VOL. 4 SEPTEMBER, 1929 NO. 6

HILGARDIA

A Journal of Agricultural Science

PUBLISHED BY THE

California Agricultural Experiment Station

CONTENTS

The Effect of Dormant Pruning on the Carbohydrate Metabolism of Vitis vinifera

A. J. WINKLER

UNIVERSITY OF CALIFORNIA PRINTING OFFICE
BERKELEY, CALIFORNIA

HILGARDIA

A JOURNAL OF AGRICULTURAL SCIENCE

PUBLISHED BY THE

CALIFORNIA AGRICULTURAL EXPERIMENT STATION

VOL. 4 SEPTEMBER, 1929 No. 6

THE EFFECT OF DORMANT PRUNING ON THE CARBOHYDRATE METABOLISM OF VITIS VINIFERA

A. J. WINKLER[1]

In previous papers[2, 3, 4] experiments were described, the results of which showed: (1) that dormant[2] pruning depresses the capacity of the vines for total growth; (2) that dormant pruning depresses the capacity of the vines for fruiting; (3) that dormant pruning reduces the quality of the fruit of some varieties; and (4) that bearing depresses the capacity of the vines for growth.

The purpose of this paper is to describe the effect of dormant pruning on the carbohydrate metabolism of the vine and to discuss the influence of this effect on growth and fruiting.

TYPES OF PRUNING USED

The plan of the plantings and the various types of pruning employed were those described in detail in the earlier papers.[2, 3] The types of pruning used on the vines from which samples for analysis were taken were:

Non-pruned, part crop: no pruning. All clusters in excess of what was thought necessary for a good crop of fruit were removed before blooming.

---

[1] Associate Professor of Viticulture and Associate Viticulturist in the Experiment Station.

[2] The depressing effect of herbaceous or summer pruning on growth and crop is generally recognized by viticulturists; see: Bioletti, F. T., and F. C. H. Flossfeder. Topping and pinching vines. California Agr. Exp. Sta. Bul. 296:369–384. 1918.

Cane-pruned, part crop: pruning similar to that commonly used in California on Sultanina (Thompson Seedless) except that about 25 per cent more wood was retained. All clusters in excess of what was thought necessary for a good crop of fruit were removed before blooming.

Normally (spur) pruned: pruning as nearly as possible that of the best accepted commercial practice with the varieties used. All clusters allowed to develop.

Severely pruned: pruning similar to that of the normally pruned vines but more severe, only the base buds being retained on the spurs. All clusters allowed to develop.

METHODS OF SAMPLING AND ANALYSIS

The woody material for analysis was collected as follows:—

The Shoots.—Two entire shoots were taken from each vine. About four inches of the basal portion of each shoot was taken for a sample. All the basal portions of the shoots from a single pruning treatment for a given date were thrown together to make one sample.

The Trunk.—Disks 3 to 6 millimeters in thickness were sawed from the similar positions in the trunks of the vines as they were being removed. Two vines were usually removed from a given pruning treatment, and in such cases the sample was made up of wood of both vines.

The roots.—Segments of the main roots at a distance of twenty to twenty-five centimeters from the root crown were collected at the time vines were being removed. Here also a single sample was made up of wood from two vines.

Preparation of the Samples.—In all the samples, the bark was separated from the wood. The material was then cut into small segments of less than one cubic centimeter in size and placed immediately in an oven with forced ventilation at 65° C. The dried material was ground so that it would pass through a 60-mesh sieve.

Analysis.—[3]For the determination of reducing substances the extraction was made with 95-per cent alcohol, while the starch was hydrolized with taka-diastase. The reductions were carried out according to the Shaffer-Hartman method.[(1)] Duplicate determinations were always made.

---

[3] The writer is indebted to Miss Isabelle D. Collins and Mr. T. C. Broyer, technicians in the Division of Viticulture, who made the chemical analyses.

THE EFFECT OF PRUNING ON THE CARBOHYDRATES OF THE VINE

Some ways in which pruning affects the vines, as shown in previous papers, are to depress the growth and to decrease the bearing and with certain varieties, to lower the quality of the fruit. The effect on the quality of the fruit is especially pronounced in the Muscat of Alexandria. The greater vine growth of the lightly pruned and non-pruned vines may be a result of more favorable nutrition of the vine over the entire season. The improvement in fruiting, on the other hand, must be due to more favorable nutrition when the individual flowers are developing and the berries setting; that is, before blooming, during blooming, and during the setting of the berries.

In the vine, the later stages in the development and opening of the flowers do not take place before and during leafing out in spring as they do with most deciduous fruits. By the time of leafing out in spring, the development of the vine flower has proceeded to the primordia of the individual flowers, but the development of the flower parts, such as anthers, style, and ovules, occurs while the vine is in leaf, and the flowers open six to eight weeks after the beginning of active growth. It seems probable, therefore, that the effects on fruiting of changes in carbohydrate nutrition could be produced only during early summer, that is, previous to the middle or end of June at Davis.

With the above facts concerning the fruiting habit of the vine, together with its responses to pruning, in mind, analytical results obtained in a study of the effects of pruning on the carbohydrate nutrition of the vine at Davis will be presented.

The Seasonal Changes in Total Carbohydrates.—During the season of 1925 series of samples of the vine parts to be analyzed were collected from the Muscat of Alexandria from January until well along in the growing season. A similar series of samples was collected from the Monukka in 1926. Owing to the similarity of the results obtained with the two varieties, only the results for the Muscat are shown in figure 1. This similarity of results for the two varieties during early summer may be illustrated by a comparison of the graphs of figure 1 with those of figure 3*A*. Also, since the effect of pruning on the seasonal change of carbohydrates in the vine parts analyzed was confined almost entirely (fig. 3) to the shoot, results for this part of the vine alone are shown in figure 1.

The graphs of figure 1 indicate two maxima and two minima in the seasonal changes in the total carbohydrates for the non-pruned,

cane-pruned, and normally pruned vines, one maximum falling in the dormant season and the other during the early part of the growing season. This, no doubt, is the normal condition for the seasonal behavior in the carbohydrates of the vine at Davis. The severely pruned vines, on the other hand, fail to show a maximum in the early part of the growing season.

Pruning affected the amount of total carbohydrates present at both the maximum of the dormant season and that of the early part of the growing season. The effect was much greater at the vegetative

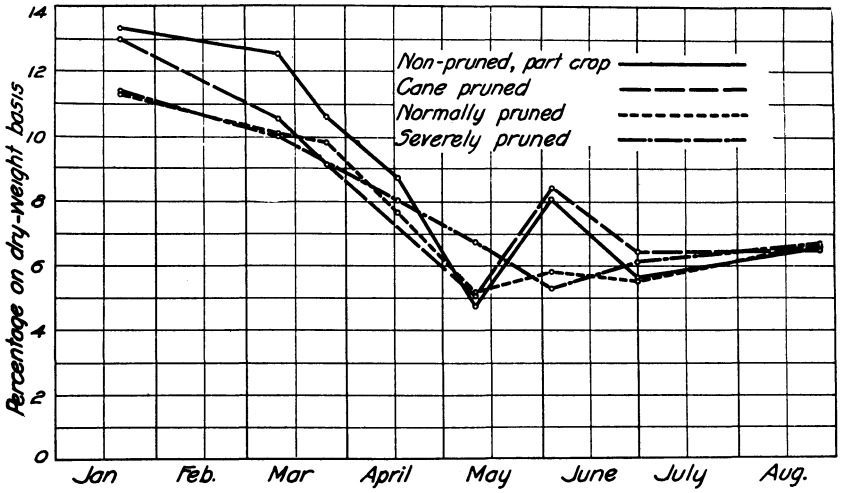


Fig. 1. The effect of pruning on the percentage of total carbohydrates in the basal portion of Muscat of Alexandria canes and shoots at various dates during 1925.

maximum. At this time the amount of total carbohydrates in the non-pruned vines was 36 per cent greater than in the normally pruned vines and 40 per cent greater than in the severely pruned vines; that in the cane-pruned vines was 44 per cent greater than in the normally pruned vines and 49 per cent greater than in the severely pruned vines. The amount of total carbohydrates in the non-pruned and cane-pruned vines at the dormant maximum was 18 and 15 per cent respectively greater than that of the normally pruned vines. At this season there was no difference in the carbohydrate content of the normally and severely pruned vines.

In the periods between the two maxima, no significant influence of pruning on the amounts of carbohydrates present is indicated. This lack of noticeable influence could probably be accounted for by differences in the rates of growth. The non-pruned vines start growth

earliest, and, owing to the many shoots that develop, the rate of growth rapidly diminishes. The more severely pruned vines, on the contrary, start growth later, and, owing to the relatively few shoots that develop, the rate of growth is rapid and continues to be so over a relatively long period. This continued rapid length growth of the severely pruned vines, no doubt, prevents the appearance of a maximum in the total carbohydrates during early summer, these materials being consumed as rapidly as they are produced.

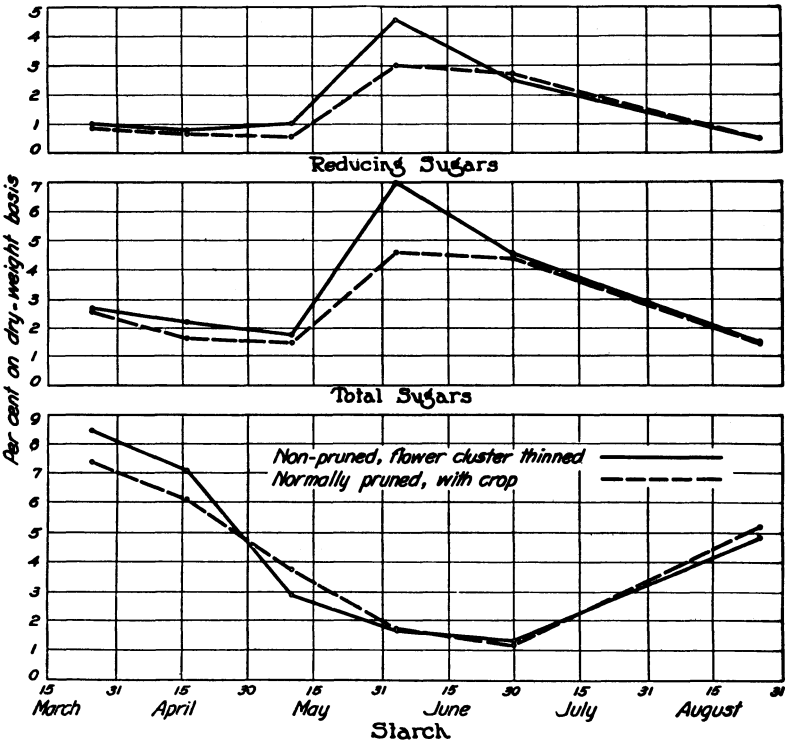


Fig. 2. The effect of pruning on the percentage of reducing and total sugars and starch in the basal portion of Muscat of Alexandria shoots.

The Amounts of Sugars and Starch Present.—By plotting graphs for each of the carbohydrates determined—namely, reducing sugars, total sugars, and starch—as in figure 2, the effect of pruning upon the changes in each of these substances is indicated. For these graphs the figures for the basal portion of the Muscat shoots are again used. Similar figures for the reducing sugars in the Monukka are shown in figure 3 *A*.

The graphs of figure 2 show that the influence of pruning, especially during early summer, was primarily, if not solely, confined to the carbohydrates in solution—sugars. There was 52 per cent more reducing sugars in the non-pruned than in the normally pruned vines on June 3, and 51 per cent more total sugars.

For starch, on the contrary, there is no indication that pruning affects the amount present during early summer. There is, however, a higher percentage of starch present in the non-pruned than in the normally pruned vines during the dormant season. This larger amount is, no doubt, of importance in connection with the greater capacity of the non-pruned vine, yet it is of questionable significance with regard to the better setting and development of the fruit which some varieties exhibit with cane-pruning or non-pruning accompanied by flower-cluster thinning. The improvement in fruiting is more closely associated with the larger amounts of the carbohydrates in solution. This association will be indicated more clearly in the following sections of this paper.

The Amounts of Sugars in the Different Parts of the Vines.—As stated, samples for analysis were collected from the shoots, trunk, and roots. The effect of pruning on the sugars in these parts of the vine during early summer is indicated by the graphs of figures 3, which represent results obtained with Monukka. As shown in figure 2, the starch content of the vine was not influenced in early summer by pruning. Also, since the direction and magnitude of the effect of pruning on the reducing and total sugars was very similar (fig. 2), only the data for the reducing sugars are included.

The graphs of figure 3*C* indicate that pruning has little or no effect on the amounts of reducing sugars present in the roots during early summer. The differences which are indicated seem to be due to differences in the time of the beginning of growth and the rates at which this substance is used for growth rather than to the type of pruning.

As indicated by the graphs of figure 3*B*, there was even less difference in the amounts of reducing sugars present in the trunks of the vines under the several types of pruning than in the roots.

In the basal portion of the shoots there was an indication of a marked influence of pruning on the amounts of sugars present. The amount of reducing sugar in this part of the non-pruned Monukka vines was slightly greater than that indicated for Muscat of Alexandria in figure 2. The amount was 33 per cent larger than that in the normally pruned vines of this variety on May 19. The graph of figure 3*A* also indicates that the changes in reducing sugars during

early summer in the Monukka follow a course very similar to that for the total carbohydrates in Muscat of Alexandria, shown in figure 1. For the Monukka there was no summer maximum in reducing sugar with severe pruning, a condition which is in agreement with that found for Muscat.

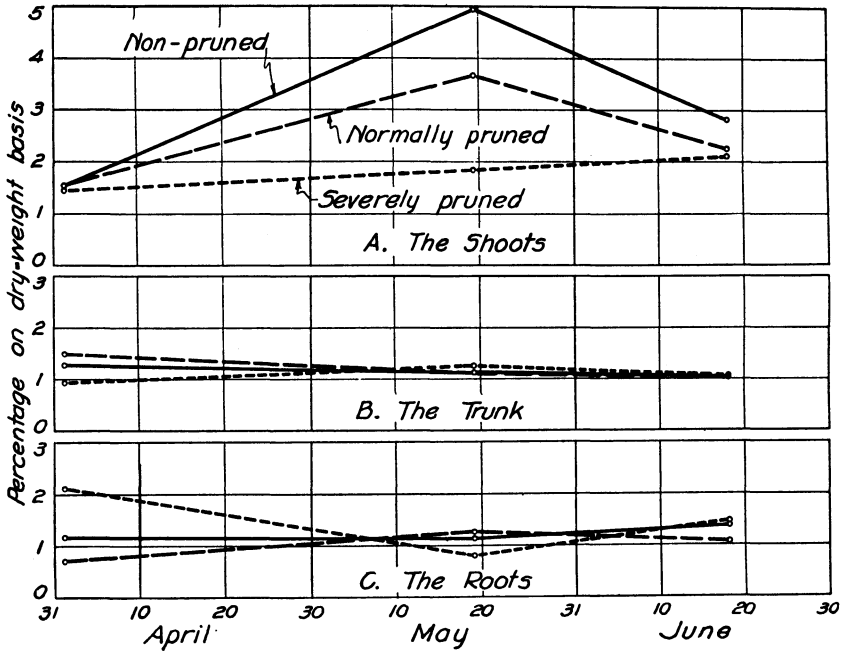


Fig. 3. The effect of pruning on the percentage of reducing sugar at various levels in the Monukka vines during early summer.

THE EFFECT OF PRUNING ON THE RATE OF GROWTH OF THE VINE

The fact noted that larger amounts of certain of the carbohydrates are present in cane-pruned and non-pruned vines than in the normally and severely pruned vines, especially during early summer, makes it of interest to inquire further into the causes of these differences in nutrition. Does the greater reserve of the dormant cane-pruned and non-pruned vines carry over to give these vines a more favorable nutrition during early summer, or does the pruning affect the rate or type of growth so as to favor the production and accumulation of sugars?

The Amounts of Reducing Sugars and Total Carbohydrates Present in the pruned Vine.—The removal of several series of vines made it possible to obtain weights of the vines both before and after pruning. From these figures, together with the analytical data, it was possible to estimate the amounts of carbohydrates contained in the vines after pruning. The average weight of vine after pruning and the percentage and total amount of reducing sugars and total carbohydrates present in two five-year-old Monukka vines under severe, normal, and non-pruning, are shown in table 1.

TABLE 1

THE WEIGHT OF DORMANT VINE AFTER PRUNING AND THE AMOUNTS OF REDUCING SUGARS AND TOTAL CARBOHYDRATES TO A VINE BASED ON DRY WEIGHT

Average of two vines

Measurements	Non-pruned	Normally pruned	Severely pruned
Weight of vine after pruning, kilos	39.10	12.70	4.50
Per cent of reducing sugars	1.25	1.16	1.13
Per cent of total carbohydrates	7.10	6.48	6.22
Weight of reducing sugars per vine, kilos	0.49	0.14	0.05
Weight of total carbohydrates per vine, kilos	2.78	0.82	0.28

Although the differences between the percentages of reducing sugars and of total carbohydrates in the non-pruned vines and those in the severely and normally pruned vines during dormancy, are relatively small, the total amounts of these substances retained in the non-pruned vines after pruning is much larger than that of the severely and normally pruned vines. They contained almost four times as much of each of these substances as the normally pruned and ten times as much as the severely pruned vines.

The larger amounts of these carbohydrate materials present in the non-pruned vines, no doubt, endows them with a greater potential capacity for growth and fruiting, yet if the rate and mass of growth produced by the vines under the several types of pruning was in proportion to the amount of wood retained at pruning, this difference in the amounts of the reserves during dormancy would not account for the differences in nutrition that exists during early summer.

The Rate of Growth.—During two seasons when Monukka vines were being removed at different intervals from May to July, weighings were made of the several parts of the vine, such as leaves, shoots without leaves, and trunk. The weights of the leaves and shoots were obtained in as short a time as possible to avoid error due to the loss of moisture. From these weighings it was possible to determine the

ratio of weight of shoots produced during early summer to total weight of the parts of the vine retained at pruning, and the ratio of weight of leaves to weight of shoots for vines of each of the types of pruning. These ratios for the non-pruned, normally pruned, and severely pruned vines are shown in figure 4.

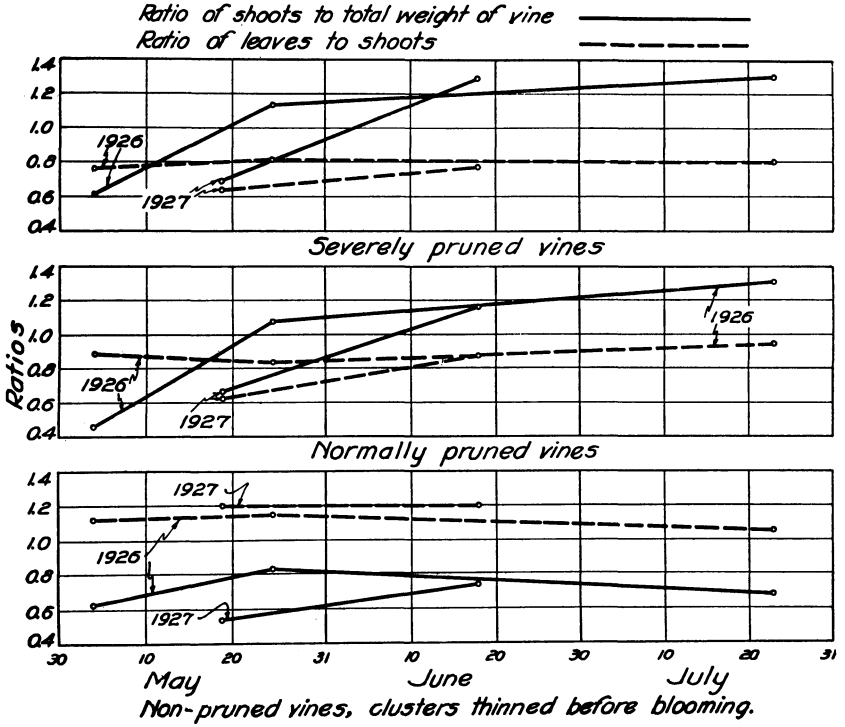


Fig. 4. The ratio of weight of shoots during early summer to total weight of the parts of the vine retained at pruning and the ratio of weight of leaves to weight of shoots.

The graphs for the severely pruned vines show that in 1926 the ratio of weight of shoot to total weight of the parts of the vine retained at pruning was 1.13 : 1 on May 25. This ratio continued to increase until on July 23 it was 1.30 : 1. At both dates the ratio of weight of leaves to weight of shoot was only 0.80 : 1. A similar condition obtained in 1927. In this season the ratio of weight of shoots to total weight of vine did not become greater than 1 so early, however, and the ratio of leaves to shoots was smaller.

In the case of the normally pruned vines, the type of growth was very similar to that of the severely pruned. The ratio of weight of

shoots to total weight of the parts of the vines retained at pruning was 1.07:1 on May 25 and 1.30:1 on July 23. For this type of pruning the ratio of leaves to shoots was slightly higher than that of the severely pruned vines, being 0.83:1 on May 25 and 0.94:1 on July 23. The ratios for the normally pruned vines during 1927 bear the same relation to those of the severely pruned vines as that just indicated for the year 1926.

In the non-pruned vines there is a complete reversal of the conditions just indicated for the severely and normally pruned vines. With this type of pruning the ratio of weight of shoots to total weight of the parts of the vine retained at pruning never attained 1. On May 25 it was 0.84:1 and on July 23 0.70:1. On the other hand, the ratio of weight of leaves to weight of shoots was greater than 1 at the earliest weighing on May 4 and remained so. Again in 1927 the ratio of weight of shoot to total weight of vine at the beginning of the growing season ranges from 0.56:1 on May 19 to 0.74:1 on June 18. On these same dates the ratio of weight of leaves to weight of shoots was 1.20:1.

The graphs of figure 4 thus show that the non-pruned vines are making *less shoot growth* in proportion to the weight of vine at the beginning of the growing season than either the normally or severely pruned vines. On the other hand, these same non-pruned vines are producing a *much greater weight of leaves* in proportion to shoots than the normally or severely pruned vines.

Rate of Total Shoot Elongation and Weight of Leaves.—Although the ratio of weight of shoots to total weight of the parts of the vine retained at pruning in the non-pruned vines was much less than that in either the severely or normally pruned vines, a condition which would tend to conserve the reserve materials of the vines, the rate of total shoot elongation under this type of pruning was much greater than that of the pruned vines owing to the larger number of shoots. The effect of pruning on the time and amount of total length growth of all shoots to a vine is shown in figure 5.

The graphs of figure 5 indicate that the type of pruning modifies both the rate of growth and the amount of total length growth. The importance of this effect is seen when the amount of length growth found at the several dates of measurement is taken into account. On May 13 the non-pruned vines had made 74 per cent of the total season's length growth, while the normally and severely pruned vines had made only 23 and 12 per cent respectively. Also, by May 13 the non-pruned vines had made 90 and 95 per cent respectively as much

length growth as the normally and severely pruned vines made during the entire season.

The figures indicate a very rapid total elongation of the shoots for the non-pruned vines during April and early May. After this, the rate of growth moderates so that very little additional elongation of the shoots occurs between July 1 and the end of the growing season. On the contrary, the rate of total elongation of the shoots of the

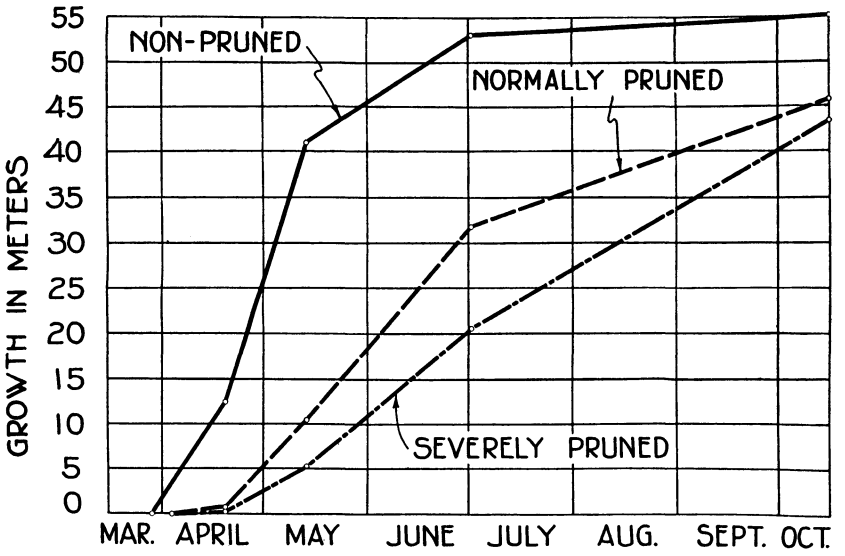


Fig. 5. The effect of pruning on the start, rate, and total length of cane growth.

severely pruned vines is very slow in April and early May. It is very rapid during the latter part of May and June and continues so with but little moderation until the end of the growing season. The growth curve for the normally pruned vines is intermediate between those of the non-pruned and those of the severely pruned vines. Yet its contour is very similar to that of the severely pruned vines.

Not only was the rate of total shoot growth greater in the non-pruned vines than in the normally pruned vines, as indicated in figure 5, but the total weight of leaves to a vine was much larger, especially during the early summer. The effect of type of pruning on the weight of leaves to a vine is shown in table 2.

The figures of table 2 show that on May 19 the non-pruned Monukka vines had produced almost five times as great a weight of leaves as the severely pruned and three times as great a weight of

TABLE 2

THE EFFECT OF TYPE OF PRUNING ON THE WEIGHT OF LEAVES TO A VINE

Variety	Date of weighings	Type of pruning and weight of leaves, in kilos		
		Severe	Normal	Non-pruned
Black Monukka	May 19, 1927	1.05	2.10	7.10
	June 18, 1927	2.70	4.50	11.60
Muscat of Alexandria	May 5, 1925	0.06	0.18	3.87
	June 24, 1925	0.85	1.54	5.97
	Oct. 15, 1925	3.06	3.47	8.80

leaves as the normally pruned vines. On June 18 the ratios of weight of leaves of the non-pruned to that of the severely and normally pruned vines was 4.30:1 and 2.58:1 respectively. The greater weight of leaves in favor of the non-pruned Muscat of Alexandria vines during May and June was even larger than that for the Monukka. The figures for the Muscat of Alexandria further show that the great advantage in total weight of leaves to a vine in favor of the non-pruned vines obtains throughout the growing season; there being two and one-half times as great a weight of leaves on the non-pruned as on the normally pruned vines, and three times as great a weight of leaves on the non-pruned as on the severely pruned vines on October 15.

The rate of growth and the total weight of leaves produced, as shown in figures 4 and 5 and table 2, clearly show that the non-pruned vines have a great advantage over the normally and severely pruned vines for the manufacture and accumulation of carbohydrates. The non-pruned vines are utilizing a smaller proportion of the available materials for shoot elongation at all stages of development, but especially during early summer, than either the normally or severely pruned vines. Then again, at all times during the growing season they have a much greater actual weight of leaves than the pruned vines, for the production of carbohydrates.

The differences in rate of growth which very markedly alter the production of leaves under the different types of pruning seem to be quite sufficient to account for the differences in the carbohydrate nutrition as indicated in figures 1, 2, and 3. These differences in rates of growth during early summer endow the non-pruned vines with a weight of leaves several times greater than that of either the normally or severely pruned vines. This is equivalent to a considerable increase in the season of leaf activity for the non-pruned vines. At the same time the growth of the non-pruned vines is exerting a smaller drain on the reserves of the dormant vines than

the less favorable growth made by the pruned vines, which, no doubt, accounts for the much higher maximum attained in the amounts of carbohydrates present in the shoots of these vines during May and June (figs. 1 and 2).

THE RELATION OF RATE OF GROWTH AND CARBOHYDRATE NUTRITION TO FRUITING

In the foregoing sections of this paper the effects of pruning on several of the carbohydrate materials and total carbohydrates present in the vine parts have been shown. It has been shown also that the effect of pruning on the rate of growth, and still more on leaf production, apparently accounts for the changes in carbohydrate nutrition. The relation of these changes in growth and nutrition to the fruiting of certain varieties of vines will now be indicated.

The Effect of Carbohydrate Nutrition on Flower Development.— In an attempt to correlate the number of leaves to a vine with the carbohydrate nutrition of its flowers and to determine the influence of this carbohydrate nutrition on flower development, the number of leaves to a vine was altered. To increase the number of leaves to a vine above that of the normally pruned vines, cane-pruning with flower-cluster removals to control the crop was employed. The excess clusters were removed about four weeks before blooming. To reduce the number of leaves to a vine below that of the normally pruned vines, defoliation was employed. All the leaves on ten normally pruned vines of Muscat of Alexandria and Monukka and four vines of Alicante Bouschet were removed two weeks before blooming. All clusters on the normally pruned vines were allowed to develop to maturity, since with this treatment crop is sufficiently controlled by the winter pruning.

At the time the first flowers on the clusters opened, samples[4] for analysis were collected. The average results for triplicate samples for reducing and total sugars, together with the percentage germination of pollen in 15 and 20 per cent sucrose media are given in table 3.

The figures of table 3 indicate a positive correlation between the number of leaves to a vine and the sugar content of the mature flowers. In the Muscat of Alexandria the amounts of reducing sugars

[4] Parts of fifteen to twenty clusters were put together for a single sample, which was weighed immediately and then plunged into boiling alcohol to which a bit of calcium carbonate had been added. The extractions and reduction were carried out the same as with the wood samples.

TABLE 3

THE EFFECT OF NUMBER OF LEAVES TO A VINE ON THE PERCENTAGE OF SUGAR PRESENT IN THE OPENING FLOWERS AND THE GERMINABILITY OF POLLEN IN MUSCAT OF ALEXANDRIA, ALICANTE BOUSCHET, AND MONUKKA

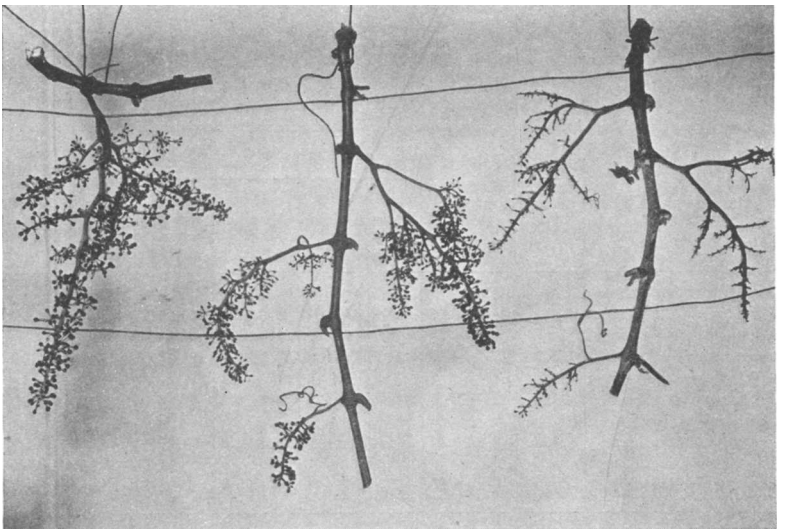
Treatment	Number of leaves to a vine		Reducing sugars, per cent*		Total sugars, per cent*		Germination of pollen, per cent	
	1927	1928	1927	1928	1927	1928	1927	1928
MUSCAT OF ALEXANDRIA								
Cane-pruned	1,700	1,950	0.80	0.97	1.50	1.67	37.0	38.0
Normally pruned	760	866	.74	.86	1.33	1.43	12.0	11.0
Defoliated	0	0	.67	.48	1.09	0.91	3.0	4.0
ALICANTE BOUSCHET								
Cane-pruned	1,650	‡	.60	.93	1.08	1.61	43.0	38.0
Normally pruned	870	‡	.46	.73	0.88	1.42	12.0	9.0
Defoliated	0	‡	0.38	0.39	0.82	0.64	1.0	3.0
MONUKKA								
Cane-pruned		3,600		0.61		1.14		46.0
Normally pruned		1,390		0.60		1.08		16.0
Defoliated		0		0.38		0.67		5.0

* Per cent of sugars on basis of the fresh weight. ‡ Leaves not counted.

present in the flowers of the normally pruned vines with leaves was 10 per cent larger than in the defoliated vines in 1927 and 80 per cent larger in 1928. The amount of total sugars in the flowers of the normally pruned vines with leaves was 22 per cent larger than in the defoliated vines in 1927 and 56 per cent larger in 1928. The amount of reducing sugars in the flowers of the cane-pruned vines was 19 per cent larger than in the defoliated vines in 1927, and 93 per cent larger in 1928; the amount of total sugars in the flowers of the cane-pruned vines was 38 per cent larger than in the defoliated vines in 1927 and 84 per cent larger in 1928. The results for Monukka and Alicante Bouschet indicate a similar condition with respect to sugar content of the mature flowers. A decrease in number of leaves to a vine was in each case accompanied by a decrease in the percentage of sugars present.

That the larger percentage of sugars present in the flowers improves their development is indicated by the figures on germinability of pollen. The pollen of the cane-pruned Muscat of Alexandria vines gave a germination of 37 and 38 per cent, that of the normally pruned vines 12 and 11 per cent, and that of the defoliated vines only 3 and 4 per cent, respectively, for 1927 and 1928. The variation in the germination of the pollen of the other varieties was similar to that of the Muscat.

A further indication of the improvement in flower development resulting from the better nutrition is shown in figure 6. This figure shows average clusters of Alicante Bouschet taken from cane-pruned, normally pruned, and defoliated vines just after the berries had set. The clusters from both the cane-pruned and normally pruned vines set a normal crop of berries. The cluster from the cane-pruned vine, however, is much longer owing to the better nutrition it had during the later stages of its development. The average length of cluster of the cane-pruned vines was $22.3 \pm .05$ centimeters, while that of the



A *B* *C*

Fig. 6. The effect of the number of leaves to a vine on the size of the clusters and the setting of the berries in Alicante Bouschet. *A*, Cane pruned, flower-cluster thinned. *B*, Normally pruned. *C*, Normally pruned, defoliated.

normally pruned vines was only $15.5 \pm .03$ centimeters. On the contrary, the clusters from the defoliated vines are shorter than those of the vines with leaves and only a few berries set. Both of these conditions may be attributed to poorer nutrition during the later stages of development of the clusters. In addition to the influence of the low percentage of sugars present in the flowers under this treatment on the development of the male parts of the flower, as shown by the germinability of pollen, there is indication that the female parts of the flower, too, are weakened. Although the pollen of these flowers was poor, there were vines with good pollen only twelve feet away which should have given these flowers, had they been susceptable to fertilization, a chance to set berries.

In the case of Monukka, not a single berry was set on the defoliated vines in either 1927 or 1928, even though their pollen gave a germination of 5 per cent. This further indicates that the female as well as the male parts of the flower are weakened by the poorer nutrition of these vines.

The Effect of Nutrition on Berry Setting and Development.— During a number of seasons data has been collected on the effect of nutrition. as influenced by the number of leaves to a vine, on the setting of the berries and further development of the clusters. The data for the seasons of 1927 and 1928 are given in table 4.

TABLE 4

THE EFFECT OF THE NUMBER OF LEAVES TO A VINE ON THE SETTING OF THE BERRIES AND THE DEVELOPMENT OF MUSCAT OF ALEXANDRIA CLUSTERS

Treatment	Leaves to a vine	Crop to a vine (kilos)	Clusters			Normal berries		Average weight of all berries, grams
			Number to a vine	Average weight, grams	Average length, cm.	Number to a cluster	Per cent of total berries	
Non-pruned, with flower-cluster thinning	3,400+	25.9±0.66	58	474±17	28.0±0.5	116±4.2	93	4.1±0.06
Cane pruned, with flower-cluster thinning	1,700	15.1±0.36	38	430±24	27.0±0.4	124±5.2	92	4.2±0.07
Normally pruned (crop limited by pruning)	760	13.7±0.57	62	211±13	20.8±0.5	45±2.6	68	3.8±0.09
Severely pruned (crop reduced by pruning)	540	8.9±0.41	44	200± 9	20.0±0.6	35±1.7	63	3.1±0.11
Normally pruned, defoliated* 2 weeks before blooming	0	5.8±0.25	53	105±11	19.0±0.4	29±2.2	52	1.8±0.07

* Leaves arising after the berries had set were allowed to develop.

The figures of table 4 show a positive correlation between number of leaves to a vine and the setting of the berries and the development of the fruit. In each of the measurements made there was a deterioration in the clusters with a decrease in the number of leaves to a vine, except in two measurements in going from the non-pruned to the cane-pruned vines. In these cases the very much larger crop of the non-pruned vines somewhat counteracted the beneficial influence of the increase in the number of leaves to a vine.

The decrease of crop below that of the non-pruned vines was 41 per cent for the cane-pruned vines, 47 per cent for the normally pruned vines, 65 per cent for the severely pruned vines, and 77 per cent for the defoliated vines. The differences in the crop of the cane-pruned and non-pruned vines and that of the vines with other treatments was primarily the result of the poorer setting of the berries on the vines with fewer or no leaves.

The effect of the several treatments on the setting of the berries is shown by the number of normal berries to a cluster. The set of normal berries to a cluster on the normally pruned vines was 175 per cent smaller than on the cane-pruned vines, and 158 per cent smaller than on the non-pruned vines. Severe pruning and defoliation two weeks before blooming reduced the number of normal berries to a cluster to 22 and 35 per cent, respectively, below that of the normally pruned vines.

Accompanying the decrease in the number of normal berries to a cluster, as the number of leaves to a vine became less, there was a decrease in both the weight of cluster and the percentage of normal berries to a cluster. The clusters of the normally pruned vines weighed 104 per cent less than those of the cane-pruned vines, and 125 per cent less than those of the non-pruned vines. Severe pruning and defoliation reduced the weight of clusters below that of the clusters of the normally pruned vines by 5 and 50 per cent respectively. The percentage of normal berries to a cluster was reduced by a decrease in the number of leaves to a vine in a similar manner to weight of cluster, the magnitude of the reduction being somewhat less.

The clusters of the cane-pruned and non-pruned vines were 35 and 40 per cent, respectively, longer than those of the normally pruned vines. Severe pruning and defoliation have had little or no effect on length of cluster. This might be expected with defoliation, since the clusters attain their full length before the flowers are mature or before blooming, and hence before the leaves were removed from the vines which were defoliated.

Despite the smaller crop and small number of berries to a cluster, there was a decrease in the average weight of berry with each decrease in the number of leaves to a vine. The berries of the cane-pruned and non-pruned vines were 10.5 and 8 per cent, respectively, heavier than those of the normally pruned vines, and severe pruning and defoliation reduced the weight of berry under that of normal pruning by 18.4 and 52 per cent respectively.

The beneficial influence of a large number of leaves to a vine on the size of cluster and the development of the berries on Muscat of Alexandria is further shown in figures 7, 8, and 9. As indicated in figures 7*A* and 8, the clusters of the cane-pruned vines are well filled with normal berries of uniform size. Figures 7*B* and 9 show that the clusters of the normally pruned vines are affected by coulure and that the berries are irregular in size, there being a considerable number of shot berries on each cluster. The cluster from the defoliated vines

fig. 7*C* coulured badly and show an increased tendency to *millerandage*—the setting of small seedless (shot) berries. On these latter clusters the normally seeded berries are also small.

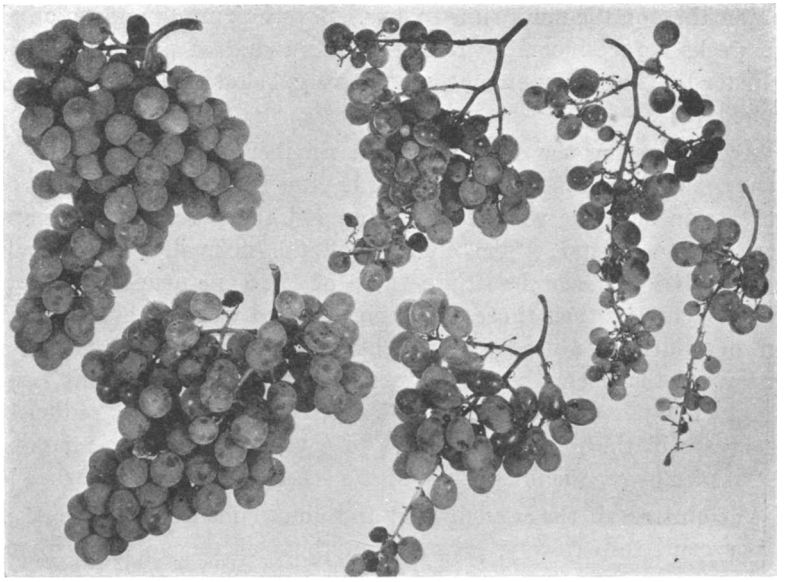


Fig. 7. The effect of the number of leaves to a vine on the size of cluster and the setting and development of the berries of Muscat of Alexandria. *A*, Cane-pruned, flower-cluster thinned. *B*, Normally pruned. *C*, Normally pruned, defoliated.

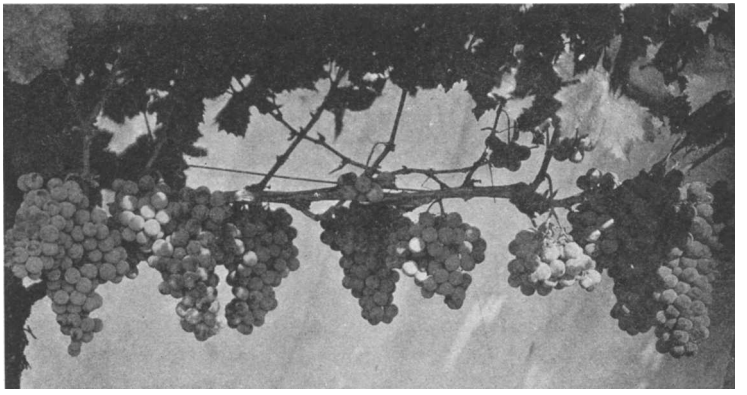


Fig. 8. An excellent crop of fruit on a single cane of a Muscat of Alexandria vine that was cane-pruned and on which the crop was controlled by flower-cluster thinning.

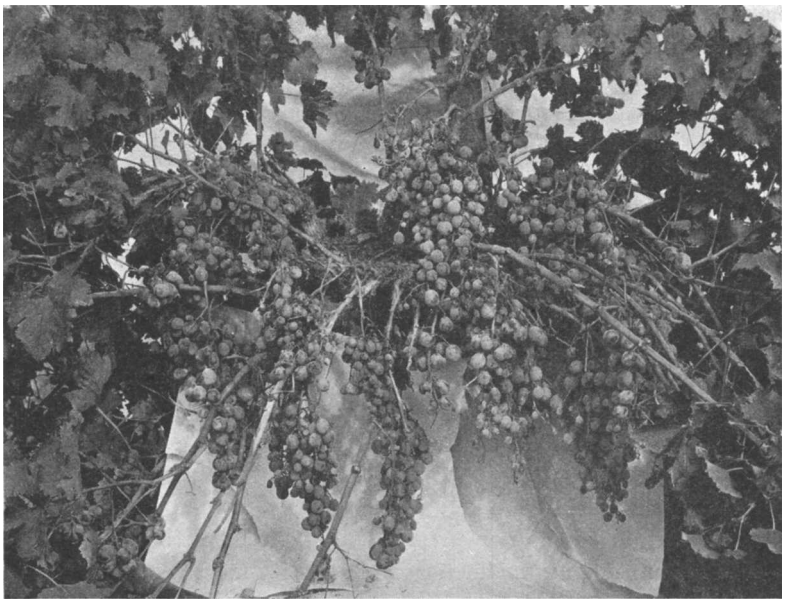


Fig. 9. The crop of a representative Muscat of Alexandria vine that was normally pruned.

SUMMARY

With Decreased Pruning the Amount of Carbohydrates Increases.— In the normal seasonal changes of the total carbohydrates of the vine there are two maxima and two minima. One of the maxima occurs in the dormant season and the other occurs during early summer.

With a decrease in pruning the amounts of total carbohydrates present were increased at each maximum, the percentage increase being greater at the maximum in early summer. The severely pruned vines failed to show a maximum in the seasonal trend of carbohydrates during early summer.

The larger amount of carbohydrates present during early summer with decreased pruning is primarily if not solely confined to the carbohydrates in solution—sugars. The amount of reducing sugars in the non-pruned vines of Muscat of Alexandria was 52 per cent larger than in the normally pruned vines on June 3, and the amount of total sugars 51 per cent larger.

The effect of pruning on the amounts of carbohydrates present during early summer was most pronounced in the shoots. The

amounts of these materials present in the trunk and in the roots were influenced very little.

With Decreased Pruning the Growth is more Favorable to the Production and Accumulation of Carbohydrates.—The non-pruned vines contain three or four times as much reducing sugars and total carbohydrates at the beginning of the growing season than the normally pruned vines.

During early summer, the ratio of weight of shoot growth to weight of vine at the beginning of the growing season is much greater for the severely and normally pruned vines than for the non-pruned vines, while the ratio of weight of leaves to shoots is much less for the severely and normally pruned than for the non-pruned vines.

Total shoot elongation proceeds much more rapidly in the early growing season on the non-pruned than on the severely or normally pruned vines. During late May and June when the rate of total shoot elongation of the severely and normally pruned vines is increasing rapidly, that of the non-pruned vines is moderating. After July 1 the non-pruned vines make very little additional shoot growth, while the shoots of the severely and normally pruned vines continue rapid growth for most of the season.

The difference in rate of total shoot elongation during early summer supplies the non-pruned vines with a weight of leaves several times greater than that of either the severely or normally pruned vines. This is equivalent to a considerable increase in the season of leaf activity for the non-pruned vines.

With Decreased Pruning the Rates of Growth and of Carbohydrate Nutrition are more Favorable to Fruiting.—Increases in number of leaves, especially during early summer, increased the percentages of reducing sugars in the mature flowers. In Muscat of Alexandria the amounts of reducing sugars in the flowers of the normally pruned vines with leaves was from 10 to 80 per cent larger than in the defoliated vines and the amount of total sugars 22 to 56 per cent larger. The amounts were still larger in the cane-pruned vines. The results with Monukka and Alicante Bouschet indicate a similar relation of leaves to increased sugar content of the mature flowers.

Accompanying the increase in the sugar content of the mature flowers there was a very marked increase in germinability of pollen. The germinability of the Muscat of Alexandria pollen was 3 and 4 per cent on the defoliated, 12 and 11 per cent on the normally pruned vines with leaves, and 37 and 38 per cent on the cane-pruned vines, respectively, during 1927 and 1928.

The figures on germinability of pollen indicate a positive correlation between carbohydrate nutrition and the development of the male parts of the flower. Figures on the setting of the berries show a similar correlation between carbohydrate nutrition and the development of the female parts of the flowers.

A decrease in the number of leaves to a vine (see table 4) has been accompanied by a smaller capacity for production, by a decrease in weight of cluster, a decrease in the number of normal berries to a cluster, a decrease in percentage of normal berries to a cluster, a decrease in the length of cluster, and a decrease in the weight of berry. There was, moreover, a great increase in the tendency to coulure in each of the varieties used, and to *millerandage,* especially in the Muscat of Alexandria.

LITERATURE CITED

[1] SHAFFER, P. A., and A. F. HARTMAN.
1920. The iodometric determination and its use in sugar analysis. Jour. Bio. Chem. **45**:349–390.

[2] WINKLER, A. J.
1926. Some responses of *Vitis vinifera* to pruning. Hilgardia **1**:526–543.

[3] WINKLER, A. J.
1926. The influence of pruning on the germinability of pollen and the set of berries in *Vitis vinifera.* Hilgardia **2**:107–124.

[4] WINKLER, A. J.
1927. Improving the fruiting of the Muscat of Alexandria by less severe pruning. Proc. Amer. Soc. Hort. Sci. **24**:157–163.

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. R. Hoagland and J. C. Martin. July, 1923.

9. Experiments on the Reclamation of Alkali Soils by Leaching with Water and Gypsum, by P. L. Hibbard. August, 1923.

10. The Seasonal Variation of the Soil Moisture in a Walnut Grove in Relation to Hygroscopic Coefficient, by L. D. Batchelor and H. S. Reed. September, 1923.

11. Studies on the Effects of Sodium, Potassium, and Calcium on Young Orange Trees, by H. S. Reed and A. R. C. Haas. October, 1923.

12. The Effect of the Plant on the Reaction of the Culture Solution, by D. R. Hoagland. November, 1923.

13. Some Mutual Effects on Soil and Plant Induced by Added Solutes, by John S. Burd and J. C. Martin. December, 1923.

14. The Respiration of Potato Tubers in Relation to the Occurrence of Blackheart, by J. P. Bennett and E. T. Bartholomew. January, 1924.

15. Replaceable Bases in Soils, by Walter P. Kelley and S. Melvin Brown. February, 1924.

16. The Moisture Equivalent as Influenced by the Amount of Soil Used in its Determination, by F. J. Veihmeyer, O. W. Israelsen and J. P. Conrad. September, 1924.

17. Nutrient and Toxic Effects of Certain Ions on Citrus and Walnut Trees with Especial Reference to the Concentration and Ph of the Medium, by H. S. Reed and A. R. C. Haas. October, 1924.

18. Factors Influencing the Rate of Germination of Seed of Asparagus Officinalis, by H. A. Borthwick. March, 1925.

19. The Relation of the Subcutaneous Administration of Living Bacterium abortum to the Immunity and Carrier Problem of Bovine Infectious Abortion, by George H. Hart and Jacob Traum. April, 1925.

20. A Study of the Conductive Tissues in Shoots of the Bartlett Pear and the Relationship of Food Movement to Dominance of the Apical Buds, by Frank E. Gardner. April, 1925.