GROWTH AND SAP CONCENTRATION [1]

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Chandler (*1*)[3] found that trees making rapid growth had lower sap concentration and that slower growth of the tree was accompanied by higher concentration. Trees which made rapid growth as a result of severe pruning in the preceding winter had a lower concentration of sap than trees which had been lightly pruned. During the summer season the concentration of the cell sap was lowest near the ground and highest in the upper part of the tree. Although Chandler's method of preparing the samples for freezing-point determinations has been adversely criticized, one must acknowledge the advance he made in our knowledge of sap concentrations in fruit trees.

Dixon and Atkins (*3*) observed that the sap of young leaves of various plants had, as a rule, a lower osmotic pressure than sap from mature leaves.

Lutman (*10*) has determined the freezing-point depressions of the sap of the potato plant with reference to its growth cycles. The variations of concentration seem to be related to the development and rate of growth of the plant.

The seed tubers when taken from storage had a relatively high osmotic pressure, but as water was absorbed the osmotic pressure dropped. As the age of the plant increases its osmotic pressure increases on account of the accumulation of inorganic salts in its cells; but when senility begins, the osmotic pressure drops, because of the loss of soluble materials. In the young plant the leaf sap is more concentrated than the stalk sap, but after the flower buds are put out and the tubers begin to grow, the stalk sap is more concentrated. With the advent of cool, rainy weather later in the season the leaves begin to grow again and their sap concentration is greater than that of the stalks. Shading the potato plant diminishes the osmotic pressure of the leaves and stalk.

Synopses of the earlier literature dealing with cryoscopic methods and with the relation of the physical environment to the concentration of the cell sap will be found in the summaries prepared by Dixon (*2*), Hibbard and Harrington (*7*), and Harris and Lawrence (*5*).

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[1] Paper No. 71, University of California, Graduate School of Tropical Agriculture and Citrus Experiment station, Riverside, Calif.

[2] It is a pleasure to acknowledge the aid which has been rendered by those associated with the progress of this work. The author's thanks are due to Messrs. L. C. Masters, R. H. Holland, and F. F. Halma.

[3] Reference is made by number (italic) to "Literature cited," p. 98.

METHODS OF EXPERIMENT

The methods of preparing and examining the material have been adapted to the needs of the work here reported. As the work of making several hundred determinations progressed, a routine procedure was followed which stabilized, if it did not remove, the sources of error. The chief object of this work has been to study comparative concentration of sap as related to the growth rate. The results obtained, though not free from error, are comparable with each other and give a satisfactory picture of an important physiological relation.

The plant material was collected in the field and packed at once in a tight container. For small samples, the container was a quart fruit jar with a screw top. For large samples, especially constructed steel cylinders, 6 inches in diameter by 14 inch tall, were used. The open end of the cylinder was provided with an accurately fitting metal cap and rubber gasket. The cap could be drawn down tightly on the rubber gasket by means of three bolts, and the cylinder was thus effectively sealed.

The samples were always collected between 9 and 10 o'clock in the forenoon, in order to avoid the possibility of diurnal fluctuations in concentration. As soon as filled, the containers were brought to the laboratory and packed in an ice-salt mixture for the preliminary freezing which killed the protoplasm and increased the permeability of the material. The supply of ice and salt was renewed as occasion required. The containers remained in this mixture for 18 to 24 hours, to insure complete freezing of the material. When the containers were removed they were washed to remove all adhering brine and wiped dry. The material was removed and ground in a small hand mill and then pressed in a strong screw press. Not more than 20 minutes were required to grind a sample and express the sap. The mill and press were heavily tinned, and there was no apparent corrosive action of the plant juices on any part of them after continued use.

The expressed sap was received in small bottles which were closed with rubber stoppers and placed on ice, in case the sap was not to be immediately used. Samples which had stood for more than two or three hours were discarded. In spite of these precautions, there was some oxidation of the plant saps and probable change in concentration; but the error, if any, due to such changes was shared to approximately the same extent by all samples and is not believed to vitiate the results.

The freezing point of the sap was determined in the usual freezing apparatus with the use of a Beckmann thermometer. At least two determinations were made upon each sample, and the average of closely agreeing duplicates was taken as the freezing point. The osmotic pressures were calculated by the method given by Harris and Gortner (*4*).

The rate of growth of the trees was obtained by measuring the length of certain selected shoots at intervals of seven days. Each shoot bore a numbered tag and was marked near the base with a line of India ink. The distance from the basal ink mark to the tip of the shoot was easily determined and recorded for each shoot.

GROWTH INCREMENTS AND SAP CONCENTRATION OF YOUNG WALNUT TREES

Determinations on the concentration of the cell sap of young walnut trees (*Juglans* spp.) were made at frequent intervals and compared with the increments in mean height of similar trees growing in the same rows. The measurements given in Table I were made upon a population of *J. regia* trees, of which the majority were propagated upon *J. nigra* rootstocks and the remainder on a variety of *J. regia* known as "Hardshell." The trees from which the material for investigation was taken were in their second season's growth. They stood in the nursery row in a fertile soil and were artificially irrigated. The first samples for determinations were taken June 8 and the last on November 12.

The growth rate of a portion of this group of walnut trees has been discussed in a recent publication (*12*) and has been shown to follow the course of autocatalytic reactions.

TABLE I.—*Mean growth increments and concentration of cell sap of walnut trees*

Date.	Mean height.	Increment of growth during preceding week.	Osmotic pressure of cell sap.
	Cm.	*Cm.*	*Atmospheres.*
June 12	62.6	12.6	16.5
19	66.6	4.0	13.5
26	73.7	7.1	18.4
July 4	87.2	13.5	9.7
11	100 8	13.6	11.4
23	125.9	[b] 15.0	10.4
30	136.7	10.8	10.8
Aug. 6	147.6	10.9	....
13	153.4	5.8	17.8
20	[a] 160.9	[a] 7.5	....
27	168.4	[a] 7.5	12.5
Sept. 4	176.7	8.3	9.2
10	184.2	[b] 8.7	8.9
17	188.1	3.9	10.2
24	191.3	3.2	18.8
Oct. 1	194.6	3.3	11.7
8	196.8	2.2	20.9
15	199.0	2.2	13.2
22	199.7	0.7	17.1
29	201.2	1.5	13.5
Nov. 5	201.2	0.0	24.4

[a] Interpolated values. [b] Calculated to 7-day basis.

The samples collected for freezing-point determinations always consisted of the total growth of a shoot of that particular season (*ab initio*) and included both stems and leaves. Toward the end of the growing season the stems were large and woody; nevertheless they were ground in the handmill and pressed like the other material. Most of the sap so obtained came undoubtedly from the cortical layers of the stems.

By referring to Table I the reader will see the nature of the results obtained in this work. The table shows the mean height of the trees (from the basal ink mark), the height increment from the preceding measurement, and the concentration of the cell sap expressed in atmospheres of osmotic pressure. The mean height increased from 62 cm. on June 12 to 201.2 cm. on October 29. The increments (calculated in each case to a 7-day basis) were far from uniform, ranging as they do from 0.7 cm. to 15 cm. The atmospheres of osmotic pressure of expressed

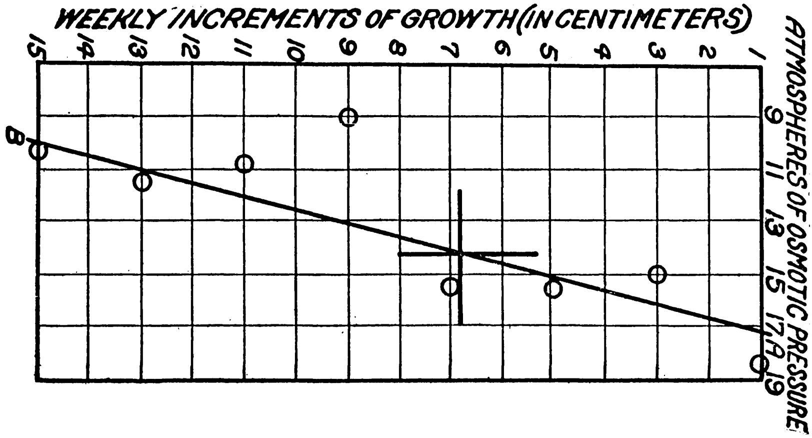

FIG. 1.—Graph showing regression of osmotic pressure on growth increments of walnut trees.

sap range from 8.9 to 24.4. Thus it will be seen that there are periodic variations in the concentration of the cell sap and in the growth rate from week to week during the season. The maximum growth rate was observed during certain weeks in July, and the maximum osmotic pressure of the cell sap was observed near the end of the growing season.

It is somewhat difficult to get a comprehensive idea of the relationship between growth and sap concentration from the array of figures given in Table I. It will be better to investigate the nature and amount of the mathematical correlation between the two sets of values. There are 19 observations in which both the increments and sap concentration were determined. While this number is rather scanty for determining correlation, the regression is remarkably linear (fig. 1), and it is believed that the correlation coefficient is trustworthy. The coefficient of correlation between the two variables is -0.557 ± 0.113. The negative correlation shows that when growth is rapid the sap concentration is lower and when growth is slower the sap concentration is higher.

These conclusions may be verified by inspection of the figures in Table I. For example, an increment of 15 cm. in the week ending July 23 coincided with a sap concentration of 10.4 atmospheres, while smaller increments coincided usually with higher sap concentrations. The small growth increments in the latter part of the season are accompanied by the highest concentrations of plant sap. The concentration of solutes in the sap tends to increase with age of the leaf, as Dixon and Atkins (*3*) discovered in the study of Ilex.

GROWTH INCREMENTS AND SAP CONCENTRATION OF YOUNG APRICOT TREES (1918)

The question of sap concentration in shoots of young apricot trees in relation to growth was also investigated. The trees from which the material was obtained had been growing in the orchard two years when these studies were started. Soon after the season's growth began, 70 young shoots were selected and marked with labels. An India ink mark was made near the base of each shoot, from which length measurements were made at intervals of seven days. At the time of making the measurements here recorded a sample of shoots was collected from adjacent trees, and these samples were used for determining the sap concentration. The samples consisted of entire shoots of that particular season's growth. The stems and leaves were ground together, and the sap was expressed. The samples were given a preliminary freezing and were treated essentially as the walnut samples were treated.

The growth and sap concentration determinations made in 1918 upon apricot shoots are given in Table II. It will be noted that where the intervals were not exactly seven days the increments were calculated to a 7-day basis in order to make them comparable. It will be noted that the rate of growth was greatest at the outset of the observations and diminished with several fluctuations to the end of the growing season. Certain dynamical aspects of this growth rate have been discussed in a separate paper (*11*) though the studies there related were based upon another set of measurements.

The concentration of the cell sap (expressed in atmospheres of osmotic pressure), although subject to some fluctuation, increased as the season advanced. The lowest concentration was observed on May 21 and the highest on October 31. The average osmotic pressure, expressed in atmospheres by months, is: May, 11.84; June, 13.66; July, 14.34; August, 15.04; September, 15.18; October, 16.48. Table II shows that the concentration of the sap, which was 12.71 atmospheies on May 2, fell to 10.87 in the next three weeks, simultaneously with rapid elongation of the shoots. The concentration at once began to rise and went up, with some irregularities, to 18.90 atmospheres on October 31.

TABLE II.—*Mean growth increments of shoots and concentration of sap of apricot trees (1918)*

Date.	Mean length.	Increment of growth during preceding week.	Osmotic pressure of cell sap.
	Cm.	*Cm.*	*Atmospheres.*
May 2	45.0	19.0	12.71
8	60.6	[b] 18.2	11.68
15	74.1	13.5	11.99
21	83.9	[b] 11.4	10.87
29	92.4	[b] 7.4	11.95
June 7	103.9	[b] 9.0	12.30
12	105.9	[b] 2.8	14.96
19	108.5	2.6	13.52
26	113.0	4.5	13.86
July 3	122.6	[b] 8.4	13.66
10	134.2	11.6	14.24
17	143.3	9.1	16.05
24	148.0	4.7	15.28
31	155.1	7.1	12.47
Aug. 7	162.2	7.1	14.87
14	167.4	5.2	14.88
21	170.0	2.6	15.17
28	173.9	3.9	15.28
Sept. 5	[a] 184.2	[b] 9.1	15.54
12	189.3	5.1	16.42
19	192.3	3.0	13.46
26	196.7	4.4	15.30
Oct. 3	199.3	2.6	15.64
9	201.0	[b] 2.0	14.52
16	203.2	2.2	14.99
23	204.6	1.4	18.36
31	206.8	[b] 1.9	18.90
Nov. 6	207.3	.5	17.66

[a] Interpolated value. [b] Calculated to 7-day basis.

The degree of association between the amount of growth in a week and the concentration of the cell sap at the end of that week is more succinctly expressed by the coefficient of correlation, which was found to be

$$r = -0.613 \pm 0.079.$$

This coefficient is of sufficient magnitude to express a strong negative correlation between growth and sap concentration. The regression of the two variables is approximately linear (fig. 2), though there is a marked tendency for the points to scatter. These determinations are based on 28 observations, however, and are regarded as somewhat more reliable than those for the walnut trees.

These observations, made at frequent intervals throughout a growing season, show that rapid growth is marked by a lower sap concentration and vice versa. In material of this kind, the concentration of the cell sap is probably due mostly to sugars and other organic compounds.

EFFECT OF PRUNING UPON SAP CONCENTRATION

The results obtained from determinations on the walnut and apricot trees are interesting and seem conclusive so far as they go, but they raise other questions which seem worthy of study.

In pursuance of these inquiries, determinations were made on the same block of apricot trees throughout the season of 1919. The growth and sap concentration were determined on two lots of trees, one of which is heavily pruned each winter while the other is not pruned at all. Needless to say, the growth of individual shoots on the heavily pruned tree, was much greater than that of shoots on the unpruned trees.

The mean length of shoots was determined at weekly intervals, as before. In the beginning, 50 shoots were selected on each lot of trees,

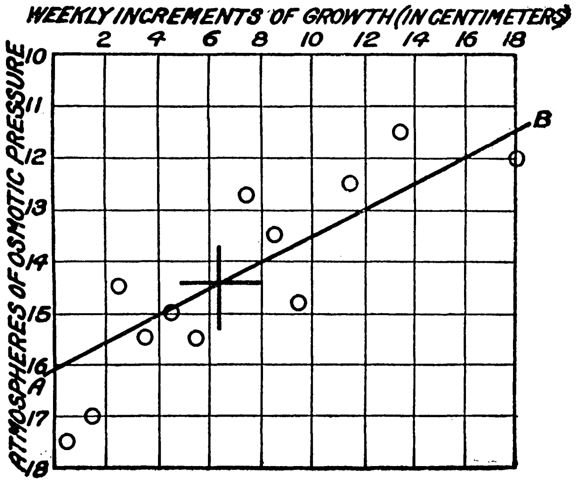

FIG. 2.—Graph showing regression of osmotic pressure on growth increments of apricot trees (1918).

but, as a result of breakage and other accidents, a number had to be eliminated. The computations are based on 33 shoots on the unpruned trees and on 28 shoots on the heavily pruned trees. The evaporating power of the air was determined by the evaporation of distilled water from a white, spherical atmometer bulb supported on a stand 5 feet from the ground in the center of the orchard. The average daily temperature was taken from the Riverside official reports, which were obtained from standard instruments located about 2 miles distant. The soil moisture was determined from composite samples taken to a depth of 3 feet throughout the area occupied by the trees in question. The sap concentration was determined by the depression of the freezing point.

A summary of the several factors is shown in Table III.

TABLE III.—*Growth and sap concentration of pruned and unpruned apricot trees (1919), with comparison of three environmental factors*

Date.	Time.	Evaporation.		Mean daily temperature.	Water added.[a]	Soil moisture.	Shoots on pruned trees.			Shoots on unpruned trees.		
		Per week.	Per day.				Mean length.	Increment of growth during preceding week.	Osmotic pressure.	Mean length.	Increment of growth during preceding week.	Osmotic pressure.
	Days.	*Cc.*	*Cc.*	*° F.*	*Acre-inches.*	*Per cent.*	*Cm.*	*Cm.*	*Atmospheres.*	*Cm.*	*Cm.*	*Atmospheres.*
Apr. 9							13			9		
16	7	350	50	62			37	24	13.82	17	8	14.49
23	14	427	61	64			60	23	13.52	25	8	13.61
30	21	185	26	57	r 0.82		73	13	11.72	29	4	13.41
May 7	28	192	27	61	i 3.40		88	15	11.00	34	5	14.52
14	35	267	38	65			102	14	11.38	42	8	13.90
21	42	246	35	65	r .72	9.18	113	11	11.60	50	8	15.19
28	49	155	22	67		9.43	121	8	12.75	57	7	13.97
June 4	56	508	72	73		8.56	132	11	13.01	63	6	14.57
11	63	455	65	72		8.39	142	10	13.82	68	5	16.73
17	69	366	61	69		8.17	148	6	15.27	71	3	17.43
25	77	808	101	81		7.53	156	8	14.76	77	6	15.94
July 2	84	447	64	73		6.78	163	7	16.60	79	2	17.88
9	91	595	85	75		5.60	174	11		82	3	
16	98	501	72	78			177	3	15.87	83	1	19.77
23	105			75	i 2.70		182	5	15.77	84	1	20.96
30	112			79		7.22	186	4	18.51	85	1	21.81
Aug. 6	119			69		6.02	190	4	14.09	86	1	17.14
13	126	496	71	76			194	4		87	1	
20	133	483	69	79	i 2.81	5.48	197	3	16.38	88	1	19.50
27	140	334	48	77		7.52	200	3	18.58	89	1	22.04
Sept. 3	147	263	38	74		6.05	203	3	17.03	90	1	16.16
24	168	350	50	74	i 2.62		208	2	19.66	94	1	21.94
Oct. 1	175				r 1.37							
8	182	260	37	72		5.92	210	1	22.73	94	0	19.40
13					i 3.80							
21	195			73		6.66						

[a] r=rain.
i=irrigation water.

The evaporation rate was at a maximum in June and July. During May the prevailing weather was cloudy, and the evaporation rate was thereby diminished. The mean monthly temperatures were as follows: April, 61° F.; May, 65°; June, 74°; July, 76°; August, 75°; and September, 74°.

The soil moisture diminished in quantity as the season advanced, in spite of the irrigations. The June irrigation was omitted on account of the ripening fruit. The figures show how the moisture content of the soil rose after each application of water.

The growth of the selected shoots on the pruned and on the unpruned trees was most rapid in the early part of the season. There were more or less distinct cycles of growth in each case, though they were more evident in the case of the heavily pruned trees. The increments in mean length are reduced to a 7-day basis. The mean growing season was approximately the same for each class of shoots, although the rate of growth of the unpruned shoots was very slow after the middle of July. Certain dynamical features of the growth rate of these trees have been described in another paper (*13*) and will not be discussed here.

The concentration of the cell sap of the two classes of shoots fell off somewhat after the observations were started, then rose, although fluctuating, toward the end of the growing season. The concentration of the sap of the slower shoots on the unpruned trees was generally higher during the season than that of the rapidly growing shoots on the heavily pruned trees, although at the end of the season the sap of the two classes was substantially similar in concentration. Thus, both comparisons show that a higher concentration of cell sap is found in slower growing shoots.

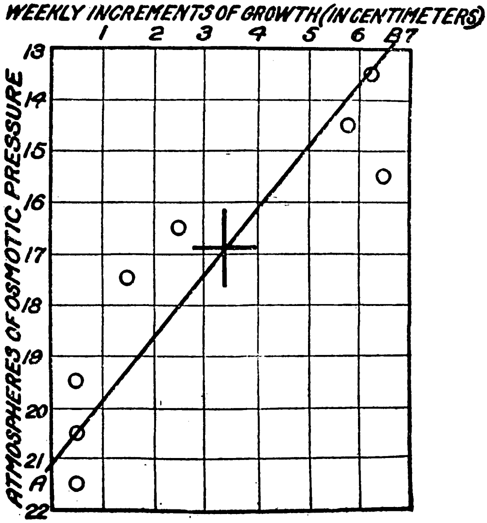

FIG. 3.—Graph showing regression of osmotic pressure on growth increments of unpruned apricot trees (1919).

In order to measure the association between growth and sap concentration I shall employ the correlation coefficient.

The correlation between concentration of cell sap and increment in length is

I. . . . . $r = -0.628 \pm 0.088$ for heavily pruned trees.
II. . . . . $r = -0.823 \pm 0.049$ for unpruned trees.

Reference to figures 3 and 4 shows that regression in the pruned trees is fairly linear, but in the unpruned trees this linearity is doubtful. In the latter case, the significance of the correlation coefficient may be more apparent than real.

It will be readily recognized that factors which contribute to the higher sap concentration of the unpruned trees are associated with the nature of the growth they made. Their slower growth and consequent diminished draft on the plastic materials of the tree should allow a greater accumulation of soluble materials in their tissues. The smaller water content of the slow-growing wood also contributes to a higher concentration in the sap.

The increased concentration of soluble materials in the sap of both classes of trees as the season advanced is to be referred in part to the foregoing factors and in part to the increase in soluble organic products of photosynthetic activity. With the increase in leaf area and the advance of the season there should be an increase in the content of soluble carbohydrates in the cell sap.

The water content of the soil has an important influence upon sap concentration of the plant (compare Hibbard and Harrington, 7). There are numerous instances to be seen in the table where the sap concentration fell after the application of irrigation water; but it will be noticed that the drop in sap concentration was not evident until, in some cases,

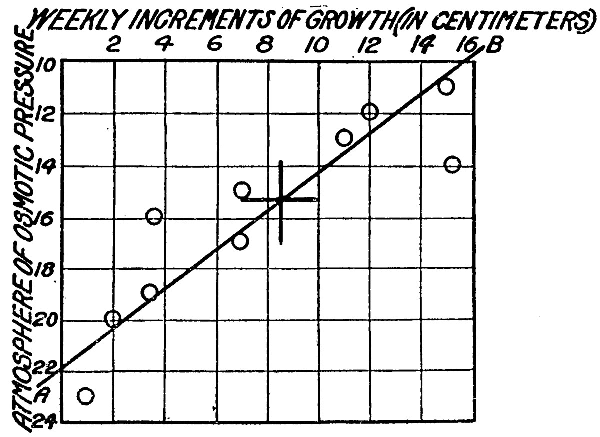

FIG. 4.—Graph showing regression of osmotic pressure on growth increments of pruned apricot trees (1919).

one or two weeks after the application of water. As the season advanced the amount of water in the soil gradually diminished, in spite of the irrigation, and there is little doubt that the gradually diminishing water supply is to some extent causally related to the gradually increasing concentration of the plant sap through the season. It is difficult to express the relationship by a correlation coefficient because the regression between the two pairs of values is not linear. After a certain moisture content (say that of saturation) is reached, a further addition of water would have no effect on the sap concentration of the tree. It may not, however, be entirely improper to attempt to express the relationship as a coefficient of partial correlation. This figure will express the relationship between growth increments and sap concentration, assuming the soil moisture to have been constant. In the case of the heavily pruned trees,

$$r_{ip \cdot w} = -0.525.$$

Taking account of the moisture factor thus reduces the coefficient from −0.628 to −0.525.

SAP CONCENTRATION IN APICAL AND BASAL REGIONS OF APRICOT SHOOTS

Determinations of sap concentration were made at weekly intervals between June 12 and December 4 in the leaves and stems of a 10-cm. zone at both base and apex of apricot shoots. The concentration, as determined by the lowering of the freezing point, is shown graphically in figure 5.

It will be seen that the sap in the apical portion of the stem was more concentrated than that in the basal region. Increases or decreases in the

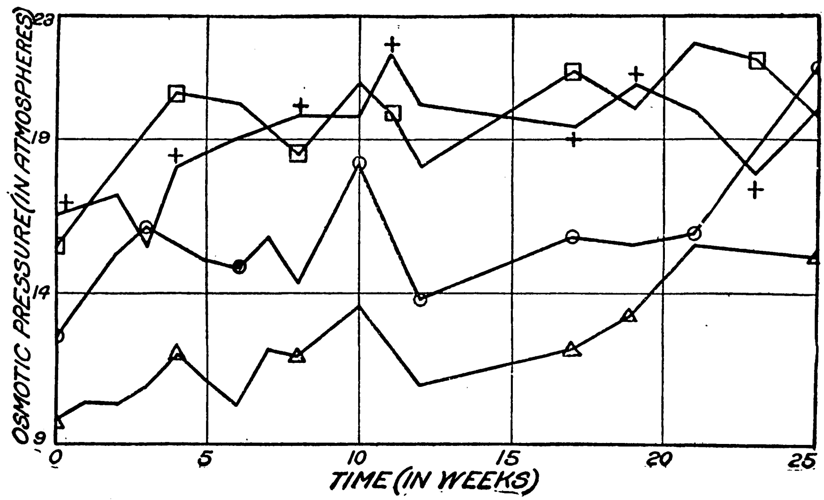

FIG. 5.—Graph showing seasonal variations in sap concentration in apricot shoots.
○=sap concentration of apical 10 cm. of stems.
△=sap concentration of basal 10 cm. of stems.
□=sap concentration of leaves from 10-cm. zone at apex.
+=sap concentration of leaves from 10-cm. zone at base.

one are approximately parallel to increases or decreases in the other. The greater divergence in the last observations is probably due to the dry condition of the samples and to the possibility of error in one or both determinations. In general, the differences between results were sufficiently great to indicate differences well outside the realm of experimental error.

The sap concentrations of the leaves from the different regions show no wide nor consistent differences, though there is a tendency for them to vary in opposite directions—that is, when one rises the other falls, and vice versa. In general, the sap concentration of the leaves was well above that of the stems at corresponding periods, a relation which was pointed out by Heald (*6*).

TABLE IV.—*Mean and root-mean-square deviations of sap concentration in apical and basal regions of apricot shoots*

Part of shoot.	Mean sap concentration.	Root-mean-square deviation.
	Atmospheres.	*Atmospheres.*
Stem, apical	15.83	2.06
Stem, basal	12.59	2.77
Leaves, apical	19.59	1.74
Leaves, basal	18.93	1.68

The mean sap concentrations, shown in Table IV, bear out the facts represented by the graphs. The sap concentration at the apical end of the shoot was higher in both stem and leaf, although there is very little difference in the leaves at the opposite ends of the shoot.

The root-mean-square deviations show that the sap concentration of the stem had a greater tendency to fluctuate about its mean value than that of the leaf. This may be taken to indicate that the sap concentration of the leaves tends to maintain an equilibrium which is not easily disturbed by fluctuations in the environment. The variation in the sap concentrations of the leaves from the middle of July on to the end of the season is within the range of experimental error. Other investigators have found that the young leaves on a plant had a lower sap concentration than the older leaves. A similar condition may exist in the apricot tree, but it would require that one should carefully select the leaves in order to demonstrate it. At the time the foregoing determinations were begun on the apricots, the shoots had made two-thirds of their growth for that season.

It thus appears that there is a gradual increase in concentration of sap from the base to the apex of a growing shoot.

There is, in some quarters, a belief that the apical leaves on young shoots are meagerly supplied with solutes and that the practice of removing the terminal half of the young shoots is justifiable at any time after mid-summer. The determinations made upon these apricot shoots seem to speak against such a belief. From the middle of the summer to the first of December there was little real difference in the sap concentration of the leaves at opposite ends of the new shoots.

The existence of a gradient in the sap concentration of apricot shoots was shown by determinations made on June 10, 1920, using a sample of young shoots having an approximate length of 120 cm. The leaves were removed and the stems were cut into four lengths of 30 cm. each. The sets were designated as A, B, C, and D. A designated the apical set of cuttings and D the basal set.

Sap-concentration determinations were made upon each of these samples separately. The concentrations expressed as atmospheres of osmotic pressure were as follows:

A	13.19
B	11.81
C	10.97
D	10.32

CONCENTRATION OF SAP IN ORANGE SHOOTS AND LEAVES

The leaves of the orange tree persist for more than one year. New shoots commonly arise from axillary buds and may attain considerable length before the subtending leaf falls. Determinations were made of the sap concentration in new shoots of the Washington Navel orange and of the old leaves subtending them. The leaves had grown to maturity in the summer preceding the appearance of the shoots and might be supposed to have some physiological relation to their axillary shoots.

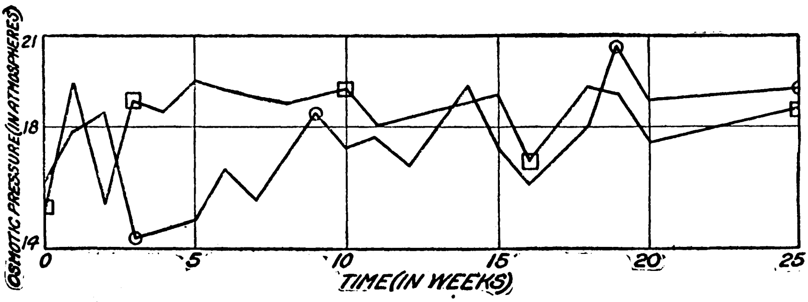

Fig. 6.—Graph showing seasonal changes in sap concentration in orange shoots and their subtending leaves.
○=sap concentration of young shoots.
□—sap concentration of the subtending leaves.

There was, however, no general relationship indicated by the sap concentration of the two members. Figure 6 represents graphically the changes in sap concentration of leaves and their axillary shoots from April 15 to October 9. During the first few weeks the sap concentration of the stem appeared to fluctuate and reached the low point for the season about May 1. From May until October there was a general tendency for the sap concentration to rise, though not to so marked a degree as was seen in the apricot. Throughout most of the summer the concentration of the leaf sap was greater than that of the shoot sap. The mean of the determinations of the leaf sap was 18.4 atmospheres and of the shoot sap 17.3 atmospheres.

The root-mean-square deviation of a series of values from their mean, as stated above, is an excellent measure of their dispersion. In this case the root-mean-square deviation of the leaf-sap concentration is 1.21 atmospheres and that of the shoot sap is 1.64 atmospheres. This shows that the concentration of sap in the leaves was subject to slightly less fluctuation during the period of the observations than that of the shoots. In all cases these leaves were not more than 1 year old and were performing the functions common to orange leaves of their age. It seems difficult to escape the conclusion that in some way the concentration of solutes in the leaves tends to reach and maintain an equilibrium, and that this equilibration occurs regardless of the variations in concentration which simultaneously take place in the adjacent shoots.

CONCENTRATION OF THE SAP IN VARIOUS LAYERS OF THE APRICOT SHOOTS

The following osmotic pressures were found in a sample collected on June 27: mature leaves, 17.12 atmospheres; cortical layers of the stem, 13.82 atmospheres; woody, subcortical layers, 10.21 atmospheres. These figures indicate that the sap of the wood is less concentrated than that of the leaves and are in entire agreement with those previously obtained. They show quite remarkable differences in the sap concentration of the different layers of the stem. The cortical layers (including the phloem) undoubtedly owe their higher concentration to their content of plastic organic substances. Although subject to variation, these relations might be expected to hold throughout the season.

SAP CONCENTRATION OF THE APRICOT TREE AFTER GROWTH CEASES

It is well known that during the progress of "ripening" the woody tissues are the seat of changes involving the translocation and deposition of many kinds of compounds. A series of determinations was made after the shoots on these trees ceased to show further elongation to see whether there were appreciable changes in sap concentration in the early part of the dormant period.

TABLE V.—*Sap concentration of apircot shoots during fall and early winter*

Date.	Osmotic pressure.	
	Unpruned trees.	Heavily pruned trees.
	Atmospheres.	*Atmospheres.*
Oct. 23	18.60	15.81
Nov. 6	19.10	17.90
20	19.00	17.20
Dec. 4	16.33	17.22
18	19.10	22.30
Jan. 29	15.85	18.75

These figures show that there are appreciable changes in the concentration of the sap even though no active growth is taking place. The changes may, however, be referred in part to changes in the amount of soil moisture present. During November and December there were light rains which did not penetrate deeply into the soil and did not affect the concentration of the cell sap of the trees. On January 4, 0.585 inches of rain fell, and on the three succeeding days 5.2 acre-inches of irrigation water were applied. The effect of this increased supply of soil moisture is seen in the lower concentration of sap in the samples taken on January 29. The effect of the increased amount of water intake was to dilute the sap of the tree, even though active growth had ceased.

SAP CONCENTRATION AND FRUITFULNESS

The observations made upon these fruit trees may throw some additional light upon the relationships between vegetative and fruiting activity of the tree. It appears that lower sap concentration is associated with abundant water intake and rapid growth. Severe pruning, which also stimulated active vegetative growth, caused *pari passu*, a lowering of the concentration of sap in the tree.

Horticulturists have long recognized that those conditions which are associated with lower sap concentration are opposed to fruit bearing in a tree. With the data now in hand it seems possible to point out some additional relationships of interest. The most rapid growth occurs in the early part of the season. The apricot shoots in 1919 made about half of their total growth in the first one-fifth of their growing period. By the time that three-fourths of the length growth had been made, the sap concentration had reached a fairly high value, which was maintained during the remainder of the season. Now it is well known that this time of higher sap concentration is the time during which the fruit buds for the following year are developing on the tree. The various lines of evidence lead to the conclusion that higher sap concentration is associated with slower growth and fruit-bud formation. At the present time, however, it seems impossible to say which one of the conditions is cause and which is effect. Differences in the sap concentration of the stem at the apical and the basal ends of the shoots are so well marked as to be unmistakable, yet it is somewhat difficult to orient one's views to fit the facts. The sap concentration of entire shoots, including stems and leaves, was lower during periods of rapid growth and higher during periods of slower growth. Yet, when we note that the sap concentration of the rapidly growing apical region of the shoot was uniformly higher than that of the slowly growing basal region, the condition seems paradoxical. The condition seems the more paradoxical when one remembers that the apical portion of the stem has a higher water content and that the content of solutes must, therefore, be correspondingly higher in order to show a higher concentration in the expressed sap.

We should remind ourselves, however, that growth is not wholly regulated by concentration *per se*. The composition of the sap, no less than its total concentration, affects the activity of the cell. Attention has recently been called to the effect on plant growth of inhibiting substances resembling chalones (*9, 14*). The absence of these growth-inhibiting substances in the apical portion of the shoot accounts in large measure for the more rapid growth of that region. There are also numerous lines of evidence which indicate that the sap of the apical region of the stem promotes vegetative growth because of its greater content of nitrogenous substances, while the slowly growing basal portion of the shoot is favorable to fruit-bud formation because of its greater content of carbohydrates (*8*). It goes without saying that we must recognize qualitative as well as quantitative differences in the plant sap in analyzing its

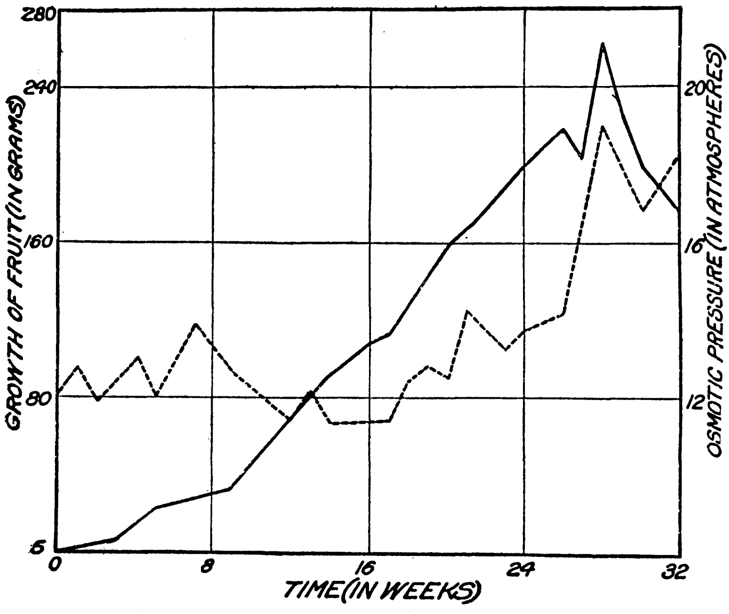

Fig. 7.—Graph showing growth and sap concentration of Golden Nugget navel oranges. Average weight of fruits is shown by solid lines, sap concentration of fruits by broken line.

effects on growth. The evidence, however, indicates that an increasing sap concentration in the shoot as a whole retards vegetative growth, while a decrease in the sap concentration of the whole shoot favors growth.

SAP CONCENTRATION AND THE GROWTH OF ORANGE FRUITS

The orange fruit was selected for study because it has a relatively long period of growth and develops on a tree which continuously bears green foliage. The variety employed is a strain of the navel orange known as "Golden Nugget." Determinations began on June 5, 1918, and were continued at weekly intervals until January 16, 1919. The mean weight of fruits on the former date was 0.39 gm. The growth rate was rather slow from the beginning of the observations until the end of the ninth week; then a period of more rapid growth set in, which lasted until the twenty-sixth week (Dec. 1). Toward the close of the period there was considerable fluctuation in the weight of fruits, largely because of errors in sampling, but the final mean weight was somewhat over 200 gm. The courses of the growth process and of the sap concentration of the fruit are shown in figure 7. During the first nine weeks, while the fruits were growing slowly, their sap concentration varied between 12 and 14 atmospheres of osmotic pressure. When more rapid growth began, the sap concentration dropped to a pressure between 11 and 12 atmospheres, but subsequently gradually rose. As the fruit approached maturity there was a great increase in its sugar content and a consequent increase in the concentration of the sap.

During the first half of the growth period it is quite evident that rapid growth is accompanied by a lower sap concentration. In the latter half of the growth period it is more difficult to ascertain the relationships between sap concentration and growth because of the fact that while the fruit is still growing it begins to accumulate increasing amounts of soluble carbohydrate.

SUMMARY

(1) Observations on the growth and sap concentration of young trees showed that the two variables have a tendency to vary in opposite directions—that is to say, rapid growth is associated with a generally lower concentration of sap in that shoot, while slower growth is accompanied by higher concentrations of sap.

(2) There was a gradual increase in sap concentration as the season advanced. In apricot trees the concentration continued to increase for some time after active growth had ceased. The accumulations of solutes in the plant sap is unquestionably related to the synthetic metabolism of the tree as the season advanced, though there is some evidence that diminished water absorption was partially responsible for the increased sap concentration.

(3) Of several environmental factors measured, soil moisture was the only one having an obvious effect upon sap concentration. The addition of water to the soil usually diminished the concentration of the plant sap.

(4) The sap concentration of shoots on trees heavily pruned was lower than that of shoots on trees not pruned, because of the more rapid growth of the former.

(5) A concentration gradient appears to exist in the shoot. The concentration of the sap in the apical portion of a stem was greater than that in the basal region. The sap concentration in the stems showed a greater tendency to fluctuate than that in the leaves.

(6) Lower concentrations of plant sap in the shoot as a whole appear to be associated with abundant water intake and rapid vegetative growth.

Higher concentrations are associated with slow growth and fruit-bud formation.

(7) The results seem to indicate that the practice of summer pruning fruit trees is not only unnecessary but may be detrimental.

(8) Observations upon the growth and sap concentration of shoots and fruits of the orange tree confirm those made on the apricot tree.

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