutralized, and made up to volume in the usual manner. Table 3 gives the results obtained.

TABLE 3  
PERCENTAGES OF REDUCING SUBSTANCES BEFORE AND AFTER ACID HYDROLYSIS OF  
FILTRATES FROM STARCH DIGESTION OF WOOD, BARK, AND  
SPURS ON A DRY-WEIGHT BASIS

Wood		Bark		Spurs	
Before acid hydrolysis	After acid hydrolysis	Before acid hydrolysis	After acid hydrolysis	Before acid hydrolysis	After acid hydrolysis
7.8	8.1	4.4	4.3	6.0	6.2
6.6	6.8	1.3	1.6	6.7	7.1
3.2	3.2	4.1	4.5	2.3	3.0
4.6	4.8	2.5	2.8	5.0	5.7
11.0	10.5	.8	1.2	6.1	6.4
9.9	10.1	2.2	2.7	1.8	2.4
2.9	3.3	11.2	12.0		

Table 3 shows that there is only a small increase of reducing substances after acid hydrolysis. The difference between the value before and after acid hydrolysis has much the same absolute value, but has a varying relative value as the amounts of starch change.

Perhaps the plant material contains sufficient buffering material to make the addition of more buffer unnecessary. This point, however, has not been determined for this material.

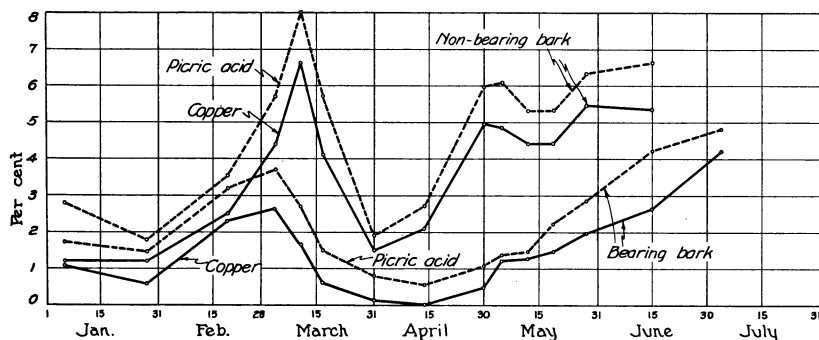


Fig. 3. Comparison of the values obtained by the picric acid and copper reduction methods for starch in bark.



The validity of the picric acid method as compared with the copper reduction method was tested in the same manner as for the alcohol-soluble reducing materials. There is no reduction of the picric acid at room temperature in the starch determination. The results of the comparison are given in figure 3. Figure 3 shows the comparison for bearing and non-bearing bark, but the other fractions show the same striking parallelism between the two methods.

*Nitrogen.*—Total nitrogen was determined on two or three grams of the ground material. The Kjeldahl-Gunning method, modified to include nitrate nitrogen, was used.

## PRESENTATION OF RESULTS

In any consideration of the results of the analyses of bearing and non-bearing trees, it is well to verify the performance of the material selected. For this purpose, a number of branches of the kind selected for analyses were tagged in the winter of 1927. At the time of full bloom in the spring of 1927, the following results were obtained:

(a) Branches selected as being in the non-bearing condition had an average of 0.1 flowers per spur.

(b) Branches selected as being in the bearing condition had an average of 5.4 flowers per spur.

The tags were left on the branches, and the same observations were made at blossom time in 1928. The following results were obtained:

(a) Branches selected as being in the non-bearing condition in 1927 had an average of 6.6 flowers per spur in 1928.

(b) Branches selected as being in the bearing condition in 1927 had an average of 0.3 flowers per spur in 1928.

The above data were obtained from about 2000 spurs of each kind. At the same time in the spring of 1928 counts were made on limbs that had been disbudded in 1927. The following results were obtained:

(a) Of the spurs that were disbudded in 1927, 58.0 per cent had formed fruit buds.

(b) Of the spurs that bore in 1927, 9.5 per cent had formed fruit buds again.

About 600 disbudded spurs were used to secure the data given above.

The problem of selecting the branches for verification of the performance was made easier because the trees were nearly all behaving as units. That is, they would be either in a very decidedly 'off' or 'on' year. This behavior was reflected in that of some of the disbudded branches. On some trees that were bearing very heavily in 1927, no fruit buds were formed; disbudding had no effect at all. On trees that could be considered as having a large but not extremely heavy crop, disbudding had some effect. However, the data presented above for disbudding are for trees of both classes and are taken only from trees that had both bearing and disbudded branches on them.

As a further check on the bearing of the trees, yield records were taken at harvest time in 1927 and 1928. These records are presented in table 4.

TABLE 4  
YIELD RECORDS OF SUGAR PRUNE TREES, IN POUNDS OF FRUIT PER TREE

Tree No.	Yields	
	1927	1928
A-2.....	134.0	0.0
A-3.....	137.0	36.0
A-4.....	167.0	65.0
A-5.....	133.0	3.0
A-6.....	24.0	134.0
A-7.....	118.0	16.0
B-1.....	87.0	5.0
B-2.....	174.0	1.0
B-3.....	80.0	24.0
B-5.....	56.0	165.0
B-6.....	30.0	68.0
B-7.....	77.0	2.0
B-8.....	83.0	5.0
C-1.....	52.0	27.0
C-2.....	158.0	25.0
C-3.....	140.0	0.0
C-4.....	2.0	65.0
C-5.....	72.0	0.0
C-6.....	89.0	0.0
C-7.....	6.0	150.0
C-8.....	119.0	12.0
D-3.....	122.0	16.0
D-4.....	103.0	74.0
D-6.....	118.0	42.0
D-7.....	18.0	130.0
E-2.....	148.0	39.0
E-4.....	67.0	141.0
E-5.....	84.0	158.0
E-6.....	48.0	137.0
E-7.....	55.0	130.0

Throughout the following tables and graphs certain designations are used. "Bearing" and "non-bearing" indicate the condition of the trees at the time the sample was taken. Thus, trees which had a crop in 1927 are designated as "bearing" in 1927, but in 1928 they furnish "non-bearing" branches. Likewise trees which had no crop in 1927 are classed as "bearing" during the whole of the 1928 season because they formed fruit buds during the summer of 1927 and were therefore in the "bearing" condition at the first sampling on January 5, 1928. It should be remembered that the designation indicates the condition of the tree for the season in which the sample was taken. "Disbudded" refers to those branches from which the fruit buds were removed in the winter of 1927. This type of material occurs only in the 1927 samples. "Spurs" refers in all cases to those spurs taken from the branches used for the wood and bark samples. "Spurs from main branches" refers to spurs taken from scaffold branches in the main body of the trees. This sample occurs only in 1928. Such terms as "bearing bark," "non-bearing wood" refer to bark or wood from bearing or non-bearing trees.

Condition of trees on sampling dates, sampling of March 2, 1927: the fruit buds were swollen, many of them showing white through the scales. March 25: the trees were in full bloom. April 6: petals were ready to fall. April 29: this was just at the beginning of the June drop. June 23: the yellow undercolor was just beginning to show; the pits had already hardened. July 29: this date is about a month before harvest, which took place the last of August.

Sampling of February 19, 1928: the fruit buds were swollen slightly. March 4: the flowers were pushing out of the bud scales almost far enough to enable one to tell how many flowers there were per bud. March 11: the flowers were about half out. March 17: the trees were nearly in full bloom. March 31: the petals had fallen. April 14: prunes that would fall in the June drop could be identified at this time. April 30: buds appeared to be formed in the axils of the leaves on the spurs. May 5: at this time the June drop was occurring and the pits were showing some signs of hardening. May 19: the pits were nearly hard on this date but could still be cut with hand shears. May 28: the pits were definitely hardened and the buds had developed brown bud scales by this time. June 15: the yellow undercolor was beginning to show on the fruit and the cotyledons had definitely developed in the seed. July 31: the fruit was harvested about ten days after this date. The period from about May 12 to May 28 is the time when there was very little increase in fresh weight or volume of the



fruit. This likewise corresponds to the period when the pits were hardening.

*Calculation of Results.*—The results for the carbohydrate fractions were obtained in all cases by the picric acid method. All color values were compared to a pure glucose standard. A curve prepared from pure glucose solution, after Willaman and Davison,<sup>(50)</sup> was used for the calculations.

No entirely satisfactory method of calculating and expressing results has been devised when only a portion of a plant has been taken, as was the case in this investigation. The carbohydrate and nitrogen fractions occurring in the spurs, wood, and bark, have been calculated as per cent dry weight, as per cent fresh weight and as the amount in the branch immediately behind the spur, assuming that these materials were equally available to each spur. In the Sugar prune the spurs are very evenly spaced along the branch (fig. 1). The carbohydrates and nitrogen in the flowers or fruit have been calculated as milligrams per flower or fruit and as milligrams withdrawn per spur. The nitrogen of the leaves has been calculated as milligrams of nitrogen per leaf and as milligrams of nitrogen withdrawn per spur.

*Moisture.*—The moisture changes have the same general seasonal trend in both years. They are shown in tables 5 and 6. The moisture increases up to the last of April or the first of May in all fractions of both bearing and non-bearing trees. In the fractions from the bearing trees the amounts remain reasonably constant for the remainder of the season. In the fractions from the non-bearing trees the moisture content begins to drop about May 1.

TABLE 5

MOISTURE CONTENT OF SAMPLES TAKEN IN 1927; PER CENT FRESH WEIGHT

Date of sampling	Bark			Wood			Spurs		
	Bearing	Non- bearing	Dis- budded	Bearing	Non- bearing	Dis- budded	Bearing	Non- bearing	Dis- budded
March 2.....	54.3	54.5	.....	41.0	42.4	.....	50.9	49.8	.....
17.....	57.8	.....	.....	42.2	.....	.....	55.6	.....	.....
25.....	59.7	57.0	57.9	43.6	41.5	42.9	60.9	59.8	62.1
April 6.....	60.4	61.6	60.3	44.9	44.6	44.8	57.8	49.6	58.2
29.....	61.7	61.9	61.2	45.3	.....	45.9	59.9	61.2	62.9
May 27.....	62.6	58.6	62.2	47.4	44.9	46.7	60.6	57.0	59.8
June 23.....	60.9	55.0	57.2	46.2	43.1	44.3	56.6	52.7	53.7
July 29.....	.....	.....	.....	.....	42.2	43.4	54.9	47.8	49.7

TABLE 6  
MOISTURE CONTENT OF SAMPLES TAKEN IN 1928; PER CENT FRESH WEIGHT

Date of sampling	Bark		Wood		Spurs		Leaves		Fruit
	Bearing	Non-bearing	Bearing	Non-bearing	Bearing	Non-bearing	Bearing	Non-bearing	
Jan. 5.....	55.1	48.1	42.9	43.2	51.3	58.0	.....	.....	48.0
28.....	54.4	55.6	41.1	41.6	50.3	50.4	.....	.....	46.1
Feb. 19.....	56.8	56.5	42.0	42.8	51.6	51.3	.....	.....	60.1
March 4.....	58.3	57.4	43.2	43.8	52.9	51.3	.....	.....	72.8
11.....	58.7	56.6	44.3	43.2	54.3	52.1	55.6	61.2	77.2
17.....	58.5	57.4	43.2	43.5	54.0	53.7	65.0	69.9	79.9
31.....	60.4	60.8	45.0	44.2	55.7	56.0	72.8	70.4	74.6
April 14.....	61.0	59.4	45.1	44.6	58.4	54.1	71.4	64.5	85.5
30.....	62.8	60.6	47.1	43.7	61.1	57.6	70.3	66.7	89.3
May 5.....	62.3	60.8	46.6	44.1	60.4	56.1	69.3	66.4	88.1
12.....	61.6	62.3	46.4	44.5	60.0	58.9	67.1	67.1	85.7
19.....	63.3	63.3	46.9	45.2	61.5	58.2	68.3	64.6	83.0
28.....	62.5	61.4	46.8	46.0	59.7	57.5	66.4	63.3	81.1
June 15.....	61.8	62.1	46.8	47.2	55.8	55.4	60.3	60.5	79.2
July 4.....	62.8	59.0	46.9	44.2	55.0	49.9	59.7	56.9	81.6
31.....	60.6	53.7	48.2	43.6	53.3	48.0	56.2	54.9	73.7

Date of sampling	Spurs from main limbs			Date of sampling	Borings		Date of sampling	Roots	
	Bearing spurs	Non-bearing spurs	Fruit		Bearing	Non-bearing		Bearing	Non-bearing
March 10.....	51.8	51.1	75.2	.....	.....	.....	.....	.....	.....
17.....	53.7	51.6	80.2	.....	.....	.....	.....	.....	.....
31.....	56.3	53.7	78.6	.....	.....	.....	.....	.....	.....
April 14.....	56.2	55.2	.....	.....	.....	.....	.....	.....	.....
30.....	58.9	54.7	89.6	.....	.....	.....	.....	.....	.....
May 5.....	58.1	54.3	88.8	May 7	42.3	41.2	May 7	63.1	60.8
12.....	58.4	55.3	87.1	June 9	39.9	40.3	June 9	59.8	55.9
19.....	59.8	55.8	84.5	.....	.....	.....	July 2	59.9	56.9
28.....	58.2	55.3	81.5	.....	.....	.....	.....	.....	.....
June 15.....	56.0	54.6	80.5	.....	.....	.....	.....	.....	.....
July 4.....	56.2	48.9	82.3	.....	.....	.....	.....	.....	.....
31.....	52.1	48.1	75.2	.....	.....	.....	.....	.....	.....

*Reducing Substances.*—The data presented in figures 4, 5, and 6 show some very interesting and consistent relationships. The curves for the different fractions of the bearing or non-bearing trees behave very much alike. Thus wood, bark, and spurs have much the same trend throughout the year. The most interesting relationship is shown when the curves for the two years are considered. It must be remembered that the trees experienced a complete alternation, so that the trees furnishing the bearing material in 1927 furnished non-bearing samples in 1928. In both 1927 and 1928 the values for the bearing trees lie below those of the non-bearing until a little after May 1, when the values for the non-bearing trees fall below those of the

bearing and remain there for the remainder of the season. This relationship holds for all fractions, wood, bark, spurs, and spurs from main limbs. The values for the disbudded material lie between the bearing and the non-bearing, especially toward the end of the season.

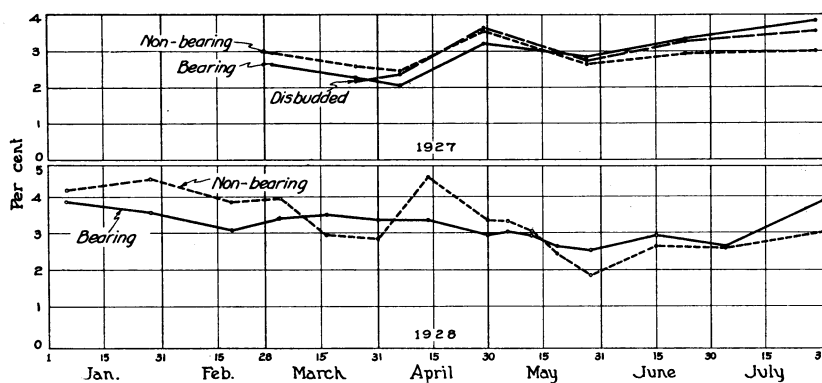


Fig. 4. Percentages of substances in bark which reduce picric acid on heating, dry-weight basis.

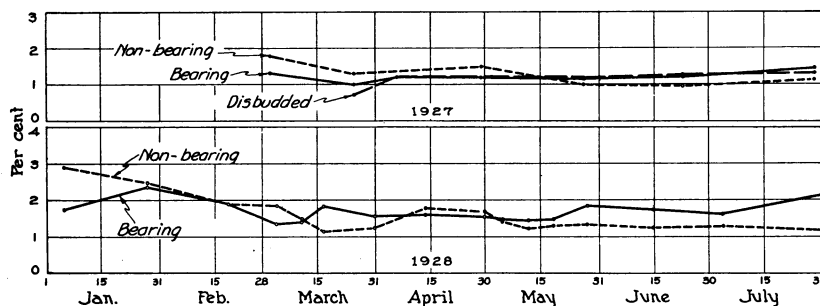


Fig. 5. Percentages of substances in wood which reduce picric acid on heating, dry-weight basis.

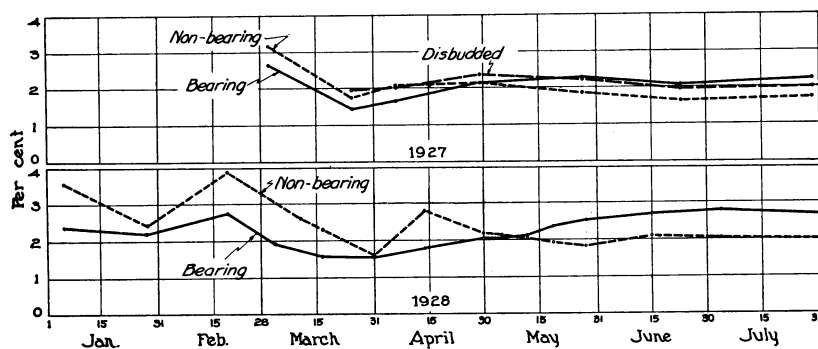


Fig. 6. Percentages of substances in spurs which reduce picric acid on heating, dry-weight basis.

*Sucrose*.—The data for sucrose are given in tables 7 and 8. Sucrose is relatively high early in the season but soon drops to a low value and remains low throughout the remainder of the period. The sucrose values are not shown by graphs.

*Starch*.—The data for starch are presented in figures 7, 8, and 9. They are of considerable interest because of the difference which occurs

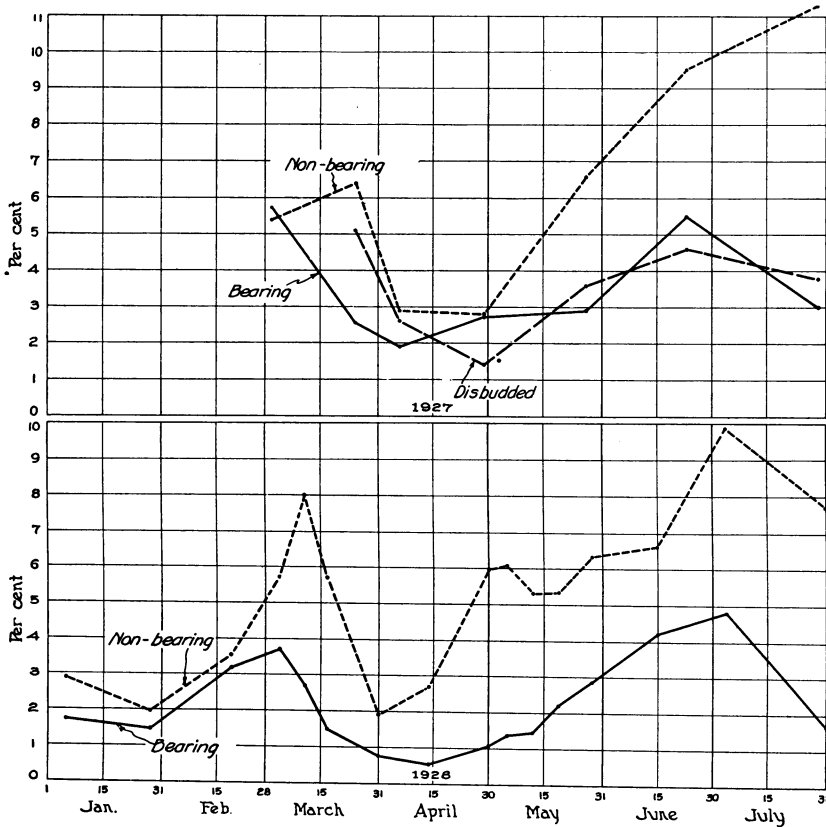


Fig. 7. Percentages of starch found in bark on a dry-weight basis.  
Starch expressed as glucose.

between the bearing and non-bearing trees, because of the distinct seasonal trend which it shows, and also because of the lack of agreement with regard to the part played by starch in fruit bud formation.

The bearing and non-bearing trees differ from each other considerably in every type of material except at the time of the first flush of growth. At least two maxima and two minima are shown. If an

accumulation of starch occurred later in the fall a third maximum and minimum in the bearing trees would appear. A third maximum and minimum have been reported by Anderson and Hooker<sup>(2)</sup> for sour cherries. The samples for 1928 were taken early enough to catch the spring maximum. The non-bearing material reaches a maximum about ten days later than does the bearing. In fact, the bearing bark and

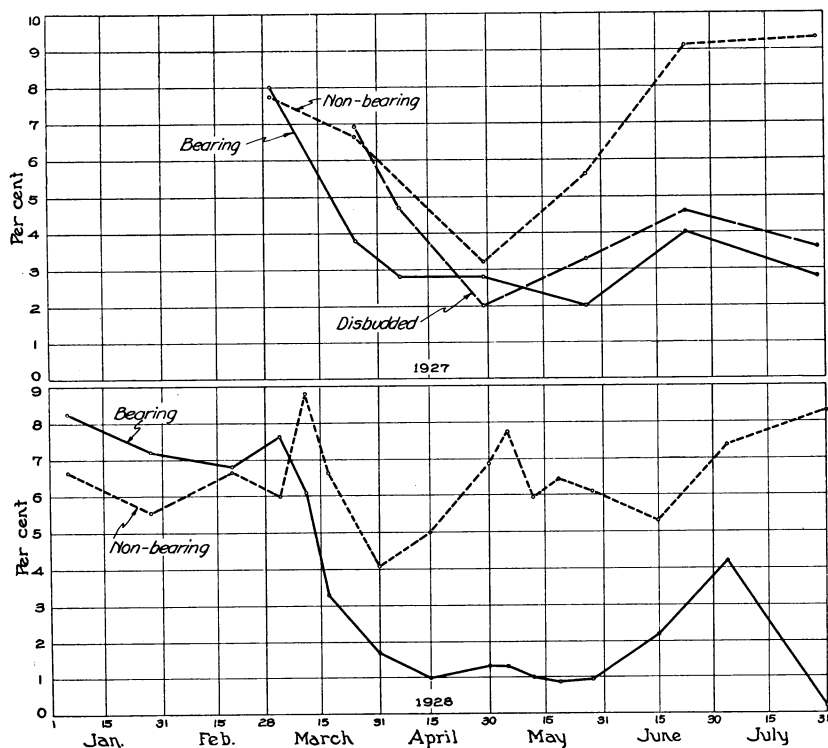


Fig. 8. Percentages of starch found in wood on a dry-weight basis. Starch expressed as glucose.

spurs do not reach a very decided maximum in the late winter before they go into the spring minimum. On the other hand, the bark and spurs of the non-bearing trees reach a very decided maximum in the late winter and then go into a spring minimum. After reaching the minimum at blossoming time, the starch in the bark, wood, and spurs of the bearing trees remains in a relative minimum until about June 1; then it rises until about July 4, when it drops rapidly to nearly zero. It was from this latter period until the last sample was taken that the fruit was ripening most rapidly and, as will be shown in a later table,

was undergoing an enormous increase in sugar content. In 1928, the fruit was harvested on August 5, just six days after the last sampling date.

The starch content of the roots and the trunk is shown in table 9. An especially great difference exists between the bearing and the non-bearing roots.

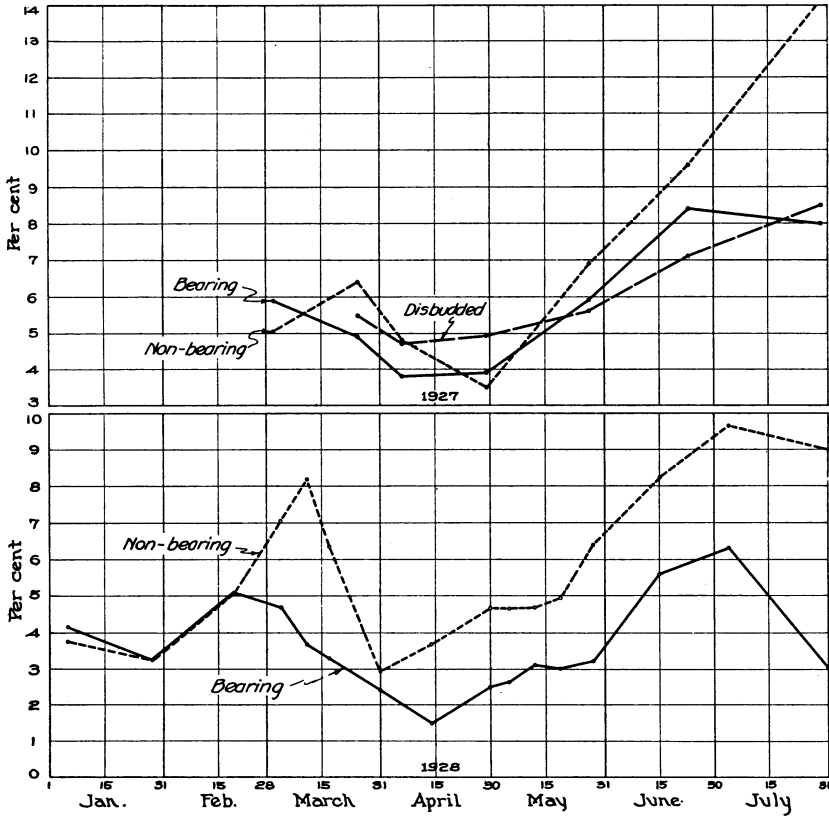


Fig. 9. Percentages of starch found in spurs on a dry-weight basis. Starch expressed as glucose.

Starch and moisture show an inverse relation throughout both 1927 and 1928. This is in agreement with the findings of a number of other investigators—Hooker,<sup>(21)</sup> Kraybill,<sup>(26)</sup> Cameron.<sup>(8)</sup>

The starch content of the disbudded branches is but little different from that of the bearing. This might be expected if heavily loaded trees would behave as a unit. The disbudded branches were taken from the same trees as the samples of the bearing material.

TABLE 7

PERCENTAGES OF SUCROSE IN BARK, WOOD AND SPURS ON A DRY-WEIGHT BASIS, 1927

Date of sampling	Bark			Wood			Spurs		
	Bearing	Non-bearing	Dis-budded	Bearing	Non-bearing	Dis-budded	Bearing	Non-bearing	Dis-budded
March 2.....	3.4	3.1			1.8		1.1	1.2	
25.....	1.2	2.87	1.9	.96	1.0	.55	2.46	3.4	.5
April 6.....	2.1	.65	1.66	.88		.32	1.3	.6	1.05
29.....	1.1	1.1	1.0	.44	.9	.52	.3	1.0	.2
May 27.....	1.2	1.86	.15	.55	.82	.4	1.04	1.2	.86
June 23.....	1.46	1.2	.9	.2	.28	.12	.8	.91	.3
July 29.....	1.0	.8	.6	.48			.74	1.2	.46

TABLE 8

PERCENTAGES OF SUCROSE IN BARK, WOOD, SPURS, AND SPURS OFF MAIN LIMBS ON A DRY-WEIGHT BASIS, 1928

Date of sampling	Bark		Wood		Spurs		Spurs from main limbs	
	Bearing	Non-bearing	Bearing	Non-bearing	Bearing	Non-bearing	Bearing	Non-bearing
Jan. 5.....	3.0	3.7	1.55	1.98	1.4	1.5		
28.....	4.1	3.8	1.7	2.2	3.4	3.9		
Feb. 19.....	3.1	3.9	1.0	2.0	.7	1.4		
March 4.....	1.9	3.0	.46	1.0	.2			
11.....			.58	.55		1.0	.6	.35
17.....	1.7	1.4	.0	.41	.1	.13	.27	.76
31.....	1.7	1.8	.0	.28	.28	.3	.59	.1
April 14.....	1.0	2.0	.1	.31	.2	.14	.69	.48
30.....	.7	1.8	.12	.30	.27	.22	.3	.1
May 5.....	1.2	1.7	.24	.30	.32	.14	.3	.22
12.....	1.2	1.5	.23	.25	.4	.0	.4	.14
19.....	1.3	1.2	.20	.32	.2	.32	.2	.13
28.....	1.3	1.5	.76	.31	.42	.27	.26	.25
June 15.....	1.4	1.4	.31	.33	.76	.14	.47	.32
July 4.....	1.6	1.4	.35	.25	.23	.53	.37	.1
31.....	.8	1.0	.3		.3	.3		

TABLE 9

PERCENTAGES OF STARCH IN ROOTS AND BORINGS FROM THE TRUNK ON A DRY-WEIGHT BASIS, 1928

	Roots		Borings from the trunk	
	Bearing	Non-bearing	Bearing	Non-bearing
May 7.....	4.5	10.6	2.6	2.9
June 9.....	6.5	13.6	1.9	2.5
July 2.....	5.4	16.7		



*Total Nitrogen.*—The data for total nitrogen are presented in figures 10, 11, and 12. The nitrogen data are consistent for the two years in wood, bark, spurs, and spurs from main limbs. In general the nitrogen values of the bearing trees lie above those of the non-

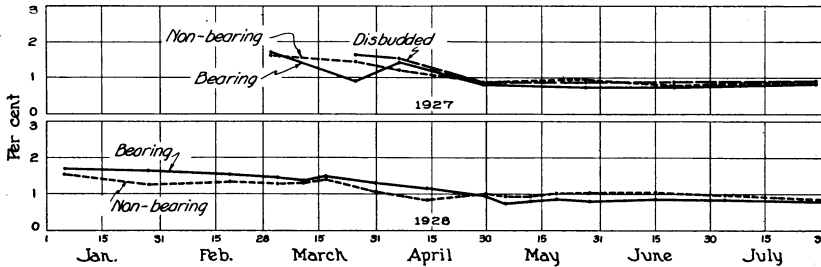


Fig. 10. Percentages of total nitrogen found in bark on a dry-weight basis.

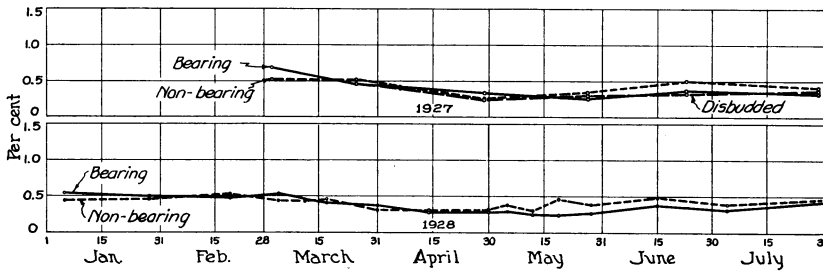


Fig. 11. Percentages of total nitrogen found in wood on a dry-weight basis.

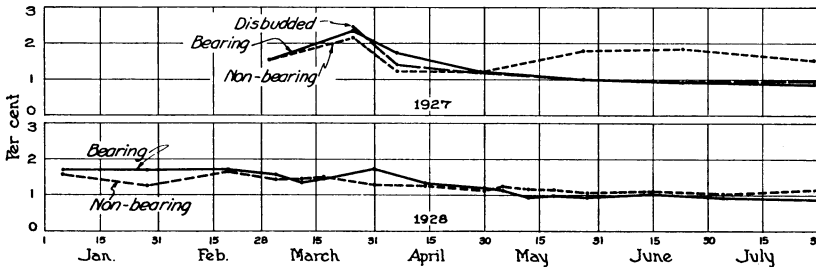


Fig. 12. Percentages of total nitrogen found in spurs on a dry-weight basis.

bearing trees for the first part of the season. Near May 1 in both years, the curves for the bearing and non-bearing trees cross, and for the remainder of the season the non-bearing lie above the bearing. The difference in the spurs for 1927 is much greater than for 1928.

If the preceding data are expressed on a green weight basis the relationships are essentially the same. In the case of total nitrogen and starch the differences are greater than when the results are

expressed on a dry weight basis. The reducing substances are brought closer together when the results are expressed on a fresh weight basis, but the relationships are the same. The results for bark for 1928 calculated on a fresh weight basis are presented in table 10. The results for the other fractions on that basis are not given, but they show the same relations as those for bark.

TABLE 10  
PERCENTAGE OF REDUCING SUBSTANCES, STARCH, AND NITROGEN IN BARK ON A GREEN WEIGHT BASIS, 1928

Date of sampling	Bearing bark			Non-bearing bark		
	Reducing substances	Starch	Nitrogen	Reducing substances	Starch	Nitrogen
Jan. 5.....	1.8	.77	.75	2.2	1.49	.70
28.....	1.7	.67	.75	2.0	.88	.56
Feb. 19.....	1.4	1.38	.66	1.7	1.54	.58
March 4.....	1.5	1.54	.62	1.75	2.43	.55
11.....		1.11	.56		3.47	.57
17.....	1.5	.62	.62	1.32	2.43	.62
31.....	1.4	.30	.52	1.17	.74	.43
April 14.....	1.3	.21	.44	1.91	1.1	.35
30.....	1.2	.39	.35	1.42	2.34	.39
May 5.....	1.2	.51	.28	1.37	2.37	.38
12.....	1.2	.56	.31	1.2	2.00	.35
19.....	1.0	.80	.32	.95	1.95	.37
28.....	1.0	1.07	.30	.77	2.43	.40
June 15.....	1.2	1.6	.34	1.06	2.50	.39
July 4.....	1.0	1.78	.32	1.12	4.06	.41
31.....	1.6	.67	.31	1.48	3.56	.41

The amounts of reducing substances, starch, and total nitrogen, in milligrams, in the bark available to each spur for 1928 are shown in table 11. The data for starch and total nitrogen show the same relationships as when expressed on either a fresh or dry weight basis.

The relationships for reducing substances are sometimes the reverse of what they were when expressed as per cent fresh weight or per cent dry weight. This method of calculation makes the assumption that each spur has an equal opportunity to draw upon the materials in the branch to which it is attached. The data are only tentatively offered in an attempt to approach the absolute amounts of the various materials which may be functioning in the metabolism of bearing and non-bearing trees. There is a remarkably uniform distribution of spurs along the branch of the Sugar prune.

*Increase of Total Sugars and Total Nitrogen in Flowers and Fruit.*—At the two sampling periods March 4 and March 11, 1928, when the flowers were emerging from the buds, both buds and flowers

were counted so that the average number of flowers per bud (1.8) was found. Buds, flowers, or fruits were counted at each sampling period. From this information the amounts of reducing substances, total sugars, and nitrogen have been determined per flower and fruit. These data are presented in table 12. The nitrogen content of the fruit increases rather steadily throughout the season. Petal fall occurred just previous to March 31. Although the table shows no appreciable increase, the fruit has gained enough nitrogen so that if any is lost at petal fall, it does not show as a loss of nitrogen per fruit.

TABLE 11

MILLIGRAMS OF REDUCING SUBSTANCES, STARCH, AND TOTAL NITROGEN IN BARK AVAILABLE TO EACH SPUR, 1928

Date of sampling	Bearing			Non-bearing		
	Reducing substances	Starch	Nitrogen	Reducing substances	Starch	Nitrogen
Jan. 5.....	11.2	4.8	4.6	7.3	4.9	2.3
28.....	13.8	5.4	6.0	11.9	5.1	3.2
Feb. 19.....	8.7	8.6	4.1	12.0	10.6	3.9
March 4.....	9.55	10.0	3.99	10.6	20.8	3.35
11.....		6.2	3.1		25.6	4.2
17.....	9.8	4.1	4.0	7.4	13.7	3.4
31.....	8.7	1.9	3.3	9.3	5.9	3.3
April 14.....	9.8	1.5	3.1	13.6	7.8	2.4
30.....	9.3	3.2	2.8	14.7	24.4	4.1
May 5.....	7.7	3.2	1.7	12.9	22.4	3.6
12.....	9.3	4.3	2.4	10.9	18.0	3.2
19.....	9.2	7.2	2.9	8.6	17.6	3.3
28.....	8.1	8.6	2.4	6.4	20.2	3.2
June 15.....	9.3	12.6	2.6	11.5	27.1	4.2
July 4.....	7.6	13.0	2.3	10.4	37.6	3.7
31.....	11.8	4.9	2.3	13.1	31.6	3.6

Three periods of rapid increase are shown in total sugars per fruit: one at full bloom, March 11 to March 17; the second from April 14 to April 30, which is about three weeks after petal fall; and the third from June 15 to until harvest. The fruit was showing some yellow undercolor on this date. The pits had definitely hardened about two weeks previously. The greatest change occurs in the last part of this period, July 4 to July 31. The increase of total sugars per fruit during this interval is enormous, being greater than the increase from January 5 to July 4, and is undoubtedly responsible for the decrease of the starch content of the branches. The drop in total sugars on March 31 results from petal fall, when a large loss occurs.

The amounts, in milligrams, of total sugars and total nitrogen in the flowers or fruit, calculated as the amount withdrawn per spur, are

shown in table 13. This table manifests the effect of both the petal fall and the June drop and shows the relatively large absolute amounts that are taken out of the spur or pass through the spur into the flowers or fruit.

As an example of the large amounts of nitrogen that pass into the flowers and fruit one calculation will be given. On March 17, at the time of full bloom, there were 400 milligrams of nitrogen in the flowers from 100 spurs. The total nitrogen in the wood, bark, and spurs directly back of these flowers was about 800 milligrams. On April 30 there were 1630 milligrams of total nitrogen in the fruit from 100

TABLE 12

REDUCING SUBSTANCES, TOTAL SUGARS, AND TOTAL NITROGEN IN MILLIGRAMS PER FLOWER OR FRUIT FOR 1928; TOTAL SUGARS PER FRUIT FOR 1927

Date of sampling	Reducing substances	Total nitrogen	Total sugar	Date of sampling, 1927	Total sugar
Jan. 5.....	.061	.032	.0895	.....	.....
28.....	.033	.038	.0926	.....	.....
Feb. 19.....	.079	.053	.082	.....	.....
March 4.....	.23	.163	.23	.....	.....
11.....	.53 <sup>1</sup>	.331	.73	.....	.....
17.....	2.49	.618	3.5	.....	.....
31.....	.97	.687	1.2	.....	.....
April 14.....	2.9	1.24	3.0	.....	.....
30.....	80.7	6.6	84.0	April 29.....	49.6
May 5.....	107.7	8.4	108.0	.....	.....
12.....	131.1	12.8	136.0	.....	.....
19.....	164.0	18.5	177.0	.....	.....
28.....	200.1	20.1	215.0	May 27.....	197.0
June 15.....	229.0	27.4	408.0	June 23.....	458.0
July 4.....	544.0	31.5	941.0	.....	.....
31.....	1193.0	40.5	1953.0	July 29.....	1900.0
.....	.....	.....	.....	Aug. 24.....	2692.0

spurs. The total nitrogen in the wood, bark, and spurs back of these fruits was about 750 milligrams. These figures do not take into consideration the nitrogen that was lost at petal fall or directly afterwards, at the first drop of fruits. The calculation shows a large increase in the amounts of nitrogen in the fruit without any appreciable change in the total nitrogen content of the woody tissues directly back of the fruit.

In table 14 are shown the absolute amounts of nitrogen in the leaves per spur and per leaf. The leaves were just emerging from the bud on March 31. The leaves from the non-bearing trees emerged a little earlier than those from the bearing. Data on the average weight per leaf and the average number of leaves per spur show that the leaves had attained approximately their full weight and number per

spur by April 30. This is also reflected in table 12. After April 30, when the leaves had attained full size, there was no appreciable change in the introgen content per leaf or in the nitrogen content of the leaves per spur. The leaves from the non-bearing trees have withdrawn a slightly greater amount of nitrogen per leaf. This amount when calculated as the amount of nitrogen withdrawn per spur is greater because of the slightly greater number of leaves per spur.

TABLE 13  
MILLIGRAMS OF TOTAL SUGARS AND TOTAL NITROGEN IN FLOWERS AND FRUIT PER SPUR, 1928

Date	Total sugars	Total nitrogen
Jan. 5.....	.96	.34
28.....	1.2	.49
Feb. 19.....	.67	.44
March 4.....	1.45	1.00
11.....	4.8	2.20
17.....	22.8	4.0
31.....	6.6	3.8
April 14.....	13.5	5.6
30.....	207.0	16.3
May 5.....	200.0	15.5
12.....	250.0	23.5
19.....	244.0	25.4
28.....	330.0	30.8
June 15.....	530.0	35.4
July 4.....	1150.0	38.4
31.....	2520.0	52.2

TABLE 14  
MILLIGRAMS OF TOTAL NITROGEN PER LEAF AND IN LEAVES PER SPUR, 1928

Date	Milligrams per leaf		Milligrams in leaves per spur	
	Bearing	Non-bearing	Bearing	Non-bearing
March 11.....			.136	.304
17.....			.233	.873
31.....	.67	.60	4.00	6.6
April 14.....	1.16	1.64	9.73	17.0
30.....	1.85	2.1	16.0	20.5
May 5.....	1.62	2.1	13.0	20.9
12.....	1.52	2.34	13.6	23.0
19.....	1.9	2.1	16.6	23.5
28.....	1.6	2.3	13.1	25.0
June 15.....		2.0		20.0
July 4.....	1.8	2.0	12.1	18.0
31.....	2.3	2.7	18.0	22.7

The same calculation that was used in computing the nitrogen removed by the fruit showed that the leaves on 100 spurs have withdrawn about 1400 milligrams of nitrogen from March 17 to April 30.

## DISCUSSION

Certain definite chemical differences have been found in the bearing and non-bearing trees which would seem at least to be correlated with the performance of the trees. These differences have occurred regularly and uniformly throughout the two years, although the trees have alternated.

The differences have occurred sufficiently early in the season to be of importance in the formation of fruit buds. If the fruit buds on the Sugar prune are formed by mid-July or early August, the factors influencing their formation are probably operative some time previous to that time.

The position which the reducing substances occupy is a peculiar one. In both years and in all types of material the reducing substances of the non-bearing trees fall below those of the bearing trees about May 1, when the June drop occurs, and remain below for the remainder of the season. If the amounts present as per cent dry weight are a basis for reasoning, this relationship of the reducing substances is not what would be expected, because the greatest deposit of starch takes place in the non-bearing material, and deposition of starch is usually thought to occur when a given concentration of soluble sugars has been reached. It is not safe, however, to reason as to conditions of concentration from amounts present on a dry weight basis or from the amount of water present in a given mass of tissue. Localization of concentrations can vary widely within the same tissue. Swarbrick<sup>(43)</sup> believes that fruit bud formation begins when a sufficient concentration of soluble carbohydrates has been attained. Since the data give no information in regard to the concentrations of the reducing substances present, it would not seem advisable to make any assumptions regarding the effect of concentration upon the formation of fruit buds in the Sugar prune. Rather it would seem preferable to say that fruit buds were formed on branches in which the amounts of reducing substances, on a dry weight basis, were lower than in branches not forming fruit buds, at the time when fruit bud formation is considered to be taking place.

Observations made in January of 1929 show that the trees that were non-bearing in 1928 set a heavy crop of fruit buds.

Nitrogen has played an important part in all the literature regarding the formation of fruit buds. Kraybill,<sup>(26)</sup> Kraybill, Potter, and others,<sup>(25)</sup> and Hooker<sup>(21)</sup> have each found that the bearing spurs of apples are relatively higher in nitrogen than the non-bearing spurs.

This condition does not agree with the one found in this investigation. Here the bearing materials have all been uniformly lower in nitrogen from about May 1 on throughout the season. Of course, as Swarbrick points out, the conditions affecting formation of fruit buds in the apple are not necessarily the same as those in the plum, since the buds are essentially different. The situation in the early part of the season, where the bearing material has a higher nitrogen content than the non-bearing, may be a case of nitrogen storage from the off year, as described by Roberts.<sup>(36)</sup> Nightingale<sup>(35)</sup> has revised the four classes of Kraus and Kraybill and has laid stress upon the relationship between *amino* acids and other forms of soluble nitrogen, not necessarily including nitrates, and the available carbohydrate supply in fruit bud formation.

The flowering and fruiting process has long been considered an exhaustive one. Howlett<sup>(23)</sup> has shown that considerable amounts of nitrogen and carbohydrates are taken out at blooming time and lost at petal fall. Over 60 per cent of the free reducing substances of the whole flower may be in the petals at full bloom. Murneek<sup>(31, 34)</sup> found that fruiting was an exhaustive process in the apple.

The present investigation has shown that there is a continuous increase in the carbohydrate and nitrogen content of the fruit from mid-winter on until harvest time. The increase in the absolute amounts of nitrogen removed by the developing flowers or fruit is greatly in excess of the amounts lost by the spur itself or by both the spur and the wood and bark behind the spur. A very large proportion of the nitrogen going into the flowers and fruit must be translocated from regions more remote than the spurs or the branches to which they are attached. This does not take into consideration the large amounts of nitrogen which go into the leaves up to the time of full development.

Another phase of the fruiting process apparently shown by the data is the relationship of the starch storage of the trees which were non-bearing in 1927. At the last sampling in 1927 they were very high in starch. They show the winter minimum which seems to be characteristic of deciduous trees, but they fail to reach a very high early spring maximum before going into the minimum at blossom time. On the other hand, the trees which were bearing in 1927 must have had a very low starch storage at harvest time; yet they show a very decided maximum in early spring. From harvest in 1927 to the time of the spring maximum in 1928 there was one great difference in the trees: those not bearing in 1927 had a heavy crop of fruit buds, while those bearing in 1927 had none.



As an example of the approximate number of flowers on a tree the following calculations have been made. Tree C-7 had 150 pounds of fruit in 1928. Each fruit averaged 18.7 grams. An average of the number of fruits per spur for the last three samplings gives 1.3. This would give 2800 fruit-bearing spurs on the tree. The data taken at the time of full bloom showed that there was an average of 6.6 flowers per spur. This, then, would give on the tree 18,480 flowers that were developing from the summer of 1927—probably a minimum because a number of spurs that had flowers did not keep any fruit past the June drop. This calculation is given only as a very rough approximation of the number of flowers that were respiring and developing. Both the trees which were bearing in 1927 and those which were non-bearing in that year must have had an equal chance for starch storage between harvest time and leaf fall. There seems to be two reasons for the failure to reach the spring maximum. One is that the demand of the fruit buds for carbohydrates was so great at this time that translocation and deposition of starch was prevented. The other reason is that the development of the fruit buds throughout the fall and winter of 1927 was sufficient to reduce the starch storage greatly. The respiration of buds and flowers is known to be considerable. Very likely a combination of the two reasons accounts for the situation. If this assumption is true, then not only is the fruiting process an exhaustive one with respect to carbohydrates during the year in which the fruit is borne, but it exerts a considerable drain on the carbohydrate reserve from the time the fruit buds are formed until the following harvest.

Further evidence of the carbohydrate drain is found in the starch content of the roots. Between the bearing and non-bearing roots there is a wide difference which agrees with that in the top. Davis<sup>(12)</sup> has found, in controlled experiments with the wheat plant, that when the temperature has been increased, other factors being the same, the top to root ratio has increased. He has attributed this to the fact that with an increase in temperature the metabolic processes have increased and more of the carbohydrates have been utilized at the point of manufacture, so that although both top and root have increased, the top has increased much more rapidly than the root. Bushnell<sup>(6)</sup> has found the same thing to be true for potatoes and has explained it in the same way. Chandler,<sup>(9)</sup> in discussing the effect of thinning and blooming on a tree, says: "Not only is the percentage of girth increase greater in a year when the tree does not bloom, but this is true also when the bloom is killed by a frost. And when trunk growth is so greatly

reduced, root growth also must be reduced, it seems, as greatly. . . . Since the thinning is done so late that the terminal buds have generally formed, it cannot influence top growth. . . . It seems possible, however, that it may influence root growth considerably." The failure of the bearing trees to store much starch in the roots very likely indicates that the carbohydrates were utilized in the top by the fruit and that the root growth was seriously hindered. This lack of root growth would correspondingly cut down the absorbing area.

This relationship between the depletion of carbohydrates in the tree by the fruit and the lack of starch storage in the roots might offer one explanation of some apparent soil troubles. A fruit tree which bears heavy annual crops and whose fruit is left on until late summer when ripe, would very likely have a large part of its manufactured carbohydrates go into the fruit. This condition would result in a much restricted root growth and a more limited absorbing surface, so that any soil deficiency would be intensified. In addition, if the tree had annual crops it might be kept relatively low in stored carbohydrates the whole year round because of the demands of the growing and respiring fruit buds.

The carbohydrate-nitrogen relationship widens in this material in agreement with the conception of the part played by such relationship in fruit bud formation. Starch is the largest variable among the carbohydrates, and the widening of the ratio in the trees producing fruit buds results very largely from the increase in the starch content. The uniform behavior of the starch content of all parts of the tree invites speculation concerning the rôle which a deposit of starch or a lack of it plays in fruit bud differentiation. If a deposit of starch in the roots is a source of available energy for root extension and for an increase of absorbing surface, then any factor, such as intake of ions or water, which depends upon the extent of the absorbing surface, may be a factor in the differentiation of fruit buds. Deposition of starch in the spurs and adjacent tissue is undoubtedly associated with an excess of energy-furnishing material which is available to the growing point and may be essential in the differentiation of fruit buds. If starch or carbohydrates be the chief factor in the changing carbohydrate-nitrogen relationship associated with fruit bud differentiation we may reasonably wonder whether the carbohydrate content might not show the same widening relationship to other elements or compounds when trees are in a condition, as these were, to produce fruit buds. In other words, when the results of the gross analysis of the tissue of fruit trees are under consideration, it seems logical to speculate regarding the validity of the carbohydrate-nitrogen ratio as

a causal agent in fruit bud differentiation. In alternate-bearing trees in the 'off' year the conditions are favorable for an accumulation of storage carbohydrates, and the relationship between the carbohydrates and any other compound or element very likely will widen. In trees in the 'on' year the converse is true because of the heavy demand of the fruit for carbohydrates. Under these conditions the relationship of carbohydrates to nitrogen or other materials, may be not a causal one but a situation accompanying the 'off' or 'on' year in alternate bearing. The causal factors may be those related to an excess of energy furnishing materials—for example root growth and extension of the absorbing surface through the soil is dependent upon energy obtained from the parts of the tree above ground. The heavy use of carbohydrates by a crop may seriously reduce extension so that any material which is dependent upon the extension and renewal of the absorbing surface may become a limiting factor in the region of fruit bud differentiation; or the supply of carbohydrates may be so low that a supply of available energy materials may be limiting in the area of fruit bud differentiation.

### SUMMARY

Samples were taken from bearing and non-bearing Sugar prune trees for two years, the same trees furnishing the material for both years.

Yield records and counts of tagged limbs which were judged to be in the bearing or non-bearing year in the winter of 1927 showed that the trees experienced a complete alternation.

Chemical analyses were made for the principal carbohydrates and nitrogen.

A determination of reducing substances on a lead acetate cleared extract by the picric acid method shows the same seasonal trend as when the reducing substances are determined by a copper reduction method. The curves for the determination of starch by the picric acid and the copper reduction methods are also parallel.

Fifty-eight per cent of the spurs that were disbudded in 1927 formed fruit buds again that year, while only 9.5 per cent of the spurs bearing in 1927 formed fruit buds that year.

Reducing substances showed small but uniform differences for both years. In all fractions after about May 1, the reducing substances in the bearing trees on a dry weight basis are greater than in the non-bearing trees.

Total nitrogen shows small but consistent differences, which are constant for all the fractions taken and for the two years. Before May 1 or thereabouts, the bearing trees have a nitrogen content higher than the non-bearing. After this date the value for the total nitrogen of the bearing trees lies below that of the non-bearing.

Starch is consistently higher in the non-bearing trees than in the bearing. After the first flush of growth the difference becomes of considerable magnitude. The data for the amount of starch present in the non-bearing trees at the close of the 1927 season and that present on January 5, 1928, along with the failure to reach a decided maximum in the spring, indicate that there is probably a considerable carbohydrate drain on a tree from the time the fruit buds are formed in the summer until the fruit is harvested the following year.

The roots of the bearing trees contain a relatively small amount of starch, whereas those of the non-bearing are high in starch. It seems reasonable to suppose that root growth is suppressed when the demand for carbohydrates, above ground, is heavy. A suppression of root growth would limit the absorbing area and possibly limit some factors, such as intake of ions or water, which may function in fruit-bud differentiation. It is suggested that fruit trees which have a heavy annual crop that remains on the trees most of the summer, may experience a shortage of carbohydrates for the roots. If the trees should be growing in a soil deficient in any ions this deficiency might be exaggerated by the suppressed root growth.

Although starch, in itself, is probably not necessary to fruit bud differentiation, its accumulation perhaps represents an excess of energy materials, which are available for processes that are necessary to fruit bud formation such as root growth with the consequent extension of absorbing surface or to furnish available energy to a growing point where fruit bud differentiation may be taking place.

Starch shows two maxima and two minima. A third maximum may be shown in bearing trees. An especially sharp maximum is shown in the non-bearing trees in the spring.

Starch content and moisture show an inverse relationship. The data for the increase of nitrogen and reducing substances per flower or fruit show a regular increase per flower or fruit from January 5 until harvest time, about the first of August. The increase of total sugars per fruit is especially heavy after the fruit begins to ripen. The increase during the three weeks before harvest is enormous and is accompanied by a corresponding depletion of starch in the branches back of the spur. Allowing the fruit to become fully ripe on the tree,

as is the custom with prunes, appears to be an especially exhaustive process, so far as carbohydrate reserves are concerned. The increase of sugar per fruit was as much from July 4 to July 31 as it was during the whole period of development of the fruit up to that time.

Some of the data presented indicate that the loss of nitrogen from the spurs and from the wood and bark adjoining the spurs cannot account for the nitrogen appearing in the flowers and fruit for a given period.

From the data obtained for the nitrogen content of the leaves, either as milligrams per leaf or as milligrams of nitrogen in the leaves per spur, it would seem that the leaves are not active competitors for nitrogen after they have attained full size.

### ACKNOWLEDGMENT

I am deeply indebted to Dr. E. L. Proebsting for his guidance and advice in organizing the investigation.

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The titles of the Technical Papers of the California Agricultural Experiment Station, Nos. 1 to 20, which HILGARDIA replaces, and copies of which may be had on application to the Publication Secretary, Agricultural Experiment Station, Berkeley, are as follows:

1. The Removal of Sodium Carbonate from Soils, by Walter P. Kelley and Edward E. Thomas. January, 1923.
4. Effect of Sodium Chlorid and Calcium Chlorid upon the Growth and Composition of Young Orange Trees, by H. S. Reed and A. R. C. Haas. April, 1923.
5. Citrus Blast and Black Pit, by H. S. Fawcett, W. T. Horne, and A. F. Camp. May, 1923.
6. A Study of Deciduous Fruit Tree Rootstocks with Special Reference to Their Identification, by Myer J. Heppner. June, 1923.
7. A Study of the Darkening of Apple Tissue, by E. L. Overholser and W. V. Cruess. June, 1923.
8. Effect of Salts on the Intake of Inorganic Elements and on the Buffer System of the Plant, by D. E. Hoagland and J. C. Martin. July, 1923.
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