



**AgEcon** SEARCH  
RESEARCH IN AGRICULTURAL & APPLIED ECONOMICS

*The World's Largest Open Access Agricultural & Applied Economics Digital Library*

**This document is discoverable and free to researchers across the globe due to the work of AgEcon Search.**

**Help ensure our sustainability.**

Give to AgEcon Search

AgEcon Search  
<http://ageconsearch.umn.edu>  
[aesearch@umn.edu](mailto:aesearch@umn.edu)

*Papers downloaded from **AgEcon Search** may be used for non-commercial purposes and personal study only. No other use, including posting to another Internet site, is permitted without permission from the copyright owner (not AgEcon Search), or as allowed under the provisions of Fair Use, U.S. Copyright Act, Title 17 U.S.C.*

TB 403 (1934)

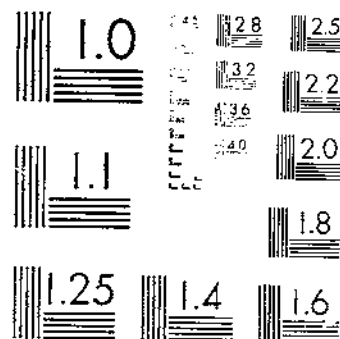
USDA TECHNICAL BULLETINS

UPDATA

HYDRION CONCENTRATION CHANGES IN RELATION TO GROWTH AND RIPENING IN

CALDWELL, J. S.

1 OF 1



**HYDRION  
CONCENTRATION CHANGES  
IN RELATION TO GROWTH  
AND RIPENING IN FRUITS**

BY

**JOSEPH S. CALDWELL**

Senior Physiologist

Division of Fruit and Vegetable Crops and Diseases  
Bureau of Plant Industry



UNITED STATES DEPARTMENT OF AGRICULTURE, WASHINGTON, D.C.



UNITED STATES DEPARTMENT OF AGRICULTURE  
WASHINGTON, D.C.

# HYDRION CONCENTRATION CHANGES IN RELATION TO GROWTH AND RIPENING IN FRUITS

By JOSEPH S. CALDWELL<sup>1</sup>

*Senior physiologist Division of Fruit and Vegetable Crops and Diseases, Bureau of  
Plant Industry*

## CONTENTS

	Page		Page
Introduction.....	1	Analytical results—Continued.....	
Review of literature.....	1	Berries.....	33
Materials and methods.....	4	Tomatoes.....	42
Analytical results.....	8	Discussion.....	43
Apples.....	5	Summary.....	49
Citrus fruits.....	20	Literature cited.....	51
Cherries.....	23		

## INTRODUCTION

The investigation of methods of preserving fruits now in progress in the fruit and vegetable utilization laboratory of the Bureau of Plant Industry has necessarily involved a study of the chemical and physicochemical methods of determining the stage of maturity of the fruit, since the stage of maturity of the material largely determines the quality of the preserved product. A rather extensive study has been made of the changes occurring in the hydron concentration of the juices of ripening fruits, in order to determine whether the hydron concentration of the juice is in any degree a dependable criterion of the stage of maturity. Since May 1927 this study has been supplemented by an investigation designed to secure a somewhat fuller knowledge of the nature and extent of the changes in active and titratable acidity of the fruit juices in the earlier stages of development. Comparative studies have been made of the relations between changes in active acidity, on the one hand, and changes in volume or weight and in chemical composition, on the other hand, in a number of fruits of widely diverse character, representing widely separated botanical groups. This bulletin reports the results of these studies.

## REVIEW OF LITERATURE

A number of workers have recently reported results of determinations of hydron concentration or titratable acidity, or both, made upon developing fruit. These data collectively indicate that both

<sup>1</sup> The writer gratefully acknowledges his indebtedness to Byron C. Brunstetter, for assistance in making many of the hydron determinations, and to C. W. Culpepper and H. B. Moon, for assistance in the chemical analyses.

active and total titratable acidity increase as growth advances, attain a maximum about the time ripening begins, and then decrease as ripening proceeds.

Bartholomew (4)<sup>2</sup> appears to have been the first worker to call attention to the large change in hydron concentration occurring in the juice of a fruit during its period of development. He made determinations of average diameter, water content, and hydron concentration upon Eureka lemons at Riverside, Calif., at intervals of 1 month from September 10 to July of the following year. There was an increase in active acidity from pH 4.46 to 2.30 (0.000034N to 0.005N)<sup>3</sup>, or to an active acidity 144 times as great as that of the initial sample, occurring in the course of 10 months of growth. Of this total, the change from pH 4.46 to 2.91, representing an increase in active acidity of more than thirty-fivefold, occurred in 2 months, and was accompanied by an increase in water content from 53.9 to 81.4 percent and an increase in volume of about 350 percent. Bartholomew has not given the results of determinations of titratable acidity and average weight of fruits and made no determinations of titratable or active acidity upon the wood or leaves of his trees. Reed and Halma (29) made determinations of hydron concentration values upon sap of fruiting wood and shoot wood of 3-year-old and 8-year-old lemon trees at intervals throughout the year and found an approximately fivefold increase in active acidity in the vegetative tissues in the course of the season.

Oppenheim and Winik (25), working at the Palestine Agricultural Experiment Station, followed the changes in sugar content and hydron concentration in the Jaffa orange throughout its development. Determinations of hydron concentration were begun on July 1 and continued at 2-week intervals until March 1, the fruit becoming fit for shipment or consumption about December 1. Beginning with pH 4.4 (0.000039N) on July 1, there was a progressive change to pH 2.8-3.0 (0.00158N-0.001N) on October 1. After this date there was a further change to a value of pH 3.5 (0.000316N) on March 1. Increase in sugar content began October 15 and continued until January 1, after which it fluctuated without definite change. Neither acidity nor sugar changes could be correlated with the occurrence of the rainy season or with other meteorological factors.

Alwood and his collaborators (1) showed that there is a large decrease in total titratable acidity in grapes during coloration and ripening, because of progressive conversion of free tartaric acid into acid potassium tartrate. Copeman (9, 10, 11) and Copeman and Frater (12) studied the changes in active and in total acidity throughout the larger portion of the period of development and found that both increased to a maximum during growth, then decreased as the fruit ripened.

Gustafson (16, 18), working at Ann Arbor, Mich., studied the rate of increase in volume and green weight and the change in percentage of dry matter in two varieties of tomatoes at weekly intervals from blooming to ripeness. Titratable acidity and hydron concentration were determined at weekly intervals and showed very little change

<sup>2</sup> Italic numbers in parentheses refer to Literature Cited, p. 51.

<sup>3</sup> In order to facilitate comparisons of active acidity values, statements of values in terms of the pH scale are followed in parentheses by their equivalents in terms of a normal solution of hydrogen ions, i.e., in terms of  $\text{Ca}^{+}$ . Similar values for the upper and lower limits of active acidity encountered in the material appear in the tables.

from the first to the third week. During the fourth and fifth weeks, however, there was a shift of hydrion concentration from about pH 4.70 to 4.30 (0.0000199N to 0.0000501N), accompanied by an increase of approximately 50 percent in titratable acidity. This was the period of most rapid growth, the fruits increasing about 300 percent in weight and in volume during this time (17). After the fifth week there was a slow increase in both active and titratable acidity, which reached a maximum about the time the fruit ceased to enlarge and some specimens had begun to turn color (19, p. 354). From this point onward titratable and active acidity declined somewhat irregularly until the fruit was ripe. The results in regard to the decrease in titratable acidity with advance in age are in agreement with those of Sando (35). The work of Rosa (32, 33) dealt with changes in ripening tomatoes and that of Appleman and Conrad (3) and MacGillivray and Ford (23) with the hydrion-concentration relations in the ripe fruit. None of these included the earlier stages.

Hartman and Bullis (20) found a slight but progressive decline in both titratable and active acidity in several varieties of cherries as the fruit passed from immaturity through ripeness to a decidedly overripe condition. Neller and Overley (24) and St. John and Morris (34) found a similar decline in titratable and active acidity in apples during the last 7 or 8 weeks on the tree; most of the decrease occurred in a relatively short period just before the fruit reached picking maturity. Overholser (26) found that pears showed a progressive increase in active acidity from the time the fruits had one twelfth to one sixth the mature weight until they approached shipping ripeness, when active acidity became stationary or decreased slightly.

The results of the workers just cited indicate that in the lemon, the orange, the pear, and the tomato there is a rather marked rise in active acidity throughout the period of rapid growth, which reaches a maximum about the time growth is completed and ripening processes set in and which is followed by a more or less pronounced decline as ripening proceeds. In the cherry, the grape, and the apple the available data do not cover the early stages of development, but the detailed studies of the later portion of the life period in these fruits show that the changes in active acidity follow a like course. It is also clearly indicated that in fruits, as in vegetative parts (15), there is no constant relation between total and active acidity values, and only the broadest general parallelism in their changes.

A number of workers have given more or less attention to the changes in water content occurring in fruits during development. Bartholomew (4) has shown for lemons and Gustafson (18) for tomatoes that during the earlier stages of growth there is a progressive and in the aggregate a rather large increase in water content, which slows down as the fruit approaches maturity.

Bartholomew (5) has directed attention to the fact that in citrus fruits there may be a withdrawal of water from the fruit by the leaves at almost any period in the life of the fruit. In periods of high transpiration this may result in loss of turgor in the afternoon, with recovery during the night; in periods of prolonged drought it may result in the withdrawal of such a quantity of water as to bring about the collapse and breaking down of the tissues adjacent to the vascular bundles (internal decline). Reed (27) has further emphasized the existence of an equilibrium of water between tree and fruit, and has

demonstrated the existence of a large saturation deficit in oranges and lemons, as a result of which they swell rather rapidly when placed in water, dilute acid or alkali, or solutions of salts such as calcium chloride or copper sulphate. Reed has further shown that this swelling is due chiefly to imbibition of liquid by the hydrophilic colloids of the mesocarp, but that the juice sacs making up the locules of the fruit have sufficient suction pressure to draw water from the mesocarp. Furr and Magness (14) measured the rate of growth in the fruit of apples on irrigated and nonirrigated plots and found that in the apple decrease in soil moisture content nearly to the wilting coefficient resulted in cessation of growth of the fruit and in some cases<sup>4</sup> in an absolute decrease in volume. H. H. Moon, in studies on peaches in progress in this laboratory, found that in a period of severe drought the young fruit first slowed down in rate of growth, reached a standstill, and then shrank in size, the reduction involving all three diameters of the fruit.

It is evident that in the peach and apple, as in the citrus fruits, there is an equilibrium in water content between fruit and vegetative parts and that under conditions of insufficient moisture supply movement of water into the fruit may slow down, stop, and ultimately reverse its direction.

#### MATERIALS AND METHODS

The work herein described was begun early in 1927. At that time the work of Bartholomew upon the lemon (4) was the only report to be found in the literature upon the changes in hydron concentration occurring in a fruit throughout the whole course of its development. The absence of similar information with respect to the early stages of development in other fruits prompted the present investigation and determined its scope. Its purpose was to determine whether changes in degree of active acidity occurring during the development of fruits follow any definite course, whether the course of such changes is similar in fruits of dissimilar character, and whether such changes are definitely correlated with increase in weight and volume and with changes in chemical composition during growth and ripening. It was therefore planned to make a rather detailed study of the apple, cherry, strawberry, tomato, orange, and grapefruit, employing where possible a number of horticultural varieties of each fruit. Material for determinations of weight, moisture content, active acidity, and chemical composition was collected at predetermined intervals throughout the course of development, beginning as soon as the fruit had set. For the purpose of gaining knowledge of the general course of changes in active acidity during growth in fruits of some other types, a less detailed study was made of the blackberry, raspberry, pokeberry (*Phytolacca americana* L.), and elderberry (*Sambucus canadensis* L.).

The general method employed in preparing material for determinations of hydron concentration was that of grinding the fruit, after removal of the seed and peel, through a food chopper equipped with a pulverizing disk, pressing the juice from the pulp through muslin in a small tincture press or by hand, and filtering or centrifuging, where necessary, to remove cellular debris. In the case of very

<sup>4</sup> Personal communication from J. R. Magness.



small samples the material was ground as thoroughly as possible with a porcelain mortar and pestle and expressed by hand. That the juices obtained by the use of a press and those expressed by hand were identical in their hydrion concentration was determined by numerous checks.

The hydrion-concentration determinations in all cases were begun within 5 to 10 minutes, usually within a shorter time, after the juice had been expressed. Simultaneous determinations were made, with certain exceptions noted hereafter, by means of a hydrogen electrode of the Bailey type and a quinhydrone electrode, the latter being used as a comparison electrode. In the majority of the fruits examined readings with the two electrodes agreeing within 0.05-0.07 pH were readily obtainable and the agreement was frequently within 0.03 pH. The juices of some fruits contain substances that react with quinhydrone, producing a drift of potential which makes the quinhydrone electrode unreliable in dealing with them. For some of these the hydroquinhydrone electrode was employed as a comparison electrode with satisfactory results; for others it was useless. The Hildebrand hydrogen electrode was used in some instances. In the case of very small fruits or limited amounts of material the modification of the Bodire and Fink microelectrode described by Brunstetter and Magoon (6) was employed after its development in 1928. As pointed out by these authors, the microelectrode may be employed both as a hydrogen and as a quinhydrone electrode, and was so used in some instances to obtain duplicate readings upon small samples. The rapidity with which several determinations could be made permitted its use as a check on the Bailey hydrogen electrode in such juices as could not be dealt with by the quinhydrone method. Some use of colorimetric methods was made for the purpose of determining the degree of accuracy obtainable with such methods upon the material in hand.

The samples for the chemical analyses were in all cases taken from the same lot of material employed for the hydrion-concentration determinations. Duplicate samples of 40 to 100 g of the finely minced material were weighed out, placed in sufficient 95 percent alcohol to make the alcohol concentration at least 80 percent, and heated to boiling. After some 6 to 8 months storage the extraction was completed by extraction with fresh 95 percent alcohol for 6 to 10 hours in Soxhlet extractors. The various determinations were made upon aliquots of the alcohol extract by the standard methods of the Association of Official Agricultural Chemists.

## ANALYTICAL RESULTS

### APPLES

Preliminary studies on apples were made in 1927 and more intensive studies in 1928 and 1929. Eight varieties were employed. These were chosen to represent a fairly wide range in chemical composition and length of developmental period, and included the standard varieties Baldwin, Grimes Golden, and Paragon; the summer varieties Williams and Rambo; the highly astringent French apples Launette and Amère du Surville, of the class termed by French pomologists the "douce-amère" group; and *Malus angustifolia* Mich., a native crab species having such exceptionally high acidity and

astringency that the fruit is inedible. In 1929 the absence of a crop of Amère du Surville, Paragon, and Williams reduced the number of varieties employed in that year to five.

Sampling was begun as soon after blooming as it was possible to feel reasonably certain that the fruits selected had begun normal development. This was a matter of some difficulty, since dropping continues through the period in which the young fruits remain practically stationary in size and is often severe after they have begun to enlarge. The trees were inspected almost daily from full bloom onward, and sampling of a variety was begun only when it became apparent that dropping of that variety had practically ceased. In Baldwin and Paragon in 1928 and in Launette and *Malus angustifolia* in 1929, persistent dropping postponed beginning of sampling until the fruits averaged 1 g or more in weight, 15 to 21 days after full bloom; with these exceptions, cessation of dropping allowed sampling to begin when the fruits averaged considerably less than 1 g in weight and were only 8 to 12 days old.

The data obtained in 1928 are assembled in table 1; those secured in 1929 in table 2. The 1927 results were confirmed in all respects by those of the subsequent years but were less complete and are therefore omitted.

TABLE 1.—Changes in hydron concentration, weight, and chemical composition of 8 apple varieties throughout development in 1928

Variety	Date	Average diameter	Average weight	Active acidity		Titratable acidity	Sugar			Astringent substances		Solids			Water as percentage of total solids	Increase in weight
				pH	CH		Reducing	Sucrose	Total	Tannin	Non-tannin	Soluble	Insoluble	Total		
		Mm	Grams			Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent
Amère du Surville	May 18	4-7	0.402	4.73	0.00001862N											
	do	8-11	.903	4.43		0.780	1.27	0.50	1.77	2.508	1.052	8.32	8.814	17.13	483.7	
	May 29	16-20	2.08	3.82		.705	2.73	.43	3.16	3.060	1.275	9.56	5.886	15.44	547.6	130.3
	June 6	20-27	8.33	3.54		.692	4.95	1.11	6.06	2.800	.995	8.76	5.711	14.47	591.1	300.4
	June 14	24-32	12.75	3.43	.0003715N	.688	3.64	.46	4.10	2.250	.810	8.08	6.319	14.40	594.4	53.0
	June 25	29-36	19.83	3.39		.520	4.17	.68	4.85	2.050	.638	8.32	7.339	15.72	536.7	55.5
	July 11		27.88	3.77		.462	2.40	2.28	4.68	1.375	.500	7.12	7.730	16.85	493.5	40.5
	July 25	40-48	38.66	3.80		.390	5.53	.31	5.84	1.160	.485	8.80	8.204	17.00	488.2	38.6
	Aug. 8	40-46	51.40	3.80		.380	5.66	1.20	6.86	1.027	.315	9.24	7.417	16.65	500.0	32.9
	Aug. 28	45-63.5	66.66	3.77		.325	5.94	1.56	7.50	.820	.262	9.56	6.296	15.86	530.5	29.6
	Sept. 24		95.29	3.80		.315	6.84	2.30	9.14	.690	.228	10.88	4.362	15.24	566.1	42.8
	May 17	11-13	1.77	3.35	.0004467N	1.173	1.26	.03	2.19	.547	.260	6.72	5.730	12.45	703.2	
Baldwin	May 22	15-18	3.00	3.28		1.220	1.00	.86	1.86	.476	.224	7.80	4.936	12.73	685.5	69.4
	May 31	19-25	7.69	3.02		1.460	2.26	.77	3.03	1.005	.348	7.24	4.994	12.23	717.6	156.3
	June 7	23-30	14.71	2.89	.001288N	1.455	2.17	.95	3.12	.584	.214	7.72	4.751	12.47	701.9	91.2
	June 14	30-35	17.85	2.91		1.370	3.05	.67	3.72	.532	.218	7.88	5.347	13.22	656.4	21.3
	June 27	35-42	33.39	2.95		1.105	3.22	1.31	4.53	.396	.164	7.44	6.415	13.85	622.0	87.0
	July 13	38-53	50.50	3.09		.900	3.82	1.57	5.39	.288	.126	7.68	7.914	15.50	541.4	78.2
	July 20		72.06	3.15		.804	4.36	1.66	6.02	.208	.087	8.60	7.632	16.23	516.0	21.1
	Aug. 10	54-63	105.71	3.15		.775	4.30	1.82	6.12	.288	.094	8.32	6.013	14.33	597.8	46.7
	Aug. 28	56-74	141.54	3.14		.622	4.84	1.87	6.71	.227	.079	8.64	5.964	14.60	584.8	33.9
	Sept. 24		173.12	3.26	.0005495N	.645	5.85	4.01	9.86	.176	.047	11.52	4.520	16.04	523.4	22.3
	May 18	7-11	.641	3.62	.0002399N	1.084	.68	.60	1.28	.792	.356	3.64	8.238	14.87	572.5	
	May 29	20-18	4.00	3.12		1.435	2.15	.82	2.97	1.5	.248	7.60	5.667	13.26	654.1	525.0
Grimes Golden	June 6	20-23	8.33	2.98		1.290	2.47	.70	3.17	1.086	.314	0.96	0.013	12.97	671.0	108.2
	June 14	23-30	13.00	2.87	.001349N	1.220	3.30	.96	4.26	.956	.580	8.40	7.308	15.70	536.9	56.0
	June 25	30-36	23.43	2.97		1.036	3.04	1.38	4.42	.627	.262	7.44	7.815	15.25	555.7	80.2
	July 9	33-38	35.16	3.07		.840	4.47	1.71	6.18	.378	.132	8.63	9.310	17.99	455.9	50.0
	July 20			3.20		.720	4.61	2.19	6.80	.295	.110	8.80	7.481	16.28	514.2	
	Aug. 3			3.24		.720	4.80	2.48	7.28	.209	.020	9.48	8.793	18.27	447.3	
	Aug. 21	43-62	84.37	3.30		.620	5.76	2.50	8.26	.190	.079	10.52	7.380	17.90	457.0	
	Sept. 24		123.75	3.54	.0002884N	.510	6.11	5.61	11.72	.196	.072	13.28	3.915	17.19	481.7	
	May 18	5-7	.348	4.79	.00001622N	.900	.80	1.10	1.90	1.821	.980	8.80	11.185	19.98	400.5	
	May 29	18-13	2.08	3.99		.764	2.46	.50	2.96	4.450	2.020	10.04	7.700	17.74	463.7	497.7
	June 6	28-19	5.26	3.75		.720	3.17	.05	3.22	4.450	1.610	9.88	7.806	17.68	465.6	152.8
	June 14	30-22	9.79	3.76		.817	3.47	1.00	4.47	5.150	1.960	11.36	8.279	19.63	409.1	86.1
Launette	June 25	26-37	10.60	3.72	.0001905N	.652	3.41	1.09	4.50	4.670	1.290	9.44	9.016	18.45	442.0	70.1
	July 11		26.0	3.96		.552	4.47	1.41	5.88	2.670	1.007	9.72	12.418	22.14	351.0	56.0
	July 25	35-40	35.0	4.08		.438	5.61	1.32	6.93	2.680	.803	10.92	11.777	22.69	340.7	34.6
	Aug. 8	42-57	56.56	4.10												61.6
	Aug. 28	49-57	68.75	4.43		.352	7.24	2.40	9.64	1.180	.382	12.28	6.207	18.48	441.1	21.5
	Sept. 24		81.79	4.31	.00004898N	.325	8.28	3.36	11.64	.910	.336	13.92	4.964	18.88	429.7	18.9

TABLE 1.—Changes in hydron concentration, weight, and chemical composition of 8 apple varieties throughout development in 1928—Con.

8

Variety	Date	Average diameter	Average weight	Active acidity		Titratable acidity	Sugar			Astringent substances		Solids			Water as percentage of total solids	Increase in weight
				pH	CH		Reducing	Sucrose	Total	Tannin	Non-tannin	Soluble	Insoluble	Total		
Paragon	May 22	Mm	Grams			Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent
	do.	11-14	1.38	3.40	0.0003981N	0.682	2.19	0.38	2.58	1.510	0.700	10.24	6.206	16.44	508.2	-----
	do.	14-17	2.44	3.29		.576	1.47	.77	2.24	1.137	.486	7.04	5.870	12.91	674.6	-----
	May 31	20-22	6.25	3.09		1.312	2.26	.87	3.13	1.472	.487	7.96	5.432	13.39	646.8	156.7
	June 7	22-28	12.50	3.00	.001N	1.405	2.42	.66	3.08	1.100	.305	7.32	5.165	12.48	701.3	100.0
	June 14	27-32	17.85	3.04		1.210	2.87	.79	3.66	1.010	.455	7.84	5.678	13.51	647.6	42.8
	June 27	30-35	24.80	3.12		.915	2.82	.62	3.44	.810	.286	7.60	6.706	14.30	600.0	38.9
	July 13	38-45	37.01	3.13		.677	3.87	1.39	5.26	.576	.193	7.64	7.993	15.63	539.7	51.6
	July 27	38-53	55.60	3.35		.678	4.40	1.03	5.52	.346	.196	8.12	7.749	15.87	542.6	47.8
	Aug. 10	42-62	76.05	3.37		.587	4.84	2.02	6.86	.330	.134	8.48	7.049	15.53	542.8	36.7
	Aug. 28	49-60	100.66	3.30		.750	4.56	2.42	6.98	.280	.062	8.92	6.577	15.49	545.5	32.3
	Sept. 24		135.50	3.37		.540	5.95	2.77	8.72	.210	.083	9.80	5.259	15.05	564.4	34.6
	May 15	3-5, 5-8	3.56	4.05	.00008318N	1.380	.65	1.00	1.65	1.688	1.110	11.60	7.675	18.27	444.3	-----
	May 29	15-12	1.85	2.97		1.456	.88	.82	1.70	2.405	1.200	9.32	4.715	14.03	612.6	419.7
Malus angustifolia	June 5	16-20	3.97	2.89		1.476	.60	.23	.83	2.305	.872	8.32	4.057	12.37	708.4	114.6
	June 18		8.00	2.65		1.866	.66	.90	1.56	2.540	.875	9.12	5.117	14.23	602.7	101.5
	June 25	33-20	9.83	2.77		1.956	.81	.72	1.53	1.973	.820	7.64	5.795	13.43	646.6	22.8
	July 17		16.00	2.50		2.390	.86	.57	1.43	2.430	.580	9.16	7.285	16.44	508.2	62.7
	Aug. 6		21.36	2.62		2.770	1.39	.81	2.20	2.000	.405	9.44	7.308	16.74	497.4	33.5
	Oct. 3		34.80	2.42	.003802N	2.520	2.81	1.45	4.26	1.280	.374	9.02	2.994	12.91	674.6	62.9
Summer Rambo	May 18	6-9	1.724	3.70	.0001905N	.940	.70	.70	1.40	1.185	.502	7.44	8.430	15.87	530.1	-----
	do.	10-13	1.47	3.45		1.360	.88	.26	1.14	1.208	.515	7.14	6.704	13.84	622.0	83.6
	May 31	21-25	9.80	2.07		1.375	2.93	.68	3.61	1.172	.394	7.84	5.376	13.21	657.0	566.6
	June 6	25-34	18.0	2.73		1.435	2.67	.34	3.01	1.063	.356	6.02	5.241	12.16	722.3	83.6
	June 14	28-40	25.0	2.74	.00182N	1.175	3.57	.39	3.96	.778	.222	7.16	6.122	13.28	653.0	38.8
	June 25	32-46	41.66	2.88		.785	4.40	1.28	5.68	.546	.208	8.16	5.151	13.34	649.6	66.6
	July 9	45-60	61.78	3.06		.565	5.32	1.54	6.86	.390	.137	8.88	6.225	15.10	562.2	48.3
	July 23		100.42	3.16		.515	6.12	1.84	7.96	.291	.109	9.36	5.257	14.61	584.4	62.5
	Aug. 3		126.9	3.24		.425	5.33	1.79	7.12	.219	.089	8.60	5.142	13.74	627.8	26.3
	Aug. 21	57-80	143.84	3.33		.409	6.84	2.20	9.04	.196	.083	10.40	4.083	14.48	580.5	13.3
Williams	May 22	6-11	.99	3.66	.0002188N	1.078	1.20	.26	1.46	.940	.487	7.36	6.381	13.74	627.8	-----
	do.	11-14	1.74	3.45		.648	.27	.53	.80	.373	.184	6.72	6.806	13.52	639.6	-----
	May 29	15-20	5.55	3.15		1.390	1.70	.93	2.68	1.240	.288	7.48	5.155	12.63	601.7	218.9
	June 6	26-30	12.50	2.96		1.315	2.36	.76	3.12	.940	.486	6.06	4.701	11.66	757.6	125.2
	June 14	28-40	25.00	2.92	.001202N	1.210	3.37	1.07	4.44	.650	.310	7.96	5.054	13.01	608.6	100.0
	June 25	37-45	40.63	2.95		.900	3.99	1.27	5.26	.449	.182	8.04	4.950	12.99	669.8	62.5
	July 9	48-55	73.76	3.05		.710	4.87	1.73	6.60	.217	.092	8.32	6.946	15.26	554.6	81.5
	July 23			3.33		.515	6.14	2.95	9.09	.251	.090	10.84	3.526	14.36	596.3	-----
	Aug. 3	( )		3.36	.0004365N	.512	5.70	4.16	9.92	.198	.079	11.64	3.253	14.89	571.6	-----

1 Soft ripe.

TABLE 2.—Changes in hydrion concentration, chemical composition, and weight of 5 varieties of apples in the earlier stages of development in 1929

Variety	Date	Average weight	Active acidity		Titratable acidity	Sugars			Tannin	Solids			Water as percentage of total solids	Increment in weight
			pH	CN		Reducing	Sucrose	Total		Soluble	Insoluble	Total		
		Grams			Percent	Percent	Percent	Percent		Percent	Percent	Percent	Percent	Percent
Baldwin	Apr. 29	0.294	3.73	0.0001862N	0.679	0.56	0.40	1.36	0.720	7.20	7.56	14.76	577.51	
	May 11	3.81	3.12		1.244	2.10	.22	2.32	.696	7.52	5.20	12.72	669.96	1,206.1
	May 20	21.07	2.88	.001318N	1.572	2.45	.57	3.02	.404	5.96	4.82	10.78	827.64	448.7
	June 10	35.3	2.90		1.431	3.47	.57	4.04	.380	6.92	6.70	13.62	634.21	67.5
	July 3	54.6	2.97		1.021	3.76	.53	4.29	.284	6.36	7.94	14.30	599.30	54.6
Grimes Golden	Aug. 16	140.7	3.22		1.055	7.16	1.23	8.39	.206	10.32	7.60	17.92	458.04	157.6
	May 7	0.833	3.42	.0003802N	.706	1.62	.44	2.06	.465	7.84	6.90	14.74	578.42	
	May 28	10.5	2.99		1.586	2.98	.26	3.24	.911	7.00	6.60	13.60	635.29	1,160.5
	June 7	15.0	2.90	.001259N	1.492	3.78	.88	4.66	.526	7.88	7.88	15.76	534.52	42.8
	June 28	46.4	3.06		1.156	4.04	.72	4.76	.284	6.75	8.15	14.91	570.69	209.3
Launette	July 23	73.2	3.16		.891	6.20	1.88	8.08	.216	9.36	8.34	17.70	464.97	57.7
	Aug. 16	91.4	3.39		.755	7.46	2.01	9.47	.193	10.93	6.94	17.87	459.60	24.8
	May 11	1.03	4.30	.00004365N	.810	2.53	.18	2.71	3.122	9.52	7.00	16.52	505.33	
	May 29	6.94	3.69	.0002042N	.574	3.18	.12	3.30	2.425	7.96	7.84	15.80	532.91	573.7
	June 10	13.16	3.79		.685	4.62	1.40	6.11	3.417	9.24	8.99	18.23	448.55	80.6
Summer Rambo	June 29	26.1	3.78		.659	4.63	.48	5.11	1.925	7.60	8.82	16.42	509.01	98.3
	July 23	43.66	4.08		.491	6.76	.88	7.64	1.274	9.28	8.50	17.77	459.60	67.2
	Aug. 16	63.5	4.23		.393	6.40	2.80	9.20	.851	11.14	7.54	18.68	435.33	45.4
	Apr. 29	0.300	4.08	.00008318N	.665	.84	.34	1.18	.505	7.44	11.88	19.22	417.60	
	May 7	2.56	3.24		1.176	1.53	.14	1.67	.783	6.64	6.23	12.87	677.00	556.3
Malus angustifolia	May 28	25.0	2.79	.001622N	1.666	3.08	.25	3.33	.592	6.44	7.21	13.65	632.60	876.5
	June 7	29.5	2.80		1.371	4.57	.40	4.97	.837	7.40	6.12	13.52	639.64	18.0
	June 28	77.0	2.89		.840	5.66	.44	6.10	.301	7.48	5.53	13.01	668.64	161.0
	July 23	134.10	3.15		.618	7.06	1.17	8.23	.280	9.24	4.83	14.07	610.73	74.1
	May 17	1.51	3.05	.0008913N	1.613	.90	.17	1.07	1.663	8.60	3.93	12.53	698.08	
Malus angustifolia	June 4	6.00	2.78		2.224	.89	.28	1.17	.588	8.20	4.08	13.18	658.73	297.3
	June 12	9.02	2.49	.003230N										60.3

Tables 1 and 2 show that in every series of samples of a variety, active acidity for the series is at a minimum in the initial sample, that is, in the youngest and smallest fruit. In several instances the sample taken on a given date was divided into two on the basis of size; in these cases the smaller fruits are lower in active acidity than the larger ones. Moreover, comparisons of the samples of a given variety obtained in the 2 years show that the active acidity of the smaller fruits is considerably below that of the larger ones.

There was in all cases a rather rapid change in hydron-concentration values in the first few weeks of sampling. In 1928 this change had nearly or quite reached its maximum in the samples taken June 14, 4 weeks after sampling began. The amount of change during this period varied widely with variety, ranging from a threefold increase in active acidity in Baldwin through a ninefold increase in Rambo to a forty-fivefold increase in *Malus angustifolia*. The initial samples of Baldwin and Rambo in 1929 were somewhat smaller and had considerably lower active acidities, and the increases during the succeeding 4 weeks were larger, more than sevenfold in Baldwin and nearly twentyfold in Rambo.

Hooker (22) found active acidity values of pH 5.4 to 5.5 in bearing spurs of apple about the time of flowering, and the writer's determinations upon young fruits with petals attached have given values ranging from pH 5.1 to 5.4 for several varieties. The active acidity of the young ovary prior to the onset of rapid enlargement appears to approximate that of the vegetative parts upon which it is borne. That this is the case for other fruits as well will be shown in subsequent sections. By the time that fruits which have set and begun to enlarge can be distinguished from those which will drop, a considerable increase in active acidity has occurred.

The increase in active acidity is almost completed by the time the young fruits are 5 to 6 weeks old, when they have a diameter of 2 to 3 cm and a weight of 9 to 18 g, or from one twelfth to one eighth the volume and weight of mature specimens of the variety concerned. The hydron concentration attained at the time the increase ceases varies widely with different varieties but appears to be fairly constant in successive years for a given variety. *Malus angustifolia* attains a maximum acidity three times as great as that of the Baldwin, Rambo, and Grimes Golden, which have maxima about six times as great as that of Launette. The varieties for which there are 3 years' records attained the following maximum values: Baldwin, pH 2.96, 2.89, and 2.88; Grimes Golden, pH 2.83, 2.87, and 2.90; Launette, pH 3.89, 3.72, and 3.69; Rambo, pH 2.97, 2.74, and 2.79, and *Malus angustifolia*, pH 2.52, 2.42, and 2.49.

After reaching these general levels, active acidity remains relatively stationary for a short period, then shows a sharp decline, which slows in rate as picking maturity approaches. *Malus angustifolia*, however, declines, then rises again. The general decline referred to has been observed in its later stages by Neller and Overley (24) and St. John and Morris (34). The length of the relatively stationary period varies with the date of maturity of the variety; in Williams and Rambo, which are commercially harvested in August and about mid-September, respectively, marked decline is apparent by July 23, whereas in the late-maturing varieties there is no very pronounced change until August or September.

The relation of the change in water content occurring in the young fruit to the concurrent change in active acidity is not immediately obvious from the usual statement of composition of the sample as made up of certain percentages of solids and of water together equaling 100 percent. It is made more obvious by recalculation of the data on moisture content, employing the total solids of the sample as a base and calculating the water present as percentage of the dry matter. This method of treatment has been applied to the data, and the results are stated in the next to the last column of tables 1 and 2. A like method has been employed with the data of subsequent tables.

In tables 1 and 2 there was in every case an abrupt increase in water content accompanying the rise in acidity and astringency, which can only mean that these increases in these constituents occur despite the opposed effect of dilution of the cell contents as a result of the rapid intake of water. The amount of the increase in water content varied widely among the varieties, and the percentage of water, calculated as percentage of the total solids, that is present at the time of maximum hydration is also somewhat variable. There was, however, a very definite relationship between the degree of active acidity attained at the peak of the upward rise and the water content of the fruit.

In the French apple Launette, the maximum active acidity attained in 1928 was pH 3.72, the sample containing 442 percent of water expressed as percentage of total solids. The rise of active acidity in this variety was from pH 4.79 to 3.72 (0.00001622N to 0.0001905N), and this rise was accompanied by an increase in water content from 400 to only 442 percent. In the other French crab apple, Amère du Surville, the maximum active acidity attained was pH 3.43 (0.0003715N), slightly less than twice that of Launette, but this higher level of active acidity is accompanied by a higher level of water content, namely, 594 percent. Five of the six remaining varieties attained maximum active acidities of the general order of pH 3.00 (0.001N), or about three times that of Amère du Surville, with an accompanying rise in water content to the general neighborhood of 700 percent. In the subsequent growth of the fruit the levels of water content reached at the stage under discussion drop somewhat. The water content of Launette fluctuates around 400 percent of the solids, that of Amère du Surville around 500 percent, and that of the other varieties around 600 percent for the remainder of the period of development, so that each variety rather early established and subsequently maintained a level of water content that was rather definitely related to the degree of active acidity existing in its tissues.

*Malus angustifolia* was unique in the course of its active acidity curve and also in its water relations. It reached a maximum water content of 708 percent on June 5, with a pH of 2.89 (0.001288N). Its active acidity continued to increase slowly throughout the season, reaching pH 2.42 (0.003802N) on October 3, but this increase was not accompanied by a further accumulation of water.

In 1929 the degree of hydration of the tissues present in the several varieties at the time maximum acidity was attained were in some cases higher, in others lower, than in 1928. As in 1928, Launette was materially lower in water content throughout the season than were the more highly acid varieties.

The degree of relationship existing between active acidity and percentage of water in the tissues is indicated by figure 1. The water in the tissues, calculated as percentage of total solids, has been plotted against the hydron concentration for all the samples of tables 1 and 2 except those of *Malus angustifolia*. (This variety was omitted for the reason that the hydron-concentration values lie entirely

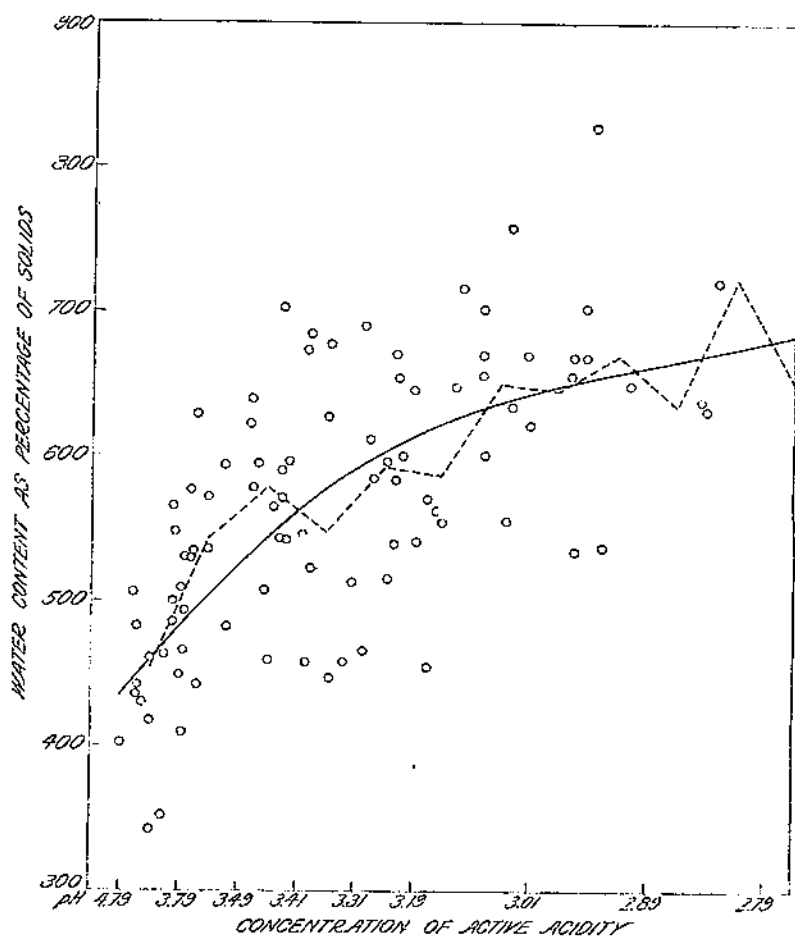


FIGURE 1.—Graph showing relationship between active acidity of expressed juice and water content of fruit, expressed as percentage of total solids, in apples during their development. Constructed from data of tables 1 and 2, omitting data for *Malus angustifolia*. The irregular line joins the group averages; the smooth line is a freehand curve averaging all the group averages.

beyond the range of those of the other varieties.) After the values for all the samples were plotted, they were averaged in groups to establish the line of group averages, and the resulting irregular line was then smoothed by a freehand curve. The slope of the curve indicates a rather high positive correlation between active acidity and percentage of water, regardless of variety or stage of development of the fruit. The slope of the curve flattens as maximum values for both active acidity and water content are reached, indicating a



lessened degree of correlation, and the scatter of the observed values about the line of regression also increases somewhat. This is exactly what would be anticipated, as it is in this region of maximum hydration that such factors as supply of water available to the plant, intensity of transpiration, and mechanical resistance to hydrational swelling offered by the anatomical structure of the fruit would exert largest effects upon the results. A considerable portion of the scatter of individual samples is attributable to varietal differences. Although the correlation is not perfect, the curve shows very conclusively that the water content of the fruit is a function of its active acidity.

The rate of percentage increase in weight of the fruit is greatest in the very young fruit and falls off rapidly with increase in age. This is apparent from the last column of tables 1 and 2, in which the increase in average weight per fruit for each interval between samplings is expressed as a percentage of the average weight per fruit at the beginning of the interval. As the intervals are not strictly uniform in length, a rigid comparison is not possible, but the data show that the percentage increase in weight is greatest in the smallest fruits sampled. Thus in 1929, sampling of Baldwin was begun when the fruits averaged 0.29 g in weight, and the increase in weight during the next 12 days was 1,206 percent, or over 100 percent per day. In the next interval the rate of increase in weight dropped to 24.9 percent per day, and in the third interval to about 6 percent. In Rambo the initial sample in the same year had an average weight per fruit of 0.39 g, the percentage increase in weight for an 8-day interval was 556.3 percent or 69.5 percent per day, in the next 21-day interval 876.5 percent or 41.7 percent per day, and in the third interval only about 2 percent per day. In the other varieties sampled in 1929 and in all the 1928 material the fruits were somewhat larger at initial sampling and the rates of increase in weight are somewhat lower, but in all cases there is a progressive decrease in the rate of increase in weight from the time sampling begins until the fruit is 5 or 6 weeks old and weighs 10 to 15 g. The period at which the fruit makes most rapid gains in total weight occurs later in the life history, when the fruit has attained one third to one half its mature weight. The distinction between percentage increase in weight and increase in total weight is shown in figures 2, 3, and 4, which include curves for both drawn from the same data.

The striking fact brought out by the graphs is the coincidence in time of the increase in active acidity, the increase in water content, and the period of most rapid percentage increase in weight. Whether these three changes begin simultaneously cannot be determined from the present data, as all three were already in progress in the youngest fruits examined, but in all cases they rise together from the first determination to the time at which maximum active acidity is reached, when water content ceases to increase, and percentage increase in the growth of the fruit abruptly slows to a fairly constant rate throughout the remainder of the period of development.

The relationship in time between changes in active acidity, water content, and rate of percentage increase in weight is presented graphically in figures 2, 3, and 4 for the 1928 series of Launette, Rambo, and *Mafus angustifolia*. These varieties are representative of the apples studied in that the level of active acidity in Launette is exceptionally

low, that in Rambo is intermediate and typical of most dessert varieties, while that of *M. angustifolia* is remarkably high.<sup>5</sup>

In Launette (fig. 2) active acidity increased more than sixfold (0.0001622N to 0.0001023N) from May 18 to 29, with a further increase to 11 times its initial concentration (0.0001778N) by June 7. In the first interval the weight increment was 497.7 percent; in the second, 152.8 percent. Active acidity was stationary by June 14, but made a further advance to 0.0001905N on June 25. The weight increments for these two periods were 86.1 and 70.1 percent, respectively. With the beginning of decline in active acidity the curve of increment in weight progressively declined. Water content rose sharply, simultaneously with the initial rise in acidity, remained

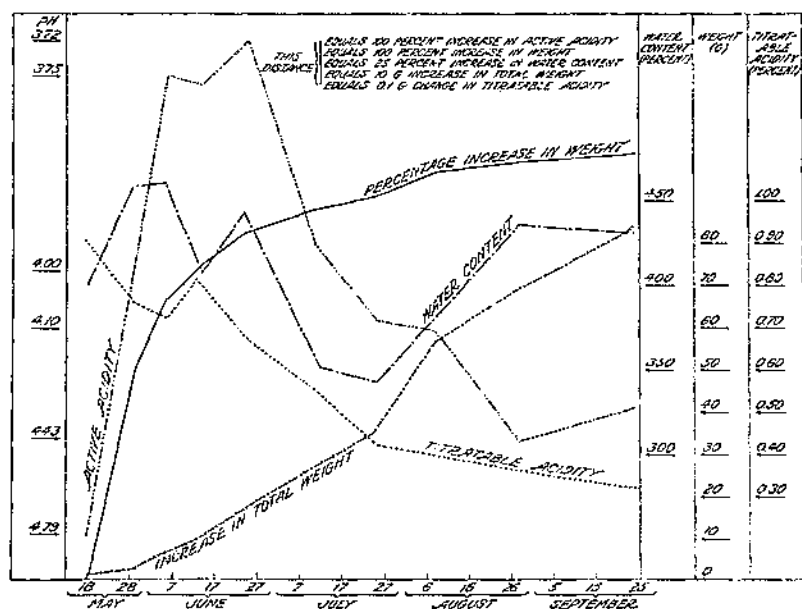


FIGURE 2.—Graph showing changes in active acidity, titratable acidity, water content, percentage increase in weight, and increase in total weight, in Launette, a French crab apple of the *douce-amère* group. The scales of the various curves are indicated on the graph.

stationary during the next interval, then declined and rose again in August and September. Titratable acidity was at the maximum in the first sample taken and declined somewhat irregularly throughout the season.

In Rambo (fig. 3) the increase in active acidity in 1928 was ninefold, from pH 3.70 to 2.74 (0.0001995N to 0.001822N). That the increase was already in progress when the fruit was first sampled is indicated by the fact that the active acidity of the initial sample of Rambo in

<sup>5</sup> Some difficulty was encountered in representing these changes by graphic methods, for the reason that they differ so enormously in magnitude. In the apples studied, the maximum active acidity attained was from 10 to 40 times the minimum concentration in the young fruit, while in the orange the maximum was over 1,300 times the minimum found. The increase in weight during the period of study ranged for the different fruits from about 10 times to more than 1,000 times the initial weight. The accompanying change in water content, expressed as a percentage of total solids, amounts at most to a doubling or tripling of the amount of water present per gram of solids. To represent these changes on the same scale is impossible. The important fact about them, however, is not their relative magnitude but their degree of coincidence in direction and in time. It therefore seemed permissible to plot them together against time, adopting for each a scale that would bring the curves within like limits and show the relation of the several processes in time. This has been done in the several graphs. The legends explain fully the scale employed in each case.

1928 had a value of pH 4.08 (0.00008318N) and rose to a maximum of pH 2.79 (0.001622N), or more than 19 times the initial concentration. Most of the active-acidity increase in 1928 occurred from May 23 to 31, and from May 31 to June 6. In the first interval the increment in weight was 566 percent; in the second, 83 percent. Water content of the tissues meanwhile rose from 530 to 722 percent of the dry matter, and titratable acidity increased from 0.94 to 1.43 percent. The curves representing active acidity, water content, titratable acidity, and increment in weight show a remarkable

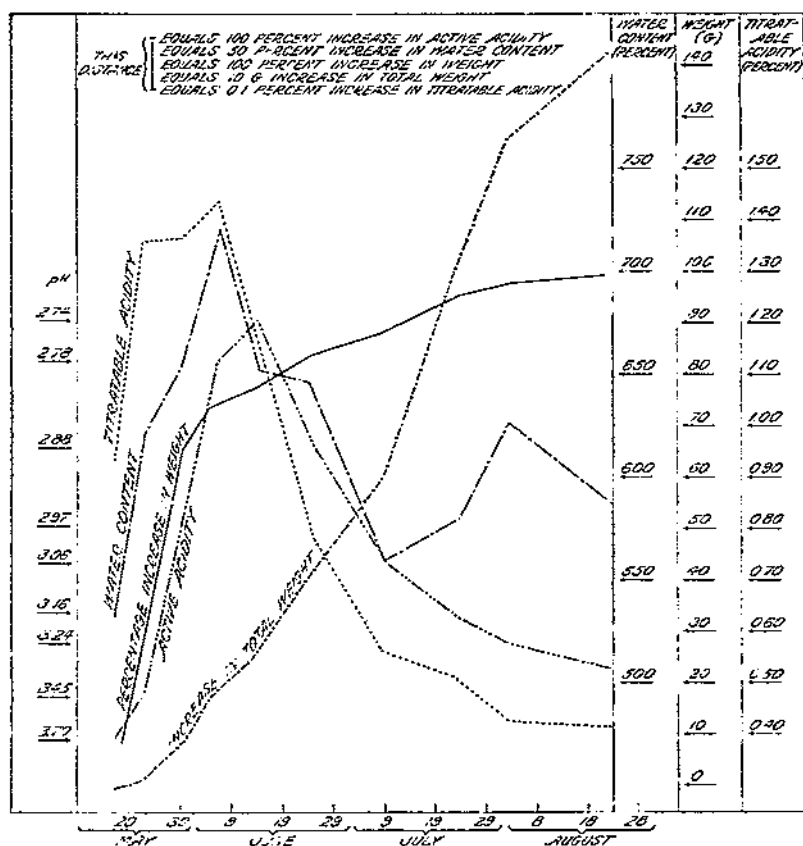


FIGURE 3.—Graph showing changes in active acidity, titratable acidity, water content, percentage increase in weight, and increase in total weight in Rambo, an early autumn dessert apple. The scales for the various curves are indicated on the graph.

parallelism in their ascending portions, the curve of increment in weight flattening sharply as the others begin to decline.

*Malus angustifolia* (fig. 4) differed from the dessert apples in that its active acidity, instead of rising rather rapidly to a maximum and then declining, continued to rise up to October 3, when it was more than 45 times the concentration found at initial sampling. The greater part of this increase occurred from May 15 to June 18 (0.00008318N to 0.002239N). This was also the period of the most rapid percentage increase in weight; the percentages being as follows: May 15 to 29, 419.7; May 29 to June 5, 114.6; June 5 to 18, 101.5,

followed by a drop to 22 percent for June 18 to 25. Water content rose rapidly from 444.3 percent of the dry matter on May 15 to 708.4 percent on June 5, after which it declined irregularly.

The degree of relationship in time between rate of rise in active acidity and rate of percentage increase in weight is shown in figure 5, which presents the data for changes in active acidity and percentage increase in weight for the Baldwin, Rambo, and Launette varieties in 1929 (table 2) in graphic form, plotted to the same scale. Not only did the period of the most rapid percentage increase in weight coincide with the period of increase in active acidity, but there was also a considerable degree of agreement between the amount of the

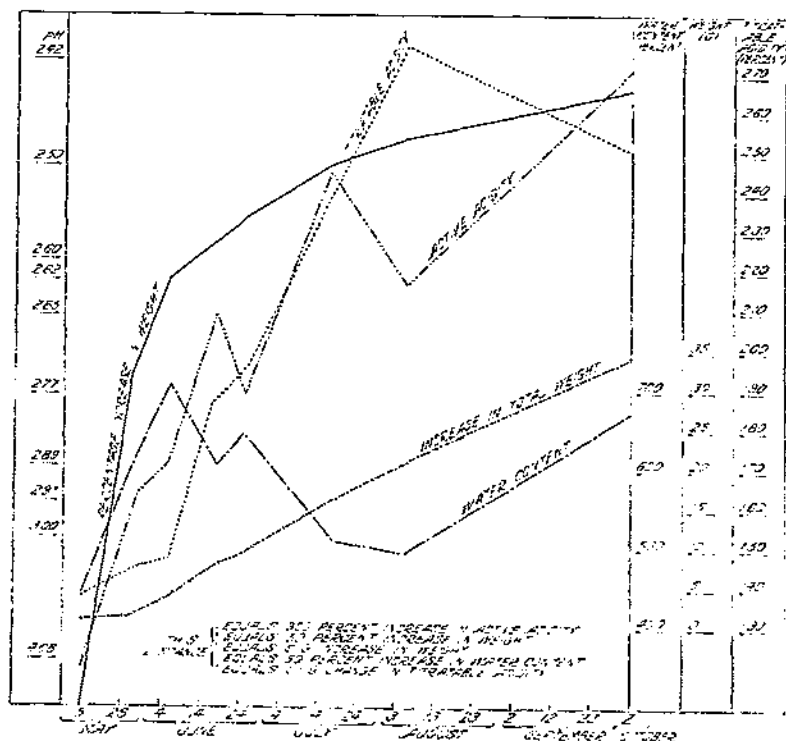


FIGURE 4.—Graph showing changes in active acidity, titratable acidity, water content, percentage increase in weight, and increase in total weight, in a native crab apple, a variety of *Malus angustifolia*. The scales for the various curves are indicated on the graph.

increase in active acidity and that of the concurrent percentage increase in weight. In Launette, active acidity increased more than fourfold in 18 days, with an accompanying weight increment of 573.7 percent. In Rambo, active acidity increased to 6.91 times the initial concentration in 8 days, with an accompanying weight increase of 556.3 percent; in the succeeding 21 days active acidity increased to 19.5 times the initial concentration, with an accompanying weight increase of 876 percent. In Baldwin, a fourfold increase in active acidity in 12 days was accompanied by an increase in weight of 1,206 percent; in the next 18 days a further increase in acidity to 7.1 times its initial amount was accompanied by a weight increase of 448.7 percent.

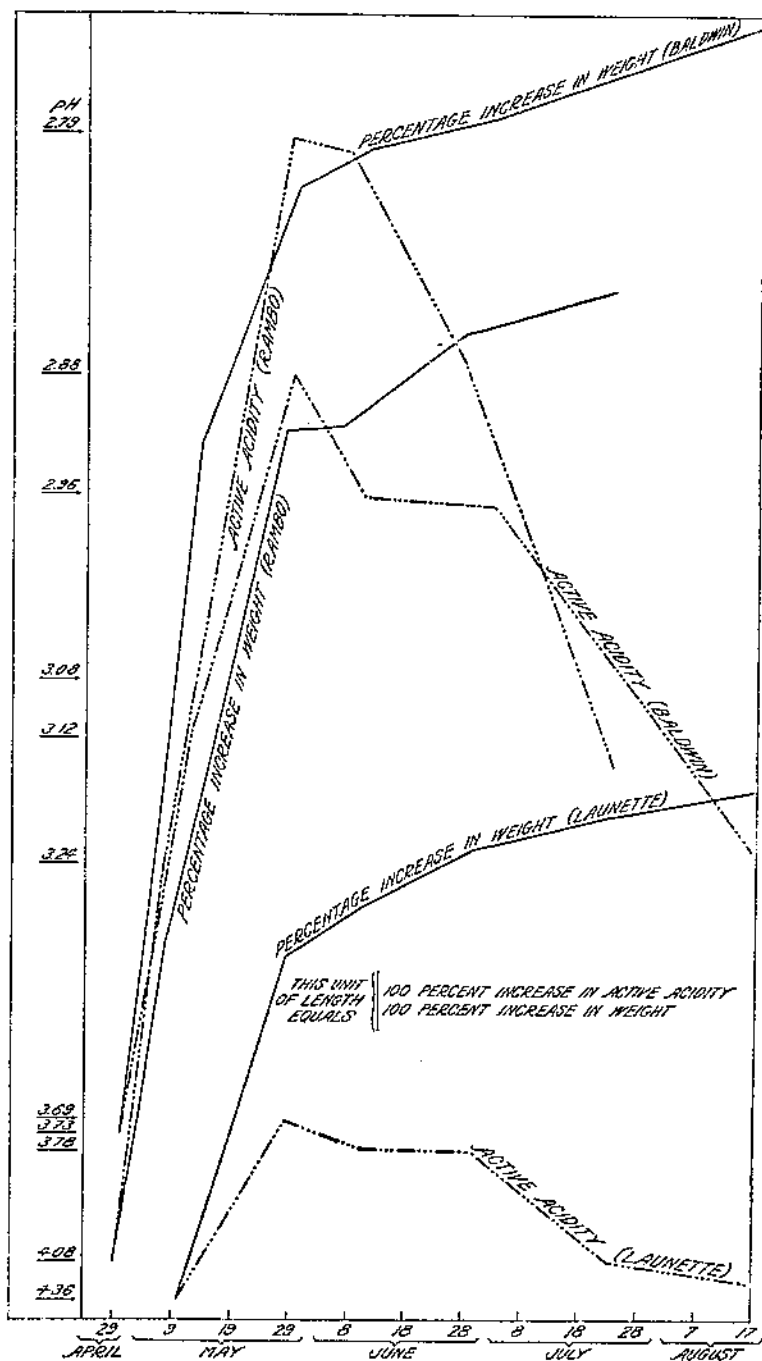


FIGURE 5.—Graph showing data for changes in active acidity and percentage increase in weight for Launette, Rumba, and Baldwin in 1920, plotted to a common scale.

The curves in figure 5 express the increase in weight per interval as percentage of weight at the beginning of the interval; hence they do not show directly the relation between the total change in active acidity and the total gain in weight during the same period. Launette increased more than fourfold in active acidity, from 0.00004365N to a maximum of 0.0002042N in 18 days, with an accompanying increase from 1.03 to 6.94 g, or 573.7 percent, in weight. Baldwin increased in active acidity from 0.0001862N to 0.001318N, or more than sevenfold, but the increase began very slightly below the maximum reached in Launette and the maximum acidity attained was 6.4 times as great as in that variety. The change was spread over 30 days, and the fruit meanwhile increased from 0.294 to 21.07 g, or 7,066 percent, in weight. Rambo increased in acid concentration in 30 days from 0.00008318N to 0.001622N, or 19½-fold, its final concentration being 8 times that reached in Launette. The accompanying increase in weight was from 0.390 to 25.0 g, or 6,310 percent.

In every instance the period of most rapid percentage increase in weight was that in which transition from a plane of low active acidity and low water content to one of high active acidity and high water content was in progress. The three changes everywhere occurred together. In some of the varieties sampling was begun very shortly after the initiation of these changes, with the result that most of their extent is indicated by the data; in others, the changes were already well under way when the first samples were taken. In every case, however, they coincided in time.

The relationship of these changes to the morphological development of the fruit is fairly clear from the work of Tetley (36), who has recently described in some detail the anatomical changes occurring in the young apple. At the request of the writer she has supplied considerable additional information as to the age of the fruit at the time of the appearance of the several stages. She divides the early development of the apple into meristematic and postmeristematic stages. In the former stage, as the name would imply, the cells are identical in appearance everywhere throughout the fruit, and nuclear divisions are abundant. This is the condition at the time the flowers open and for a few days afterward. The postmeristematic stage begins about the time the fruit has set and is indicated by the appearance of vacuolation in groups of cells scattered irregularly through the flesh while nuclear division continues elsewhere. As vacuolation proceeds, nuclear divisions become less frequent and rapid increase in size of cells presently sets in, resulting in the rapid enlargement of the fruit.

In a personal communication under date of January 3, 1931, Miss Tetley supplies the following data in regard to her material, which are quoted by permission:

Variety Wagener. May 26, 1927. Flowers opening. Diameter of apples 3 mm. End of meristematic stage.

June 2. Diameter 6 mm. Vacuolation taking place, together with nuclear divisions. Increase in size of cells beginning.

June 10. Rapid increase in size of cells beginning, also formation of large intercellular spaces.

Variety Court Pendu Plat. May 29 to June 9, 1927. Approximate date of meristematic stage.

June 6. Vacuolation of cells, together with nuclear division.

June 16. Marked vacuolation of cells, increase in cell-size noticeable.

June 16 to August 7. Large increase in size of cells and intercellular spaces.

It thus appears that in Wagener and Court Pendu Plat growing in the vicinity of Leeds, Yorkshire, England, the meristematic stage passes over into the stage of vacuolation within 6 to 10 days after blooming, and marked vacuolation and increase in size of cells are established 14 to 17 days after. The youngest fruits secured in the present work in 1929 did not exceed 10 to 12 days of age, whereas the 1928 samples ranged from 14 to 20 days. The material was therefore just entering upon the postmeristematic stage of vacuolation and increase in cell size. The fact that active acidity is minimum in the youngest and smallest samples obtained (Baldwin and Summer Rambo, 1929) and rises rather rapidly with increase in age makes it highly probable that vacuolation and rapid increase in cell size is the anatomical accompaniment of the onset of rapid increase in weight, in water content, and in active acidity.

Tables 1 and 2 show that the sugar content of the young apple remains low until the period of rapid increase in active acidity and water content has passed. It then begins a rather slow, irregular increase which continues until 4 to 5 weeks before the fruit reaches picking maturity, when accumulation of sugars materially increases in rate. The data indicate that in the apple three fairly well defined phases may be distinguished with respect to sugar: (1) An initial phase in which the sugar content remains low by reason of the fact that development of the structural framework of the fruit converts it into other forms as rapidly as it enters the fruit; (2) a succeeding phase, in which gradual accumulation occurs because transport into the fruit exceeds the demand for structural materials and the rate of starch formation; and (3) a final phase, in which an accelerated rate of transport into the fruit, together with some production of sugar from the insoluble solids, results in rapid accumulation. Throughout the life of the fruit respiration is a factor limiting the rate of accumulation of sugars; but too little is known of the respiratory rate of fruit attached to the tree, particularly of fruit in the earlier stages, to determine precisely the extent of this influence.

In the young fruit titratable acidity increases to a maximum which is usually attained before active acidity has reached its maximum. Almost immediately afterwards it begins to fall off at a rate which increases somewhat with the approach of picking maturity. In general, the titratable acidity of picking-ripe fruit is about one third that of fruit 4 to 5 weeks old. In the native crab species *Malus angustifolia*, however, titratable acidity increased throughout the entire season and showed only a very slight decrease in mid-October. It is unlike other varieties, also, in the fact that in October samples active acidity was practically unchanged or even increased.

The total-solids content of the fruit is high in the youngest sample taken and declines with increasing age, reaching the minimum at approximately the time at which the fruit attains maximum active and titratable acidity and maximum astringency; that is, about the fifth or sixth week of life. From this point total solids make rather slow and irregular but definite gains, which reach a maximum when the fruit is 10 to 13 weeks old (July 9 to 26 in the varieties here employed); afterward total solids decline somewhat with the approach of maturity.

Total astringency, which includes the total content of materials oxidizable by potassium permanganate at room temperature, follows a course paralleling the change in titratable acidity. From the initial sampling there is a rapid increase which reaches a maximum about the time titratable acidity becomes maximum in amount; there is then a progressive decrease which becomes more rapid as maturity approaches. The nature of the materials concerned in these changes is conjectural. Estimated in terms of the conventional factor for tannin, their amount is extremely large, amounting at the end of May to about 10 percent of the total solids in Paragon, Williams, and Grimes Golden, and to 20 and 25 percent, respectively, of those of Amère du Surville and Launette (table 1). The early stages of development of the orange and grapefruit and of the strawberry are characterized by a high content of permanganate-oxidizable material, but neither the relative nor the absolute amounts approach the enormous quantities present in the French cider apple Launette.

#### CITRUS FRUITS

Bartholomew, working with Eureka lemon (4) found that in 4 weeks (Sept. 10 to Oct. 10) the hydron concentration for this fruit shifted from pH 4.46 to 2.91 (0.0000346N to 0.000123N) with an accompanying change of water content from 53.9 to 75.4 percent. In the succeeding 6 months there was a gradual increase of active acidity to pH 2.30 (0.005N) and of water content to 88.9 percent (4, table 1). It was considered desirable to repeat the work of Bartholomew on several varieties of orange and grapefruit, in order to determine whether an abrupt change in acidity and water content is a usual occurrence in these less-acid fruits of the citrus group.

Collections<sup>a</sup> of 3 varieties of orange and of 2 varieties of grapefruit were made at the fruit disease field station at Orlando, Fla., at approximately weekly intervals from June 7 to November 21, 1927. Immediately after being picked, the fruits were wrapped, packed in moistened paper, and forwarded by parcel post to the laboratory at Washington, D.C. All were received in good condition. Determinations of hydron concentration and preservation of samples for analysis were made on the day of receipt, which was usually the third or fourth day from the date of picking.

Two series of samples were taken. The most complete of these consisted of fruits from the June bloom of an unnamed seedling orange and of a seedling grapefruit. At the time the first collection was made (July 15) the fruits of the orange ranged from 0.5 to 1.0 cm in diameter and averaged 0.20 g in weight. Those of the grapefruit were slightly larger and averaged 0.25 g in weight. Twelve collections were made, the last on November 21. The fruit was still immature at that date, but the removal of the workers and the temporary closing of the station made continuation of sampling impossible. The results are presented in table 3.

In addition to the June-bloom fruit, for which analyses are presented in table 3, collections of fruit from the first spring bloom (February bloom) of the same trees were made, beginning June 7 and continuing at intervals of about 3 weeks through November 21.

<sup>a</sup> Secured through the kindness of Frederick A. Wolf, formerly of the Office of Fruit Disease Investigations, Bureau of Plant Industry.



The first samples taken were consequently 12 to 14 weeks old, but were very much larger than June-bloom fruit of like age. The quantities of fruit received on June 7 and 22 were unfortunately so small that all the material was required for the hydrion-concentration determinations and no analyses could be made. The later collections were larger in amount and analytical samples were taken. No samples were collected after November 21, when fruit of the spring bloom of these varieties is moving to market in some quantity. The fruits comprising the last collection were yellowing but were still somewhat immature. Results of analyses showed a close similarity in all respects to those for the later stages of the June-bloom fruit, as will be seen from the data for the seedling orange and the seedling grapefruit presented in table 4. Apparently, at the time the earliest samples were taken, a period of fairly rapid change in active acidity was in progress in both fruits, which was practically ended before it was possible to obtain sufficient material for analysis.

TABLE 3.—Changes in weight, hydrion concentration, and chemical composition of June-bloom oranges and grapefruit in 1927

Species	Date	Average diameter	Average weight	pH		Titratable acidity	Sugars			Astringent substances			Solids			Water in pulp	Water as percentage of total solids	Increase or decrease in weight
				Pulp	Whole fruit		Reducing	Sucrose	Total	Total	Tannin	Non-tannin	Soluble	Insoluble	Total			
		Centimeters	Grams			Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent
Seedling orange	July 15	0.5-1	0.20		4.96	0.66												
	July 22	.7-1.2	.33		5.17	.66	1.60	1.10	2.70	0.880	0.155	0.725	8.80	23.81	32.61	67.39	206.6	65.0
	July 30	1.0-1.7	2.0		5.31	.66	1.98	.00	1.98	.757	.019	.738	8.32	19.47	27.79	72.21	250.8	506.0
	Aug. 3	1.9-2.5	4.5		5.78	.66	1.70	.26	1.96	1.025	.278	.747	6.84	17.00	23.84	76.16	319.4	125.0
	Aug. 10	1.9-2.7	6.9	4.87	5.76	.69	2.18	.98	3.16	1.110	.351	.759	8.16	19.04	27.20	72.80	267.6	53.3
	Aug. 12	2.1-3.3	10.0		5.33	.76	2.50	.64	3.14	1.042	.052	.990	8.24	17.54	25.78	74.22	287.9	44.9
	Aug. 20	2.6-3.7	18.5		4.79	1.16	2.73	.13	2.83	.705	.057	.648	6.16	17.10	23.26	76.74	329.9	85.0
	Sept. 2	2.3-3.9	26.2	3.60	3.99	1.16	2.12	.46	2.58	1.084	.138	.946	7.43	12.95	20.39	79.61	390.4	41.6
	Sept. 14	3.6-4.1	32.1	3.10	3.36	2.48	2.00	.72	2.72	.543	.031	.512	7.92	7.73	15.65	84.35	539.0	23.6
	Oct. 1	4.0-4.5	67.9	2.66	2.91	2.72	1.63	.78	2.31	.492	.077	.415	7.54	5.75	13.59	86.41	645.8	109.5
	Oct. 24	5.5-5.8	81.1	2.72	2.75	2.98	2.44	.96	3.40	.443	.043	.403	8.68	4.79	13.47	86.53	642.5	19.4
	Nov. 21	5.8-6.8	101.7	2.67	2.83	2.27	2.98	2.76	5.74	.398	.027	.371	8.96	3.68	12.94	87.06	672.8	25.4
	July 15	.5-1.5	.25		4.73													
Seedling grapefruit	July 22	1.0-1.5	.43		5.53	.73	.60	.30	.80	1.040	.195	.845						72.0
	July 30	1.7-2.0			5.56	1.03	1.30	.64	1.94	1.380	.575	.805	13.28	11.14	24.42	75.58	309.5	
	do	2.5-2.9	5.01		5.47	.74	1.15	.33	1.48	.770	.068	.702	13.12	9.09	23.11	76.89	332.6	1,065.0
	Aug. 3	2.5-3.3			5.76	1.05	1.30	.20	1.50	1.560	.450	1.110	12.08	10.53	22.61	77.39	342.2	
	Aug. 10	3.4-3.8	21.6	4.89	5.74	.77	1.42	.76	2.18	1.160	.355	.805	11.28	13.81	25.09	74.91	298.5	391.0
	Aug. 14	4.1-4.6	38.4		5.62	.74	1.40	.18	1.58	.800	.098	.702	9.00	14.21	23.21	76.79	330.7	56.1
	Aug. 24	4.5-5.5	60.0		5.05	.52	1.25	.52	1.77	.647	.055	.592	7.00	11.99	19.59	80.41	410.4	56.2
	Sept. 2	5.3-6.0	90.6	3.70	4.35	.92	2.12	1.50	2.62	.572	.212	.360	8.40	7.14	15.54	84.46	543.5	51.0
	Sept. 14	5.9-6.8	90.2	3.60	4.23	1.50	2.66	1.68	4.34	.399	.039	.360	8.04	5.81	13.85	86.15	622.0	7.5
	Oct. 1	7.8-9.4	240.6	3.53	4.31	1.75	2.59	2.71	5.30	.444	.054	.390	9.08	4.37	13.45	86.55	643.5	166.7
	Oct. 24	7.5-9.6	220	3.13	3.47	1.68	2.52	2.24	4.76	.427	.036	.391	8.36	3.89	12.25	87.75	716.3	8.5
	Nov. 21	9.0-9.5	244.7	3.01	3.27	1.76	2.96	3.35	6.31	.380	.007	.373	9.52	3.88	13.40	86.60	646.2	11.2

<sup>1</sup> 0.000004898N.<sup>2</sup> 0.00001349N.<sup>3</sup> 0.001778N.<sup>4</sup> 0.002138N.<sup>5</sup> 0.00001288N.<sup>6</sup> 0.000001738N.<sup>7</sup> 0.000977N.<sup>8</sup> 0.000537N.

TABLE 4.—Changes in weight, hydron concentration, and chemical composition of February-bloom oranges and grapefruit, from June 7 to Nov. 21, 1927

Species	Date	Average diameter	Average weight	pH		Titratable acidity	Sugars			Astringent substances			Solids			Water in pulp	Water as percentage of total solids	Increase or decrease in weight
				Pulp	Whole fruit		Reducing	Sucrose	Total	Total	Tannin	Non-tannin	Soluble	Insoluble	Total			
		Centimeter	Grams			Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent
Seedling orange	June 7	2.0-2.5	7.8		1 3.48													
	do.	3.5	26.0		2.93													233.3
	June 22	4.5-5	61.2		2 2.80													135.4
	July 15	3.5-5	57.5		3.03	2.31	1.86	1.15	3.01	0.417	0.036	0.381	7.54	4.20	11.74	88.26	751.8	-6.0
	Aug. 10	4.5-5.5	65.7		3.06	1.66	2.74	1.23	3.07	.488	.062	.426	8.60	5.60	14.20	85.80	604.2	14.2
	Aug. 26	5.5-6.4	103.6	3 2.92	3.15	1.61	2.64	.61	3.25	.465	.032	.423	7.36	6.72	14.08	85.92	610.2	57.6
	Sept. 12	5 8	97.6	4 2.70	3.16	2.04	2.64	1.60	4.24	.420	.042	.378	7.88	4.78	12.66	87.34	689.8	-5.8
	Oct. 1	5.6	130	5 2.76		2.26	2.50	4.10	6.60	.730	.070	.660	8.48	4.23	12.71	87.29	686.8	33.2
	Oct. 24	5.8-6.5	122	6 3.07	3.16	1.58	3.44	2.79	6.23	.431	.075	.356	9.04	2.84	11.88	88.12	741.7	-6.1
	Nov. 21	6.2-7	152.2	7 3.22	3.35	.96	5.40	4.54	9.91	.358	.016	.342	11.20	2.42	13.62	86.38	634.2	24.7
	June 7	1.0-5.5	51.0	8 3.03														26.8
Seedling grapefruit	June 22	5.0-5.5	61.7		3.41													153.4
	July 12	7.0-8	164		3.44	1.50	1.75	1.65	3.40	.514	.026	.488	8.20	4.96	13.16	86.84	659.8	53.4
	Aug. 10	8.5-10.6	251.6		3.40	1.34	1.64	2.02	3.66	.478	.038	.440	7.60	6.66	14.26	85.74	601.2	72.2
	Aug. 24	10.2	433.3		3.43	1.60	2.12	1.99	4.11	.513	.068	.445	7.80	7.26	15.06	84.94	564.0	-29.5
	Sept. 13	8.8-9.7	305.2	7 3.49	3.38	1.53	2.79	2.30	5.09	.424	.044	.380	8.40	3.63	12.06	87.94	729.1	60.8
	Oct. 1	9.7-10	491		3.11	1.31	2.78	3.92	6.70	.710	.070	.640	9.04	2.42	11.46	88.54	772.6	5.9
	Oct. 24	9.5-10.4	520		3.35	1.67	4.10	2.18	6.28	.370	.034	.336	9.45	2.92	12.40	87.60	706.4	-17.1
	Nov. 21	10.8-11	431		3.15	1.50	3.80	4.16	7.96	.365	.009	.356	10.04	2.27	12.31	87.69	712.3	

<sup>1</sup> 0.0003311N.

<sup>2</sup> 0.00198N.

<sup>3</sup> 0.001202N.

<sup>4</sup> 0.001095N.

<sup>5</sup> 0.0006026N.

<sup>6</sup> 0.0001175N.

<sup>7</sup> 0.0002042N.

<sup>8</sup> 0.0007762N.

<sup>9</sup> 0.0004467N.

Less complete series of samples of the February-bloom fruit of two varieties of orange, Homosassa and Parson Brown, and of Royal grapefruit were obtained. Sampling was begun on June 7 and continued to September 14, when it had to be discontinued. The results of the analyses of these partial series show for the period covered such close agreement with the series of table 4 that the data need not be presented. In the Parson Brown and Homosassa oranges the hydron-concentration values for the pulp changed from 2.93 and 3.33 on June 7 to 2.73 and 2.88 on July 12, respectively, and afterward remained nearly stationary. In the Royal grapefruit the hydron-concentration value of the pulp changed from 3.76 on June 7 to 3.23 on July 12 and reached 3.09 on August 26, remaining at the same value on September 14. In the Homosassa and Parson Brown oranges, as in the seedling orange, change in active acidity had largely been completed by the end of June, whereas in both the grapefruits it continued at a slower rate into August.

The preparation of the material for analysis presented some difficulties. In young fruit less than 2.5 to 3 cm in diameter, the segments of the pulp are so small and widely separated that a large quantity of fruit is required to yield sufficient pulp for analysis. As the quantity of available fruit was limited, it was necessary to make up the samples for analysis, without attempting to separate pulp from peel, by cutting slices through the center of a number of fruits. After September 2 the fruits had reached such size that the pulp could be separated from the peel, rag, and seeds, and the samples preserved for analysis on and after that date consisted of pulp only. Before September 2 the determinations of hydron-concentration values were made upon juices obtained by grinding the entire fruit in a food chopper and expressing the juice with a tincture press. After that date determinations upon juices so obtained were supplemented by determinations upon juices from the pulp alone.

The determinations of hydron concentration were made in duplicate with two Bailey hydrogen electrodes, and agreed within 0.05 pH. The juice of immature oranges contains substances which react with quinhydrone; consequently, quinhydrone could not be used for determining the hydron concentration.

The data of table 3 on changes in active acidity of whole fruit and of pulp, in water content, in total weight, and in percentage increase in weight per interval for seedling orange and seedling grapefruit are represented graphically in figures 6 and 7, where they are plotted against time.

For both fruits there is a period, which extends up to August 12 for the orange and to August 16 for the grapefruit, in which the active acidity of the fruit at first decreases and then fluctuates irregularly at levels markedly below the initial values. Water contents also fluctuate, showing a small net gain. During this period the fruit makes very rapid gain in weight; the oranges increase from 0.20 g to 10 g, the grapefruit from 0.25 g to 38.4 g. This increase occurs almost wholly in the mesocarp, the segments of the pulp remaining very small and widely separated. When hydron-concentration determinations upon the pulp were first attempted, on August 10 and 16, the pulps of individual fruits weighed less than 1 g each and it was difficult to secure sufficient juice for the determinations.

About mid-August rather abrupt changes in the relative volume of mesocarp and pulp set in. The pulp began to increase at a rate considerably greater than that of the accompanying increase in volume of the fruit, so that, as development proceeded, the mesocarp tissues were compressed into a progressively thinner and thinner enveloping layer. Hydrion concentration rose very rapidly in the orange and less rapidly in the grapefruit. From August 10 to October 1, the pulp of the orange increased 158-fold in active acidity (pH 4.87 to 2.66), subsequently changing very little. The acidity of the whole

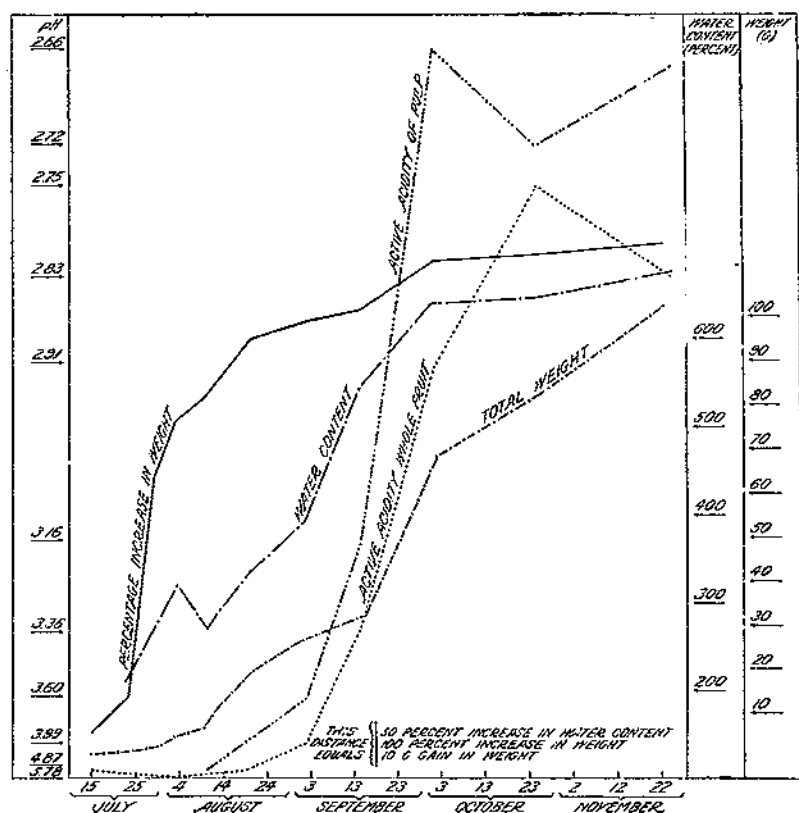


FIGURE 3.—Graph showing changes in active acidity, water content, total weight, and percentage increase in weight for seedling oranges, June bloom, from data of table 3. The scales of the various curves are indicated on the graph.

fruit increased less rapidly and continued to rise until October 23. The active acidity of the grapefruit increased more slowly and the rise was still in progress on November 21, at which time it had reached pH 3.27 for the whole fruit and pH 3.01 for the pulp. These values are equivalent, respectively, to 309 and 76 times the corresponding active-acidity concentrations found on August 10. At all stages the acidity of the pulp was higher than that of the whole fruit, and the amount of increase in acidity during any interval was considerably greater in the pulp. The fruit was still quite immature when circumstances compelled discontinuance of sampling on November 21. The fruit from

the February bloom was at that time market ripe. The hydron-concentration data for the later samples of this fruit (table 4) show maximum acidity values of pH 2.70 for the orange (pulp) on September 12 and pH 3.11 for the grapefruit (pulp) on October 1; afterward there was a decrease in acidity, which was much more pronounced in the orange. This would indicate that the June-bloom fruit had nearly or

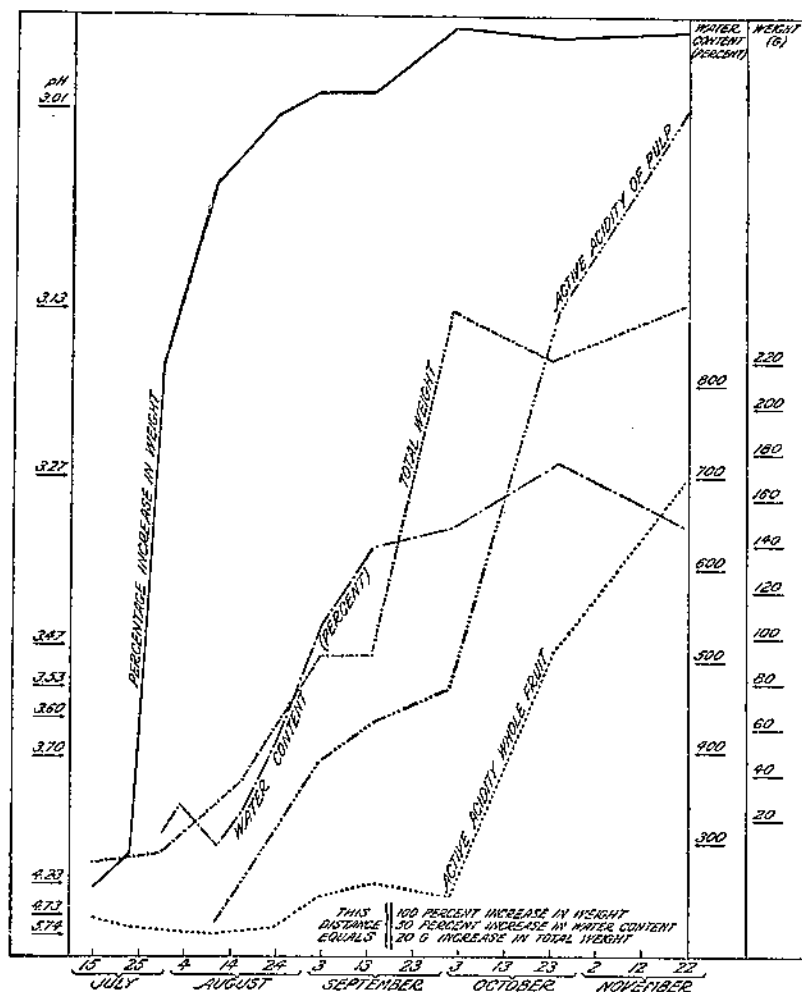


FIGURE 7.—Graph showing changes in active acidity, water content, total weight, and percentage increase in weight for seedling grapefruit, June bloom, from data of table 3. The scales for the various curves are indicated on the graph.

quite attained its maximum active acidity in the samples taken November 21.

The increase in active acidity in the June-bloom fruit was accompanied by a rapid rise in water content, which between August 10 and October 1 increased in the orange from 267 percent to 635 percent and in the grapefruit from 298 percent to 643 percent, calculated as percentage of dry matter. After October 1, water content fluctuated

within fairly narrow limits. Data for the February-bloom fruit (table 4) indicate that although the water content of the fruit fluctuated considerably in the last 3 or 4 months prior to picking, the general level maintained during this period was not greatly above that reached by the June-bloom fruit in October and November.

The graphs (figs. 6 and 7) show that the increase in active acidity and the increase in water content coincided in time. In the orange both began about August 10 and were completed about October 1; in the grapefruit both continued up to October 23, when water content began to drop off somewhat despite a continued rise in acidity. The crab apple (*Malus angustifolia*) showed similar behavior.

The earlier development of the citrus fruits differs from that of apples in one respect (figs. 6 and 7). In apples the period of maximum percentage gain in weight coincides with the period of most rapid increase in active acidity and in water content. In both orange and grapefruit (June bloom), however, the maximum percentage increase in weight occurred from July 22 to 30, and the rate fell off progressively in the succeeding intervals. Throughout this period the active acidity remained stationary or decreased, and water content made relatively small gains. By the time the rise in acidity and in water begins on August 10, the curves of percentage growth rate have become markedly flattened. They are somewhat irregular throughout their later course, but show no consistent relation to the concurrent changes in acidity and in water content. As already suggested, this difference between the citrus fruits and the apple is probably due to the fact that the citrus fruit consists of two highly distinct regions, mesocarp and juice sacs, or pulp, which do not develop together. Up to a diameter of 2.5 to 3.5 cm the increase in size of the fruit is almost wholly due to growth of the mesocarp; the glandular hairs which later develop into the pulp meanwhile remaining nearly constant in amount and making up only a very small percentage of the total volume of the fruit. The rate of increase in weight during this period of growth of the mesocarp is initially very high but falls off rapidly from week to week (figs. 6 and 7).

Increase in volume of the pulp begins simultaneously with the rise in active acidity and the large and sustained rise in water content. In every sample of June-bloom fruit taken after August 10, the pulp made up a larger proportion of the entire fruit than in the preceding sample. During the period from August 10 to October 1, the fruit was transformed from a structure consisting chiefly of mesocarp with a small percentage of pulp into one consisting chiefly of pulp. The rapid increase in volume of pulp was concurrent with the rapid increase in active acidity and in water content. This fact is suggested by the irregular form of the growth curve but is not clearly evident because of the inclusion in the total weight of the slower-growing mesocarp. Unfortunately, the full significance of the change in relative volume of mesocarp and pulp was not immediately recognized, so that determinations of weight of the two tissues separately throughout the series were not made. Such data if available would yield two curves, that for the mesocarp rising abruptly in July and flattening in August, and that for the pulp having its steepest portion in September.

The data of table 4 show a very decided decrease during October and November in the titratable acidity of the ripening orange, while

those of the grapefruit show little change. Collison (8) found much smaller decreases in titratable acidity in the several varieties of grapefruit which he studied than in various orange varieties examined over the same period, which extended from October 1 to the following May. Hawkins (21) found a slow decrease in titratable acidity in grapefruit picked at 4-week intervals from July 27 to November 1, followed by a slight increase in the December 1 samples. With respect to changes in both active and titratable acidity the grapefruit appears to stand in an intermediate position between the lemon, in which no appreciable decrease in either occurs with the oncoming of maturity (4, 7), and the orange, in which there is a marked decline in both as ripening proceeds.

The general results in the present study are in complete agreement with those of Bartholomew (4) and of Oppenheim and Winik (25) in showing that in both oranges and grapefruit there is a rather abrupt and large increase in both active and titratable acidity during the period of most rapid growth, accompanied by an abrupt rise in water content. This transition occupies only a few weeks, and it carries the fruit from the condition of high solids and low water content, with low active and titratable acidity, characteristic of the young fruit, to the condition of low solids and high water content, with high active and titratable acidity, characteristic of the full-grown fruit. Both before and after this period of rapid change there is a period in which all these changes occur at comparatively slow rates. It is only after the rapid changes have been completed that any appreciable accumulation of sugars or reduction of insoluble solids begins.

#### CHERRIES

Five varieties of cherries, namely, Baumann May, Montmorency, Napoleon (Royal Ann), Nouvelle Royale, and St. Medard, were employed. Baumann May is an early sweet cherry of small size and mediocre quality, now passing out of cultivation; Nouvelle Royale is a late hybrid Duke, supposedly a cross of Early Richmond and May Duke; St. Medard is a black sweet variety of French origin that does not appear to have been introduced into cultivation in the United States; Napoleon is the most popular firm-fleshed sweet cherry; Montmorency, the most widely grown sour cherry. The varieties employed were chosen to represent early, late, sour, and sweet varieties insofar as the available material permitted.

The studies were begun in 1927 and continued for 3 years. Material for analysis was collected in each year, but no material of Napoleon or of Nouvelle Royale was available in 1929. The results of the analyses of the 1928 and 1929 series are presented in table 5.



TABLE 5.—Changes in hydron concentration and chemical composition of cherries throughout development

Series and variety	Date	Average diameter	Color or condition	Average weight	Active acidity		Acidity of fresh juice	Sugars			Titratable acidity	Astringent substances		Solids			Water as percentage of total solids	Increase in weight
					pH	Cu		Reducing	Sucrose	Total		Total	Non-tannin	Soluble	Insoluble	Total		
1928 series:		Mm		Grams			Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	
Baumann May	May 5	6-9		0.176	4.79	0.00001622N		2.65	1.05	3.70	0.472	0.258	0.193	5.80	5.045	11.745	751.8	
	May 15	8-9.5		.577	4.20		0.951	3.00	.32	3.32	.500	.232	.194	5.96	11.915	17.875	459.0	
	May 21	10-14	White	1.58	3.51	.000300N	.038	4.81	.55	5.36	.750	.138	.082	8.04	2.194	10.234	877.5	
	do	15-18	Red	2.22	3.54		.850	6.09	.39	7.08	.652	.080	.040	0.72	1.645	11.265	788.0	
	May 24	17-18.5	Dark red	2.63	3.53		.843	8.20	.44	8.64	.786	.092	.053	11.40	1.070	13.070	665.1	
apoleon	May 29		Soft ripe	2.68	3.76	.0001738N	.815											
	May 5	3.5-8		.121	4.74	.0000182N		.08	1.50	2.48	.632	.490	.332	5.100	0.522	11.622	700.5	
	May 15	10-12		.04	4.40		.620	2.64	.20	2.84	.417	.458	.358	5.320	0.425	11.745	751.8	
	May 21	10-14		1.04	4.24		.717	1.77	.30	2.10	.530	.446	.273	4.640	0.724	14.364	595.3	
	May 28	12-15	Whitening	1.60	4.05		.817	2.46	.46	2.92	.622	.358	.268	4.920	10.101	15.021	565.7	
St. Medard	June 5	16-18	Red	3.23	3.60		.018	5.15	.52	5.67	.752	.207	.135	7.720	1.845	9.565	940.0	
	June 22	10-20	Ripe	4.19	3.42			7.98	.77	8.75	.634	.183	.108	13.120	1.339	14.459	591.5	
	May 18		Canning ripe		3.38	.0004169N												
	May 8	5-8		.480	4.52	.0000302N	.884	2.70	.62	3.32	.664	.482	.244	6.080	0.362	12.442	703.8	
	May 16	7-9		.780	4.16		.884	2.78	.38	3.16	.555	.480	.308	5.720	8.801	14.521	588.7	
Montmorency	May 21	14-11		1.06	3.77		1.125	2.07	.00	2.07	.645	.405	.164	4.640	11.897	16.537	504.9	
	May 28	15-16	White	3.00	3.25		1.206	0.08	.13	0.21	.975	.222	.073	8.120	2.814	10.934	814.9	
	May 31	16-18	Red		3.44		1.313	0.20	1.73	8.02	1.098	.207	.070	0.36	1.700	11.060	804.1	
	June 5	19-21		4.17	3.19		1.534	8.20	.56	8.76	1.255	.177	.063	10.68	1.387	12.067	729.2	
	June 7	20-22	Ripe	4.49	3.18	.0006607N	1.782	9.20	.57	9.86	1.205	.215	.089	12.48	1.216	13.696	630.0	
Nouvelle Royale	June 9	20-22			3.36	.0004365N												
	May 8	2-4		.231	4.74	.0000182N												
	May 16	6-8		.590	4.23													
	May 21	8-12		.635	4.11		.877	2.69	.50	3.19	.604	.861	.412	0.280	9.013	15.293	554.0	
	May 28		White	.735	4.21		.964	1.40	.24	1.73	.682	.701	.320	4.960	13.390	18.326	445.8	
Nouvelle Royale	June 5	10-14	Full red	1.22	3.56		1.092	1.24	.40	1.64	.717	.070	.346	5.040	20.095	25.135	207.9	
	June 18		Canning ripe	3.51	2.91	.00123N	1.641	1.10	.93	2.03	1.100	.782	.348	4.960	4.333	9.293	976.4	
	June 22			4.40	3.06	.000871N	1.960	8.62	.84	9.46	1.645	.438	.187	15.32	1.375	16.695	499.1	
	May 16	6-7		.82	4.31	.00004808N		2.60	.16	2.76	.635	.424	.193	0.80	0.980	16.780	495.0	
	May 28			1.35	4.08		1.005	1.86	1.26	3.12	.780	.313	.157	5.28	14.756	20.036	399.2	
Nouvelle Royale	June 5	17-18		3.84	3.34		1.192	8.80	.30	9.10	.901	.122	.049	10.92	1.900	12.520	698.7	
	June 15		Ripe	3.96	3.28	.0005348N	1.561	9.40	.90	10.36	1.040	.177	.093	10.52	1.346	11.866	743.1	

TABLE 5.—Changes in hydron concentration and chemical composition of cherries throughout development—Continued

Series and variety	Date	Average diameter	Color or condition	Average weight	Active acidity		Acidity of fresh juice	Sugars			Titratable acidity	Astringent substances		Solids			Water as percentage of total solids	Increase in weight
					pH	Cn		Reducing	Sucrose	Total		Total	Non-tannin	Soluble	Insoluble	Total		
1929 series:		Mm		Grams			Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent
Baumann May.	Apr. 27	6-10			4.30	0.00035012N		2.20	0.58	2.78	0.860	0.380		5.84	11.073	16.913	491.26	
	May 6		Greenish white		3.20	.000631N		4.37		4.38	.874	.276		6.84	2.379	9.219	984.72	
	do.		Reddened		3.42			6.24	.16	6.40	.800	.231		8.60	1.443	10.043	895.72	
	May 10		Firm ripe		3.58			8.25	.17	8.43	.880	.208		10.76	1.465	12.225	717.99	
	May 13		Full ripe		3.52			10.42	.14	10.56	.981	.212		13.92	1.035	14.955	568.87	
Montmorency	Apr. 27	6-9			4.26	.00005495N		2.13	.64	2.17	.833	.968		5.00	6.028	11.028	806.78	
	May 6				4.08			2.15		2.15	.961	.743		5.36	12.401	17.761	463.03	
	May 14			0.83				1.28		1.28	.941	.864		5.44	18.251	23.691	322.10	
	May 22			.90	3.91			.61	.03	.64	.927	.575		3.64	15.364	19.004	426.21	8.4
	May 27		Whitening	1.25	3.35			1.70	.04	1.80	.954	.346		3.80	3.288	7.088	1,310.84	38.8
	June 3			2.17	3.21			3.08	.02	4.00	1.222	.335		6.52	1.886	8.406	1,089.62	73.6
	June 7		Light red		3.01	.0009772N		7.13		7.13	1.626	.407		10.92	1.286	12.206	719.27	56.6
	June 11		Full ripe	3.40	3.10			8.12	.18	8.30	1.740	.393		12.16	1.406	13.566	637.14	
	Apr. 27	9-10			4.10	.00007943N		2.55	.00	2.61	1.055	1.006		6.00	5.900	11.900	740.34	
	May 6	11-12			3.36			2.31	.14	2.45	.941	.554		5.08	12.048	17.128	483.84	
St. Medard	May 14				3.08			3.89	.08	3.97	1.183	.416		6.16	1.928	8.288	1,106.56	
	May 17		Reddish white		3.32	.0004786N		5.51	.03	5.54	1.357	.376		8.16	1.418	9.578	944.06	

Insofar as possible, sampling was begun when the young fruits were 6 to 8 mm in length and from 4 to 6 mm in diameter and still retained the "husk." As the stones had not begun to harden, their separation from the flesh was tedious and difficult.

In cherries there is a progressive increase in active acidity from the youngest fruits obtainable up to those of full size. In the smallest fruits obtained the hydrion concentrations of the juices obtained were on the general level of those of aqueous extracts of the twigs, and differed very little with variety; in 1928 the value for the smallest fruits of Napoleon and Montmorency was 4.74, for Baumann May 4.79, and for Nouvelle Royale and St. Medard 4.31 and 4.52, respectively. There was a very rapid rise in active acidity with increase in size, attaining a maximum about the time the chlorophyll disappeared and the fruit began to redden, and decreasing somewhat as the fruit became fully ripe. The amount of the change differed with the variety. In Montmorency the change from pH 4.74 to 2.91 (0.0000182N to 0.00123N) represents a nearly seventyfold increase in active acidity; in Napoleon, Baumann May, and St. Medard active acidity showed an increase of twentyfold to twenty-threefold, and in the series of Nouvelle Royale, which is lacking in very early samples, the increase was more than tenfold. The time occupied by the change ranges from 40 days in Montmorency to 16 days in Baumann May, but in all cases the major portion of the change occurred in a shorter period, which was also the period of most rapid percentage increase in weight. Moreover, the change was in every instance practically completed before the beginning of the rapid increase in sugar content characteristic of the ripening period. In all cases there was a progressive increase in titratable acidity up to red ripeness, after which it usually declined somewhat as the fruit became overripe, as was likewise found to be the case by Hartman and Bullis (20).

The changes in active acidity, water content, and percentage increases in weight for Montmorency, a sour cherry, and St. Medard, one of the sweet varieties, are represented graphically in figure 8, the curves being drawn to the same scale. In both fruits the curve representing active acidity rises from the date of initial sampling until May 21 in Montmorency and May 28 in St. Medard, when it broke downward, then resumed its rise until red ripeness was reached. The curve representing percentage increase in weight has a similar break; in both varieties it rises sharply during the initial rise in acidity, then flattens somewhat as acidity ceases to rise, the rate of increase in weight varying with the fluctuations in rate of acidity increase. In both varieties water content decreases from initial sampling until the stone has hardened, then rapidly rises.

The increase in active acidity in the sour cherry Montmorency reaches a maximum nearly twice as high as that in the sweet variety St. Medard. It also undergoes greater decrease during ripening, so that the concentration in the ripe fruit is slightly less than twice that in St. Medard. The rise of water content in the St. Medard (to 814 percent) is less than that in Montmorency (to 976 percent), but its decline is also very much less, so that the water content at full ripeness is considerably higher in St. Medard than in Montmorency.

In all the varieties, as in Montmorency and St. Medard, there is a rapid hydration of the tissues accompanying the period of most rapid increase in acid concentration. This is also the period of most rapid

percentage increase in weight, chiefly due to intake of water. In the St. Medard, the most rapid increase in active acidity occurred between May 21 and 28. On May 21 the weight of the flesh was 1.06 g, of which 0.175 g was solids and 0.885 g was water. On May 28 the flesh weighed 3.00 g, of which 0.328 g was solids and 2.672 g water. While the solids increased 87 percent the water content increased 201 percent. In Montmorency the most rapid increase in acidity occurred between June 5 and 18. In this period the solids present per fruit increased only 6.5 percent (0.306 g to 0.326 g) while the water increased 248 percent (0.914 g to 3.184 g). A similar change occurred in the other varieties, resulting in a condition of maximum hydration of the fruit about the time chlorophyll disappeared and reddening had

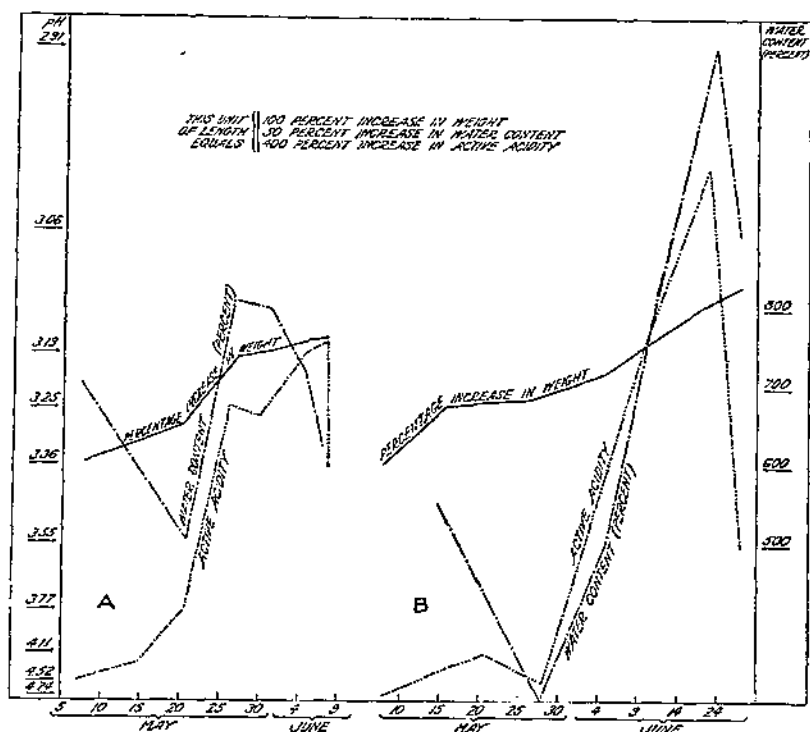


FIGURE 8.—Graph showing changes in active acidity, water content, and percentage increase in weight in St. Medard (A) and Montmorency (B) cherries during development and ripening, from data of table 5, plotted to common scale.

set in. As ripening proceeded there was a marked decline in water content as sugars accumulated in the fruit.

The course of the change in water and solids in the cherry differs somewhat from that in other fruits. In the very young fruits there is an initial stage of rather high moisture content, followed by a very abrupt decline. As the fruit whitens, water content again rises rapidly to a maximum, then declines as the fruit becomes fully ripe. The firm-fleshed varieties Napoleon and Montmorency attain a somewhat higher water content in the whitening period than do the other varieties studied, but return to the general level of the others by the time they are fully ripe.

At various periods collections of leaves and of fruiting spurs and twigs were made in order to secure some data on the range of hydriion concentration in the vegetative parts. As it was impossible to express any liquid from the pulp resulting from grinding leaves or twigs in a food chopper, the ground material was transferred to beakers, covered with a measured quantity of distilled water, macerated for 30 minutes, and pressed in a tincture press. By prolonged pressure it was possible to remove about 95 percent of the added water from the ground twigs, but only about 80 percent could be recovered from the excessively viscous leaf pulp. Hydriion determinations were made upon these aqueous extracts (table 6). A second extraction with water yielded values differing by only 0.01 to 0.04 pH from those obtained with the first extracts.

A few hydriion determinations made upon the expressed juice of the crushed seeds indicated that the active acidity of the very young embryo is low and that it rises to a maximum about the time the fruit becomes full grown and declines again at full ripeness, but the determinations were too few to be conclusive.

TABLE 6.—*Hydriion concentration of leaves, young wood, and seeds in cherries*

Variety	Date	Part	pH
Napoleon.....	May 5, 1928	Leaves, water extract.....	4.74
	do.	Wood, 1-year twigs.....	4.40
	May 8, 1928	Leaves, water extract.....	5.75
St. Medard.....	do.	Wood, season's growth.....	4.33
	May 27, 1927	1-year stems.....	4.80
	Apr. 27, 1928	Seeds of fruits 6-9 mm in diameter.....	5.44
	May 5, 1928	Leaves, water extract.....	5.41
	do.	Wood, 1-year twigs.....	4.51
Baumann May.....	May 6, 1929	Seeds of slightly reddened fruits.....	3.85
	May 13, 1929	Seeds of full-ripe fruits.....	5.33
	May 27, 1928	Seeds of whitening fruits, average weight 1.25 g.....	4.57
Montmorency.....	June 7, 1928	Seeds of full-ripe fruits.....	5.20

## BERRIES

### STRAWBERRIES

The strawberry was chosen for study as a fruit having a very short developmental period, since it passes from the flowering stage to full ripeness in approximately 4 weeks.

A portion of the material collected for a comparative study of the biochemistry of development in the strawberry was utilized in the present work. Three commercial varieties, namely, Dunlap, Howard 17, and Progressive, were sampled in 1927. Four pickings at intervals of 5 to 8 days were made, beginning when the largest berries on the plants were 10 to 12 mm in diameter and continuing until the fruit was fully ripe. The berries were transferred to the laboratory immediately after being picked, and each picking was graded into two or more lots on the basis of size and apparent maturity; no determinations of volume or weight were made. A portion of each lot was preserved for chemical analysis; the remainder was ground and expressed for the hydriion determinations, which were made with the Bailey hydrogen electrode.

The results obtained in 1927 led to a repetition of the work in 1928. Studies were made on the same varieties as well as on a number of others, and sampling was begun at an earlier stage in the development of the fruit. Blooming began 6 to 10 days later in 1928, and at the first sampling on May 17 it was possible to collect berries not more than 4 to 8 mm in diameter and having the withered petals still adhering to them.

The analytical data for the 1927 series are assembled in table 7. The results for the 1928 series are so completely in agreement with those of the 1927 series that it seems unnecessary to present the analytical data in full. The results of the determinations of hydron concentration, titratable acidity, and water content are assembled in table 8.

TABLE 7.—Changes in hydrion concentration and chemical composition of 3 varieties of strawberries at various stages of development in 1927

Variety	Date	Diameter	Active acidity		Titratable acidity	Sugars			Astringent substances			Solids			Water	Water as percentage of total solids	Stage of development
			pH	Cm		Reducing	Sucrose	Total	Total	Tannin	Non-tannin	Soluble	Insoluble	Total			
Dunlap	May 12	10-12	3.68	0.0002089N	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Very hard green.
	May 20	10-12	3.68	0.0002089N	0.910	1.25	0.23	1.48	1.070	0.652	0.418	4.48	8.79	13.27	86.72	653.5	Do.
	do	12-15	3.57	0.0002089N	.983	1.13	.39	1.52	.740	.476	.264	4.08	8.15	12.23	87.76	717.5	Dark green.
	do	15-20	3.57	0.0002089N	.942	1.41	.35	1.76	.510	.300	.210	4.04	7.28	11.32	88.67	783.3	Do.
	May 28	15-20	3.48	0.0002089N	1.050	1.54	.12	1.66	.482	.276	.206	4.20	0.83	11.03	88.97	806.6	Whitening.
	do	18-25	3.48	0.0002089N	1.082	1.92	.37	2.29	.378	.230	.148	4.56	4.92	9.48	90.52	954.7	25 percent pale red.
	do	18-28	3.35	0.0002089N	1.030	2.28	.30	2.58	.274	.148	.126	4.76	3.93	8.69	91.31	1,050.7	Fairly deep red.
	do	18-28	3.43	0.0002089N	.942	3.22	.46	3.68	.290	.210	.080	5.72	3.69	9.41	90.59	962.7	Soft ripe.
	June 3	18-28	3.34	0.0004571N	.740	3.32	1.10	4.42	.254	.128	.126	5.76	3.08	8.84	91.16	1,031.2	Very hard.
	May 12	10-12	3.98	0.001047N	.844	1.80	.38	2.18	1.294	.920	.370	5.00	6.44	11.44	88.36	772.3	Do.
	May 20	10-12	3.68	0.001047N	.840	1.92	.51	2.43	.620	.390	.230	4.64	5.34	10.08	90.02	902.0	Hard green.
	do	12-20	3.31	0.001047N	.864	2.40	.50	2.90	.480	.304	.176	5.00	4.66	9.66	90.34	935.2	Whitening.
Howard 17	do	16-21	3.20	0.001047N	.920	2.79	.71	3.50	.340	.210	.130	5.60	3.08	8.68	91.32	1,052.0	40 percent pale red.
	May 28	25-30	3.35	0.001047N	.918	3.06	.69	3.75	.260	.170	.090	5.80	2.89	8.69	91.31	1,050.7	75 percent pale red.
	do	25-30	3.39	0.001047N	.945	3.52	.84	4.36	.274	.162	.112	6.56	3.09	9.65	90.35	936.2	Pale red.
	do	25-30	3.18	0.001047N	1.050	3.66	1.20	4.86	.350	.180	.170	6.44	3.25	9.69	90.31	931.9	Do.
	June 3	18-25	3.15	0.0007586N	.930	4.10	1.48	5.58	.280	.160	.120	8.20	2.77	10.97	89.03	811.5	Firm ripe.
	do	25-31	3.12	0.0007586N	.726	4.08	1.39	5.48	.262	.152	.110	7.04	2.80	9.84	90.16	916.2	Full ripe.
	do	25-31	3.36	0.0007586N	.936	1.67	.16	1.83	.839	.604	.335	4.57	7.60	12.17	87.83	721.6	Very green.
	May 20	11-15	3.48	0.0003311N	.994	1.90	.45	2.35	.562	.322	.240	4.56	6.55	11.11	88.89	800.0	Dark green.
	do	13-19	3.38	0.0003311N	1.160	2.64	1.08	3.72	.350	.232	.118	5.80	4.40	10.20	89.80	880.4	Whitening.
	May 28	12-25	3.23	0.0007586N	1.050	2.81	1.04	3.85	.274	.164	.110	5.84	3.83	9.67	90.33	934.1	60 percent red.
	do	15-21	3.12	0.0007586N	1.218	2.60	1.11	3.71	.340	.190	.150	6.20	3.81	10.01	89.98	898.9	25 percent red.
	June 3	15-22	3.19	0.0007586N	.911	3.30	1.14	4.44	.238	.150	.088	6.20	3.20	9.40	90.60	963.8	Deep red.
	do	15-22	3.22	0.0007586N	.852	3.97	1.92	5.89	.324	.206	.118	7.32	3.16	10.48	89.51	854.1	Full ripe.
Progressive	do	18-27	3.27	0.000537N	.852	3.97	1.92	5.89	.324	.206	.118	7.32	3.16	10.48	89.51	854.1	Full ripe.

TABLE 8.—Hydric concentration, titratable acidity, and water content of 5 varieties of strawberries at various stages of development and ripening in 1928

Variety	Date	Diameter	Stage of development	Active acidity		Titratable acidity	Water as percentage of total solids
				pH	CH		
		<i>A/m</i>				<i>Percent</i>	<i>Percent</i>
Howard 17	May 17	6-10		4.37	0.00007079N	0.681	533
	do	10-12		3.95		.771	683
	do	12-15		3.71		.879	600
	May 29	18-30	Nearly white	3.23			894
	do	18-30	Tinged red one side	3.13	.0007413N	.921	985
	do	18-30	½ surface red	3.21		.900	977
	do	25-30	All red	3.14			945
	June 11	25-30	Firm red	2.95	.001122N	.924	
Progressive	do	25-32	Full ripe	3.06		.931	913
	May 17	6-12		4.24	.00005754N		584
	May 29	15-18		3.31	.0004898N		840
	do	21-25	Nearly soft ripe	3.37			
	June 11	25-30	Dead ripe and soft	3.50		.763	695
	May 17	4-6	Petals still on	5.10	.00000704N		
Chesapeake	do	6-10		4.47			452
	May 29	7-12		3.80			
	do	15-18		3.55			708
	June 11	25-28	¼ to ½ red	3.10	.0007943N	1.025	641
	do	25-28	Ripe	3.27		.984	754
	June 20		Dead ripe and overripe	3.51		.703	813
New York	May 17	5-8		4.31	.00064898N		346
	do	8-12		4.02			498
	May 29	17-22		3.39			758
	do	26-30	Green	3.24			787
	do	21-28	½ surface red	3.22	.0006026N		
	do	18-27	Light red	3.22		1.125	
	June 11	18-27	Good ripe	3.57		.897	733
	do	18-27		4.04			348
Portia	May 17	5-11		4.93	.0000912N	.809	546
	do	11-17		3.45			781
	May 29	12-15		3.35			876
	do	18-28	Whitening	3.32			1,072
	do	25-30	Half red	3.21	.0006106N	.938	974
	June 11	18-29	Light red	3.38		.844	974
	do	20-30	Full ripe	3.34		.837	1,007
	June 20		Dead ripe				

Table 7 shows that in all the varieties active acidity increases from the earliest stages to the attainment of full size and the beginning of development of color, then becomes more or less stationary, and decreases slightly as the fruit becomes fully ripe. There is a concurrent change in the same direction in titratable acidity and a very decided increase in the amount of water, made more apparent when water is expressed as percentage of total solids (table 7).

Table 8 shows the data on active acidity and water content at somewhat earlier stages in the development of the fruit. Both active acidity and water content were materially lower in the initial samples than in the preceding year. In all cases active acidity increased up to the point at which the fruit lost its chlorophyll and began to redden, remained fairly stationary as the fruit ripened, and decreased somewhat as the fruit became soft ripe. Water content increased somewhat irregularly up to a maximum which was reached as the fruit began to redden.

In the 1928 series of Chesapeake, in which the young fruits employed for the first sample had the petals still attached and for the most part unwithered, the extreme range of rise of acidity was from pH 5.10 to 3.10 (0.00000794N to 0.000794N) at half ripeness, a hundredfold increase. In Howard 17 the range of active acidity was from pH 4.37 to 2.95 (0.00007079N to 0.001122N), an increase of more than fifteen-



fold. It appears certain that determinations at equally early stages for the other varieties would have yielded similar results.

The relationship between the hydrion concentration and the percentage of water in the tissues of the strawberry is shown graphically

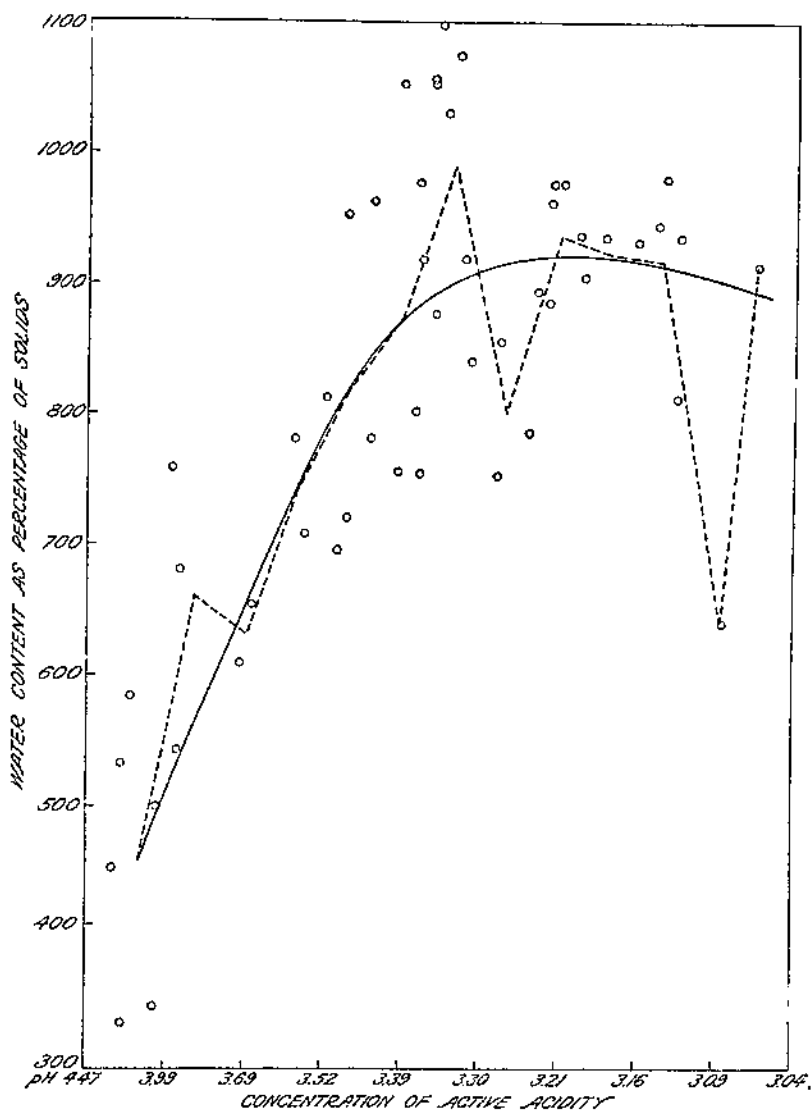


FIGURE 9.—Graph showing the degree of relationship between active acidity and percentage of water present in the tissues for strawberries. All data of tables 7 and 8 are included. The irregular line is the line of group averages; the curve is a smooth freehand curve.

in figure 9. In constructing the graph, all the data of tables 7 and 8 were used. These constitute determinations of hydrion concentration and water content for 51 samples, which comprise 8 series collected in 2 years and include 6 varieties of fruit taken at all stages of development from that at which some of the petals of the flower were still

adherent to that of full maturity. The values for water content were plotted against those for concentration of active acidity, and the group averages were determined and plotted as an irregular line on the graph. The curve, drawn freehand, indicates a very high degree of positive correlation of water content with active acidity at all concentrations of the latter below pH 3.24 (0.0005754N). From this point onward it becomes practically horizontal for active-acidity values between pH 3.24 and 3.06 (0.0005754N and 0.000871N). The downward trend of the right-hand end of the curve in the graph cannot be considered significant, since it was determined from a few values for one variety only. It may be regarded as a horizontal line, indicating that further increases in active acidity beyond hydron-concentration values of about 3.24 do not result in increased absorption of water. A number of factors which may be operative in producing this result were suggested in discussing the curves for apples (p. 13). Other factors suggest themselves. The limit of imbibitional capacity of the hydrophilic colloids under the influence of acids may lie below the maximum value of active acidity reached in some varieties, as appears to be the case in the grapefruit, the native crab apple, and the Eureka lemon. In some varieties of strawberry the rise of active acidity continues well on into the ripening period, during which the hydrophilic colloids are progressively reduced in comparative and absolute amount. The accumulation of sugar in the course of ripening is much more rapid than at any previous period in the life history and to a correspondingly greater degree affects the percentage of water present. Since some or all of these factors, as well as the environmental factor of available water supply, may affect the results, it is clear that the relationship between active acidity and amount of water in the tissues is very close and is consistently maintained throughout the development of the fruit.

In the work with strawberries the age of the fruit making up any given sample was not known, since the blossoms could not be tagged as they appeared. The earlier samples were consequently made up of berries of unknown age but apparently at a like stage in development and falling within stated limits as to size. Later, as whitening and reddening set in, fruits in identical stages as determined by color were placed together regardless of size. Determinations of average weight per fruit were not made. Data for accurately determining the rate of percentage increase in volume or weight in relation to time are lacking, but it is apparent from the rate of increase in mean diameter of the fruits that the percentage increase in volume is most rapid in the period in which active acidity and water content are increasing most rapidly.

#### BLACKBERRIES

In order to gain a general idea of the course of active-acidity changes in the blackberry, a series of hydron-concentration determinations upon the Snyder variety was begun on May 26, 1927 (table 9); at that time most of the petals were still adherent and the fruits were not more than 1 to 1.5 mm in diameter. It was somewhat difficult to express sufficient liquid to permit of determinations with both Bailey and quinhydrone electrodes. It was found that the values obtained were unaltered when the determinations were repeated after the juice had been diluted with an equal volume of distilled water. Readings of pH 4.79 (0.00001622N) (Bailey) and pH 4.76 (quin-

hydrone electrode) were obtained on May 26. On May 31 readings of pH 4.81 (Bailey) and 4.79 (quinhydrone) were obtained upon fruits at a like stage, while older berries, 3 to 4 mm in diameter, gave a value of pH 4.45 with both electrodes. Later determinations showed a rapid increase in active acidity until the fruits were practically full grown and greenish white, showing no trace of red. At this stage the value for active acidity was pH 2.46 (0.003467N). As the fruit ripened the active acidity decreased to pH 3.06 in very soft ripe fruit. The change from pH 4.06 to 2.46, representing a more than thirty-ninefold increase of active acidity, occurred between June 6 and June 30; during this time the fruits increased from sixfold to twelvefold in volume. Determinations of active acidity upon the expressed juices of young shoots and leaves on May 26 and on July 25 gave values of pH 4.98 and 4.86, respectively, indicating that the active acidity of these parts remains rather constant throughout the period of development of the fruit. Moreover, these results indicate that the very young fruit begins its existence with an active acidity very closely approximating that of the vegetative parts, and progressively departs from this value as growth proceeds. The maximum acid concentration found in greenish-white berries on June 30 (pH 2.46, or 0.003467N) is more than 213 times that in berries with petals still attached on May 26 (pH 4.79, or 0.0001622N).

TABLE 9.—Hydrion concentration of Snyder blackberry at various stages of development in 1927

Date	Part	pH	CN
May 26	Twigs and leaves	4.98	0.0001047N
26	Berries, petals just falling	4.79	0.0001622N
31	do.	4.81	
31	Berries, 3-4 mm in diameter	4.45	
June 6	Berries, 5-8 mm in diameter	4.06	0.0008710N
22	Berries, 12-15 mm, greenish white	2.70	0.01095N
30	Berries, 15-18 mm, greenish white	2.46	0.003467N
July 18	Berries, full grown, chlorophyll out, no red	2.56	0.002754N
18	Berries, hard red, no black	2.58	
18	Berries, firm ripe	2.78	0.01666N
18	Berries, soft ripe	2.91	
25	Berries, full ripe, very soft	3.06	0.0008710N
25	Leaves and petioles	4.86	0.0001380N

The series was repeated in 1928, and samples were taken for analysis. The analytical data are presented in table 10. The initial sample was about equal in age and size of berries to the second sample of 1927, and had an almost identical hydrion-concentration value—4.50 as compared with 4.45. As in the first series, active acidity rose rapidly to a maximum at the time the fruit had become distinctly red but was still firm and without blackish tinge, and then declined as the fruit reddened. The maximum acid concentration reached was 55 times that of the youngest samples taken. Water content rose abruptly as the fruit reddened, and subsequently declined as sugar began to accumulate in the fruit.

TABLE 10.—Changes in hydron concentration, water content, and chemical composition of Snyder blackberry and a wild dewberry throughout development

Variety	Date	Diameter	Stage of development	Active acidity		Sugars			Solids			Water as percentage of solids
				pH	CH	Reducing	Sucrose	Total	Soluble	Insoluble	Total	
Snyder blackberry	May 31	<i>Mm</i>				<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>	<i>Percent</i>
	June 8	3-4	-----	4.50	0.00003162N	1.64	0.85	2.49	6.49	9.72	16.21	505.0
	June 18	4-9	-----	4.12		1.37	1.08	2.45	6.20	17.17	23.37	328.0
	July 2	12-14	-----	3.67		.26	1.16	1.42	2.44	9.67	12.11	725.0
	July 16	17-20	Faint red	2.76	.001738N	.34	.76	1.10	2.92	9.66	12.52	698.7
	June 5		Ripe	2.86		4.24	.87	5.11	8.20	6.38	14.58	586.0
	June 19		Inflorescence and leaves	4.91	.0000123N							
	June 27	3-6	-----	4.77	.00001698N	1.38	.0	1.38	5.72	11.03	16.75	497.0
Wild dewberry	June 5	5-7	-----	3.58		.82	.74	1.56	2.92	13.95	16.87	492.8
	July 5		Whitening	3.12		.88	.64	1.52	5.96	15.08	21.04	375.3
	July 13		Underripe	2.87	.001349N	5.10	1.60	6.70	5.28	6.67	11.95	736.8
			Full ripe	3.22	.0006026N	5.24	1.48	7.72	9.96	4.88	14.84	573.8

## DEWBERRIES AND RASPBERRIES

Concurrently with the work upon blackberries, determinations were made in 1927 upon Cuthbert, Latham, and Ranere raspberries, an unnamed purple raspberry, a wild dewberry, and a wild black raspberry. The limited amount of material of Latham and Ranere raspberries precluded the making of close series and the taking of samples for analysis, but such samples were taken in the case of the others, and the work was repeated in 1928. The results from the 1928 series of the dewberry are presented in table 10. The results with the various raspberries are so nearly identical in general character with those for the blackberry and dewberry that presentation of the data is deemed unnecessary. In all varieties the active acidity was low in the youngest sample taken, rose rapidly during the period of most rapid increase in size to a maximum attained as chlorophyll disappeared and the development of pigmentation began, and decreased as ripening proceeded. In the dewberry the increase was approximately eightyfold; in the various raspberries it ranged between fifteenfold and fiftyfold. In all varieties there was a very marked increase in water content with the attainment of maximum acidity, followed by decrease as ripeness was reached.

## ELDERBERRIES

Collections of elderberries (*Sambucus canadensis* L.), in 1927 were accompanied by collections of leaves and petioles, shoots of the current season's growth, and 1-year-old stems. The hydrion-concentration values for these vegetative parts were practically identical at the three tests (table 11). The largest berries obtainable on July 1 and 7 were 3 to 4 mm in diameter; on July 16 many of the berries were 6 to 7 mm in diameter—a sevenfold to tenfold increase in volume—and showed all stages of coloration from bright green through greenish red to dark red. A marked change in active acidity had occurred in the interval, the increase being twelvefold in the greenish fruits to more than twentyfold in the greenish-red fruits. On August 2, faintly reddened berries showed an active acidity more than 31 times as great as that of the sample taken July 7. Determinations of moisture content were not made.

TABLE 11.—Hydrion concentration of elderberry at various stages of development in 1927

Date	Part	pH	Cu
July 1	Leaves and petioles.....	5.36	0.00004305N
1	Young stems, season's growth.....	5.41	.00000380N
1	Berries, 3-4 mm in diameter.....	4.89	.00001288N
7	Berries, 2 mm in diameter.....	4.96	
16	Berries, 5-6 mm in diameter.....	4.05	.00008913N
16	Berries, full grown, 6-7 mm but green.....	3.87	
16	Berries, greenish red, half ripe.....	3.02	.0002306N
16	Berries, dark red, firm.....	3.73	
16	Leaves and petioles.....	5.40	.000003407N
16	Young stems, season's growth.....	5.49	.000003246N
16	Woody 1-year stems.....	5.47	
Aug. 2	Berries, full grown, faintly reddened.....	3.44	.0003031N
2	Berries, dark red.....	3.75	
2	Berries dark red, after 48 hours in laboratory.....	3.64	
2	Berries, deep black.....	3.93	.0001175N
2	Berries, black, soft, and shriveling.....	4.64	
2	Leaves and petioles.....	6.50	

Partial repetition of the series in 1928, with especial attention to securing younger fruits, resulted in samples in which the petals were mostly unwithered and the ovaries were about 2 mm in diameter. In these fruits the hydron concentration was 5.36 (0.000004365N), practically the same as that of the leaves and young stems. Faintly reddened berries had a hydron concentration of 3.41 (0.0003981N); fully ripe berries, a hydron concentration of 3.77. The change in active acidity in the course of development of the fruit is consequently somewhat greater than is indicated by the results of table 11, the active acidity of the faintly red berries being 90 times as great as that of the young fruits with petals attached.

## POKEBERRIES

Hydron-concentration determinations were made July 19, 1927, upon the following parts of the pokeberry (*Phytolacca americana* L.): Leaves, terminal portions of shoots, racemes in which flowers were just opening, and berries 0.5 to 2 mm in diameter from which the petals had not yet wholly fallen away. These determinations yielded closely accordant values ranging from pH 5.49 to 5.57. The basal portions of stalks were more acid (pH 4.91). There was very little change in hydron concentration until the fruit had become practically full-grown and somewhat reddened, when the active acidity began to rise, attaining its maximum as the fruit became full soft ripe. The hydron-concentration values obtained for fruits of corresponding stages on September 26 and October 20 are not identical, but they agree in showing that active acidity doubled or tripled concurrently with the filling of the originally thin film of pulp with water, which accompanies ripening. The results are shown in table 12.

TABLE 12.—Hydron concentration in pokeberry at various stages of development

Date	Part	pH	C <sub>H</sub>
July 19	Leaves.....	5.55	0.00002818N
19	Stalks, terminal 12-18 inches.....	5.49	.000003236N
19	Stalks, basal halves.....	4.91	
19	Racemes, some flowers open, others just opening.....	5.49	.000003236N
19	Berries, 0.5-2 mm, petals not fallen.....	5.57	.000002692N
19	Berries, 4-6 mm in diameter.....	5.65	
Aug. 3	Berries, 8 mm in diameter, green.....	5.83	
Sept. 26	Berries, 8 mm, green.....	5.46	
26	Berries, full grown, slightly reddened.....	5.19	.000006457N
26	Berries, black but firm.....	5.29	
26	Berries, black, soft ripe.....	5.16	.000006918N
Oct. 20	Racemes, petals beginning to fall.....	5.62	
20	Berries, 1-3 mm in diameter.....	5.67	.000002138N
20	Berries, 3-5 mm in diameter.....	5.55	
20	Berries, full grown, green.....	5.55	
20	Berries, full grown, light red.....	5.33	
20	Berries, full grown, dark red.....	5.15	.000007079N
20	Berries, black, soft ripe.....	4.98	.00001047N

## TOMATOES

A very considerable amount of work was done in 1927 and 1928 on several varieties and types of tomato. The work was carried out along lines essentially identical with those followed by Gustafson in the work described in his 1928 paper (18), not then published. At intervals of 4 to 7 days fruit from blossoms tagged at opening was collected, and determinations were made of weight, hydron concentra-

tion, water content, and chemical composition. The results confirmed Gustafson's statements as to the course of the changes in active acidity and water content; it therefore seems unnecessary to present the data in detail.

In general, the situation found to prevail in the other fruits herein studied holds for the tomato, namely, that increases in active acidity and in water content coincide in time and that the period of their rise is also that of the most rapid percentage increase in weight. It was discovered rather early in the study that these changes are not confined to a definite period in the life of the fruit but are so largely controlled by environmental factors that their occurrence may be delayed for several weeks or even until ripening changes are setting in. Study of this fact led to the further discovery that definite gradients in hydrion concentration and in water content between the several regions of the fruit are established early in the life of the fruit and are maintained throughout its development and maturation. The results of these studies are to be prepared for separate publication.

### DISCUSSION

The data presented in the foregoing sections presents in outline the course of changes in hydrion concentration occurring during development in a number of fleshy fruits, as well as on the accompanying changes in volume and composition and particularly in water content. The fruits employed were purposely chosen to include a wide diversity of types with respect to period of development, botanical relationships, and structure of fruit, and include true drupe or stone fruits, such as cherry and elderberry; aggregates, as the blackberry and raspberry; a torus (strawberry); a true berry (tomato); a compound berry (pokeberry); a hesperidium (orange, grapefruit); and a pome fruit (apple). In consequence, generalizations that are valid for the material in hand may reasonably be assumed to apply broadly to the fleshy fruits as a class.

Studies by various workers of the active acidity conditions at various seasons of the year in the vegetative and fruiting branches of a number of species have brought out the fact that there is in all perennial fruit trees a reduction of active acidity of the expressed sap to a minimum during the dormant period and a rather abrupt rise with the resumption of growth. In the lemon, Reed and Halma (29) found that active acidity increased from pH 6.15 to 5.40. Anderssen (2) found changes in the expressed sap of pear branches of about 0.4 pH, the reaction of the tracheal sap meanwhile increasing 0.7 pH in pear and 1.0 pH in apricot. In both cases the change was rather abrupt and the maximum values reached (pH 5.3 in pear, pH 5.4 in apricot) remained fairly constant for 2 to 3 months following full bloom, after which they slowly declined. Hooker (22) found that maximum active acidity in bearing, nonbearing, and barren spurs of apples occurred from March to June, then declined to a minimum during the fall and winter. Other workers have confirmed his results.

In all the fruits studied in the present work it appears that the young fruits at setting and for a variable but always brief period after enlargement begins are low in their active acidity. In the orange, grapefruit, apple, strawberry, and tomato, the hydrion-concentration values of the juices of the youngest fruits obtainable are of the same

order of magnitude, and in several instances practically identical with those obtained from juices of the fruit spurs, leafy branches, and other vegetative parts of the plant concerned. During this period the fruit is characterized by a high content of total solids consisting predominantly of insoluble materials. Variation in content of water is confined to a relatively narrow range, showing no rapid increase. In the cherry, blackberry, and dewberry there is an initial stage of high water content followed by a decrease which establishes a relatively high value for total solids.

This period of relatively stable conditions is succeeded by a period of markedly rapid increase in active acidity which is always of relatively short duration as compared to the entire life of the fruit. The increase in active acidity during this period varies widely among the various types of fruits herein studied. The greatest increase is found in the orange, where the increase is more than 5,200 percent; the smallest increase in — pokeberry, where it is but 250 to 400 percent. In most of the fruits for which the series of samples at all approaches completeness for the early stages, active acidity undergoes a rapid increase to a concentration 10 to 50 times that of the youngest fruits procurable. Any adequate explanation of this rapid rise in active acidity must await further investigation; the present study establishes the fact of its general occurrence in fruits of widely varying types.

The period in the life history of the fruit at which the most rapid change in active acidity occurs varies considerably in the different fruits. In fruits with a short developmental period, such as cherries, strawberries, and blackberries, the period of rapid increase in active acidity is practically the same as the period of the most rapid increase in size and culminates as the fruit begins to show indications of ripening. In apples, the increase in active acidity is practically completed when the fruit has attained one tenth to one eighth its normal size and weight at maturity. In citrus fruits, the period of rapid increase in active acidity is preceded and followed by a period of some length in which there is little change. In the tomato, the period of transition normally occurs about midway in the life history of the fruit but may be postponed until much later.

With the rapid increase in active acidity is associated a rapid and rather large increase in water content of the fruit, which usually begins to be evident shortly after the change in active acidity appears and which may continue to increase in rate after the rapid change in acidity has ceased, or may attain a maximum simultaneously with the attainment of maximum active acidity. In the apple and the citrus fruits the second of these situations prevails; the abrupt increase of active acidity is accompanied by an equally abrupt rise of water content of the fruit to a maximum. A similar situation exists in the cherry and in the strawberry. In both fruits the rise of active acidity is paralleled by a rapid accumulation of water in the tissues, which reaches a maximum simultaneously with the attainment of highest acidity. In the tomato, the concurrence in time between attainment of highest acidity and highest water content is not exact, as might be anticipated from the fact that each of the several regions has a characteristic hydron concentration and water content. In all other fruits for which determinations of water content have accompanied hydron-concentration determinations, there has been a striking concurrence in time of the upward trend of these values.



The period in which these changes are in progress is also the period of most rapid percentage increase in weight (figs. 2-5, 8). That the absorption of large amounts of water is chiefly responsible for the increase in total weight is immediately obvious from the sharp decline in percentage of total solids. It is only after the point of maximum water content is reached that the formation of new material begins to contribute to the weight of the fruit at a rate comparable to that of the absorption of water. That is, the period of most rapid growth is predominantly a period of absorption of water up to a maximum which is usually subsequently reduced somewhat by an increase in the rate of accumulation of solids as maturity of the fruit is approached. A rather significant fact with respect to this period of rapid hydration of the fruit, and one to which we shall return in the subsequent discussion, is that the degree to which hydration proceeds is very definitely correlated with the level of active acidity simultaneously developed in the tissues.

It has been pointed out repeatedly in the preceding sections that the most rapid gain in weight upon a percentage basis takes place simultaneously with the most rapid increase in active acidity and in water content, so that the steepest portions of the three curves coincide in time. Before the active acidity begins to change, the fruit is increasing its volume by the addition of solids and of water at approximately equal rates, with the result that the water-to-solids ratio remains fairly constant. In the period of changing acidity the rate of water intake exceeds that of accumulation of solids and the water-to-solids ratio rises. When active acidity ceases to rise, the rate of water intake decreases and may drop below the rate of accumulation of solids. It is probable that in developing plant parts in general the period of rapid cell enlargement is one in which rapid hydration of the tissues is in progress.

That the period of increase in water content does not depend upon any external factor such as occurrence of precipitation or amount of soil moisture is evident from the 1928 results. The month of May was subnormal in rainfall, and the soil was becoming distinctly dry on the 26th, when a rainfall of 1.11 inches occurred. There was no further precipitation until June 16, by which time the soil was again quite dry. The abrupt rise in water content in the early cherry occurred from May 15 to 20; that in the midseason variety, from May 21 to 28; that in the late cherry and the blackberry, about June 5 to 15. In strawberries and in a number of apples the increase in water content was well advanced before the occurrence of rain. That it is not a dilution effect resulting from a sudden increase in the water supply available to the plants is therefore clear. That the levels of water content reached in the apples Launette and Amère du Surville are markedly below those of the more highly acid Rambo, Baldwin, and Grimes Golden, despite the identity of their conditions as to rainfall and soil moisture supply, is also significant in this connection.

All the facts appear to point to the conclusion that the sudden increase in water content of the fruit is due to the development of a new force within the fruit which is powerful enough to draw water from the vegetative tissues regardless of the supply available to the root system.

That the mechanism here involved is one of swelling of hydrophilic colloids under the influence of progressive increase in active acidity

seems to be a conception in accordance with all the facts. The young fruit is exceedingly high in its content of hydrophilic colloids, since the protoplasmic proteins, cellulose, hemicellulose, pentosans, tannins, and protopectins are strongly hydrophilic. Although little is known of the isoelectric points of these individual constituents, it seems clear that for some of them the point of minimum swelling lies somewhere along the scale between pH 4 and the neutral point. The young fruit begins its development with a hydron concentration approximating that of the vegetative tissues of the plant; that is, somewhere in the region pH 4.5 to 6.0. At this time it has a relatively low water content, which shows fluctuations of some magnitude, probably gaining or losing water to the vegetative tissues as these gain or lose in water content. As the active acidity of the fruit tissues begins to rise well above that of the vegetative tissues, the earlier process of give and take with respect to water becomes one of steady absorption into the fruit because of the greater magnitude of the force of imbibition exerted by the acid-swollen colloids and also because of the transformation of a considerable portion of the free water into bound water as it enters the tissues. That a physical force of large magnitude is active at this stage of development is evident from the fact that the young fruit is able to take large amounts of water from the vegetative parts. That the liquid present during the period of rapid increase in water content is largely held by the swollen colloids is evident from the fact that liquid can be expressed only with difficulty and is very highly viscous, setting to a gel after standing a few minutes. In the later stages of development these characters disappear.

Reed and Bartholomew (28) have called attention to the existence in young fruits of lemon, apple, and tomato of thick walls which give the reactions for pectose, and such histological studies as those of Tetley (36) have shown the existence of walls of this character in the apple. Reed and Bartholomew found that these young walls have marked imbibitory properties, swelling to such an extent when placed in water that their boundaries become indistinct. They are considered by Reed and Bartholomew as being important paths for the translocation of water, and these authors point out that the distribution of water between wall and protoplasm is an equilibrium between the imbibitional power of the cell wall and the suction pressure of the protoplast.

It would seem that we have here an approach toward an explanation of the paradox that the water content of a fruit reaches its maximum when soluble carbohydrates and other constituents capable of contributing to osmotic pressure are at a minimum and that it later decreases when soluble carbohydrates are rapidly accumulating. The water of the young fruit is bound by the colloidal micelles; the nonliving structural elements as well as the protoplasmic colloids participate in the process insofar as their several isoelectric points lie below the levels of active acidity attained in the young fruit, so that the rise of acidity increases their imbibitional capacity. In forming this conception of the process it is not necessary to attribute a definite isoelectric point to the fruit as a whole (13, 30, 31, 37) but merely to consider the known behavior of the several hydrophilic colloids present in the cells when they are isolated and treated with solutions of increasing hydron concentration. Furthermore, the

mechanism is exactly that which is operative in maintaining the water level of the vegetative portions of the plant. The difference is that the active acidity of the growing fruit mounts to a level markedly higher than any recorded for the vegetative tissues of any nonsucculent, and is accompanied by a rise of water content to corresponding levels. In Hooker's (22) study of the bearing and nonbearing spurs of apple, there was a very rapid increase in water content to a maximum of about 65 percent in mid-May, concurrently with rise of active acidity to a maximum, followed by a progressive decline to less than 50 percent in midwinter. In barren spurs, which show a much smaller rise in active acidity, the rise in water content was very markedly less, only 52 to 54 percent (22, *fig. 1 and table 25*).

As already stated, the percentage of water taken up by the several fruits during the period of transition bears a rather direct relation to the degree of active acidity attained, being least in an apple of low maximum acidity (Launette, maximum pH 3.75, maximum water content 465 percent), intermediate in one of medium acidity (Amère du Surville, pH 3.43, maximum water content 594 percent), and closely approximating 700 percent in all the fruits, regardless of species or variety, in which active acidity rises to the level of pH 3.00. This very strongly suggests that a force of identical character is operative in all these cases, as would be true were the cell proteins and the pectose of the walls the chief agents concerned. The fact that water content rises to very considerably higher levels in the cherry, strawberry, and especially in the tomato than it does in the apple and the citrus fruits, notwithstanding the higher acidity of these last-named fruits, does not necessarily render this conception untenable. In any fruit the swelling of the hydrophilic colloids under the influence of a given degree of active acidity takes place against a mechanical resistance due to the structure of the fruit, which may limit the rate and determine the degree of the process. That such mechanical resistance may restrict the degree of hydration to a fairly uniform upper limit in fruits of essentially identical structure is suggested by the results with apples.<sup>7</sup> The higher degree of hydration found in strawberries and cherries may result from an anatomical structure offering less resistance to swelling or from a difference in the amount and character of the hydrophilic colloids concerned. In the tomato it is known that the jellylike pulp surrounding the seeds is a colloid having such enormous capacity for imbibing water that it holds 1,800 to 1,900 percent of its dry weight at a hydrion concentration of 4.10 to 4.39 (23).

Some fruits, as the Eureka lemon studied by Bartholomew and the native crab apple and the grapefruit, studied here, ultimately attain a very high active acidity by a gradual increase following the period of rapid rise. Such further increase is not attended by a corresponding rise in water held by the tissues, the water content remaining fairly stationary at a level no higher than that found in fruits very much lower in active acidity. This fact does not necessarily invalidate the theory that the swelling of hydrophilic colloids under the influence of increasing acidity is responsible for the earlier intake of water. The capacity of any colloid to swell under the influence of acids has an

<sup>7</sup> The breaking of drought during the growing period is often followed by general splitting of fruit. That certain varieties split badly, as Champaign among peaches and Stayman Winesap among apples, under conditions that do not result in splitting in other varieties, may indicate an anatomical structure offering less mechanical resistance than that of other varieties, or a higher content of hydrophilic colloids.

upper limit beyond which further increase in the active acidity of the solution does not result in further absorption of water. In the fruits herein discussed this upper limit appears to be near pH 2.8 to 3.0. Increase in water content continues with increasing acidity up to somewhere near this value, then practically ceases in those fruits (grapefruit, native crab apple, and lemon) in which acidity rises to higher levels.

It has already been pointed out that the water content of the fruit usually decreases somewhat from the maximum attained during the rise of acidity, and that the amount of this decrease is in general broadly parallel with the decrease in hydron concentration which is occurring during the same period. Aside from the decrease in water-holding capacity of the colloids which would result from reduction of acidity, at least two other factors may be involved in this change. The proportion of living protoplasm to the total bulk of the fruit continually decreases as later development proceeds. This is true in even greater degree of the nonliving cell-wall constituents, namely, the hemicelluloses, pectins, and tannins and related substances, which not only cease to increase in relative amount but undergo a very considerable decrease through conversion to simpler products, including sugars, as maturity approaches. This progressive decrease in amount of both living and nonliving colloidal material may play a considerable part in the reduction of water content of the fruit as it approaches maturity, and may account for the fact that the vegetative tissues withhold or even withdraw water from the fruit in periods of insufficient water supply, as observed by Bartholomew (5) in lemons and by Furr and Magness (14) in apples. In fruits in which there is rapid accumulation of sugar as the fruit ripens, there may be a final rise in water content for which the increasing osmotic pressure of the cell solution is responsible.

Concurrently with the shift to higher levels of active acidity and of water content there is an increase in total titratable acidity, which occurs at a much less regular rate and during a much less definite period. This increase was observed in every fruit studied, with the exception of two of the apple varieties for which the series of samples was lacking in early stages, so that its occurrence in these varieties at a period prior to the beginning of sampling is a possibility. There was no relationship between the increase in active acidity and that in titratable acidity as regards amount and only a very general relation as regards time; one may be stationary or decreasing at the time of the most rapid increase in the other. In the grapefruit of table 3, for example, titratable acidity increased very little from October 1 to November 21, a period in which the concentration of active acidity in the pulp increased more than threefold.

The period of transition from the plane of low active acidity and low water content in all the fruits studied is one of low and rather constant values for sugar content, and the sugar present is predominantly in the form of reducing sugar. During this period, sugar is used up in the construction of new tissues almost as rapidly as it is transported into the fruit. At the close of the transition period accumulation of sugar begins. In the apple the initial increase is primarily in reducing sugars, followed later by increase in sucrose; in the orange and grapefruit there is a rather sudden increase, due almost wholly to increase in sucrose; in strawberries, blackberries, and cherries

the increase in sugar content is almost wholly in the form of reducing sugars and the sucrose content may even decrease as the fruit matures. These facts at least suggest that carbohydrate may be transported into the fruit in the form of reducing sugars and that in the short-lived fruits there is no subsequent conversion to sucrose, though such conversion occurs in the slow-maturing fruits such as apple and citrus.

The period of later development following that of rapid change varies greatly in length but is marked by the same general sequence of events. In the citrus fruits this period lasts several months. At the beginning of this later period active acidity fluctuates somewhat, with a tendency to increase slightly; later it becomes relatively stationary; and then slowly decreases as the fruit approaches picking maturity. Water content fluctuates somewhat irregularly, as would be anticipated from Bartholomew's (4) discovery that water is withdrawn from the fruit into the vegetative organs whenever there is a deficiency of available soil water, but shows a clear tendency to remain somewhere near the general level established in the transition period. The rate of increase in total weight decreases rather sharply at the outset of the period, the curve becoming nearly a straight line (fig. 6). Total solids in the orange and grapefruit show a progressive decrease which at first is rapid as a result of decrease in insoluble solids, the soluble solids meanwhile remaining nearly stationary. The rate of decrease of total solids later becomes slow because gains in soluble solids nearly or quite offset the slow decrease in insoluble solids. Astringency shows a rather irregular course, but there is a considerable net decrease. Titratable acidity declined markedly in the orange, but remained unchanged in the grapefruit up to the end of the period of sampling, which, unfortunately, was terminated by circumstances before the fruit had become tree ripe.

In the apple the changes during this period are in broad outline identical, the chief differences being that active acidity declines very considerably, more than is the case in any of the citrus fruits, the curve of rise and decline showing in all varieties the mountain-peak character indicated in the graphs (figs. 2, 3, and 4). It is notable that water content in all cases drops from the maximum attained in the transition period to somewhat lower levels, and that the curve of change in water content roughly parallels that of change in active acidity, taking the same mountain-peak outline. Total solids show a slow and somewhat variable increase, as increase in soluble solids and decrease in insoluble solids vary in their relative rates throughout the period.

In the strawberry and the cherry there is a rather sharp decline in water content as sugar accumulates in the ripening fruit. In both fruits this decline is preceded by a period in which both active acidity and water content are nearly constant; afterward both decline, the decrease in water content preceding the decrease in acidity. In these respects the varieties represented in the graphs are quite in accord with the others dealt with in the work.

#### SUMMARY

In a large number of the fleshy fruits, including oranges, grapefruit, apples, strawberries, blackberries, raspberries, elderberries, pokeberries, and cherries, the young fruits at setting and for a short period

thereafter have a hydron concentration rather close to the general level found in the vegetative parts and fruiting structures of their respective plants. During this period of low acidity the fruit has a high solids content. Morphologically it is the period in which rapid and general cell division is in progress.

This period is succeeded by a period of transition, always of short duration, as compared with the entire developmental period of the fruit, in which the active-acidity content of the young fruit very rapidly rises from the low values of the vegetative structures to the high values of the developing fruit. In the fruits herein discussed, this increase in active acidity ranges from less than tenfold in strawberries to more than eightyfold in the citrus fruits.

Concurrently with the beginning of the rise in active acidity or soon afterward, the fruit begins to absorb water at a rapid rate, so that the percentage of solids is reduced and the fruit attains a condition of maximum hydration. This condition is reached simultaneously with the attainment of maximum active acidity or very shortly thereafter. The degree to which hydration proceeds during this period is very definitely related to the degree of active acidity developed.

The period of rapid rise in active acidity and in water content coincides with the period of the most rapid percentage increase in weight and volume. The three curves representing (1) increase in active acidity, (2) increase in water content, and (3) rate of percentage increase in weight begin to rise simultaneously, or nearly so, and swing upward together. With the attainment of maximum values for active acidity and water content, however, there is a very marked decrease in the rate of percentage increase in weight.

The consistent relationship found to exist between rate of growth and changes in active acidity and water content in fruits of widely dissimilar morphological character and length of life very strongly suggests that the rapid increase in active acidity may bear a causal relation to the period of the most rapid percentage increase in weight. The very large alteration in hydron concentration markedly increases the imbibitional capacity of the protoplasmic colloids and of such cell-wall constituents as the pectins, which have isoelectric points well below the levels of active acidity here encountered. There is thus set into action a force capable of attracting and holding considerable quantities of water. The magnitude of this force increases with increase in hydron concentration, thus accelerating the rate of water intake and of increase in weight and volume; the period of most rapid growth (on the percentage basis), therefore, is also a period of progressively increasing hydration.

After rising abruptly to a maximum, active acidity ceases to increase and remains nearly stationary for a period which varies in length for the different fruits. Water content also ceases to increase and remains nearly stationary. The point at which active acidity and water content cease to rise coincides in time with the marked flattening of the curve of percentage increase in weight.

From this point onward there is little or no increase in the protoplasmic colloids, and the formation of primary cell walls ceases. Consequently, the amount of material capable of marked swelling in the presence of acids becomes relatively stationary or begins to decrease. Moreover, the decline of metabolic activity results in a

lessened production of acids, as shown by a decrease in the hydron concentration of the tissues. With a decrease in the active acidity of the cell sap and a cessation of formation of substances capable of strong swelling under the influence of acids, the fruit is no longer able to maintain the highly hydrated condition; later development is accompanied by a progressive decline in water content closely paralleling the decline in active acidity, which continues to picking maturity.

A working hypothesis is presented, namely, that variations in water absorption by the hydrophilic colloids of the young fruit, caused by changes in hydron concentration of the tissue fluids, may be a factor of prime importance in determining the form and slope of the growth curve of the fruit. Although this hypothesis may require modification when more detailed studies have been made of the early stages of growth in fruits, at present it appears to offer an explanation of all the known facts.

## LITERATURE CITED

- (1) ALWOOD, W. B., with the collaboration of HARTMANN, B. G., EOFF, J. R., INGLE, M. J., and SHERWOOD, S. F.  
1916. DEVELOPMENT OF SUGAR AND ACID IN GRAPES DURING RIPENING. U.S. Dept. Agr. Bul. 335, 28 p.
- (2) ANDERSSSEN, F. G.  
1929. SOME SEASONAL CHANGES IN THE TRACHEAL SAP OF PEAR AND APRICOT TREES. *Plant Physiol.* 4:459-476, illus.
- (3) APPLEMAN, C. O., and CONRAD, C. M.  
1927. THE PECTIC CONSTITUENTS OF TOMATOES AND THEIR RELATION TO THE CANNED PRODUCT. *Md. Agr. Expt. Sta. Bul.* 291, 17 p., illus.
- (4) BARTHOLOMEW, E. T.  
1923. INTERNAL DECLINE OF LEMONS. II. GROWTH RATE, WATER CONTENT, AND ACIDITY OF LEMONS AT DIFFERENT STAGES OF MATURITY. *Amer. Jour. Bot.* 10:117-126.
- (5) ———  
1926. INTERNAL DECLINE OF LEMONS. III. WATER DEFICIT IN LEMON FRUITS CAUSED BY EXCESSIVE LEAF EVAPORATION. *Amer. Jour. Bot.* 13:102-117.
- (6) BRUNSTETTER, B. C., and MAGOON, C. A.  
1930. A MICROELECTRODE FOR THE RAPID DETERMINATION OF THE HYDRION CONCENTRATION OF EXPRESSED JUICES FROM SMALL AMOUNTS OF PLANT TISSUE. *Plant Physiol.* 5:249-256, illus.
- (7) CHACE, E. M., WILSON, C. P., and CHURCH, C. G.  
1921. THE COMPOSITION OF CALIFORNIA LEMONS. U.S. Dept. Agr. Bul. 993, 18 p., illus.
- (8) COLLISON, S. E.  
1913. SUGAR AND ACID IN ORANGES AND GRAPEFRUIT. *Fla. Agr. Expt. Sta. Bul.* 115, 23 p.
- (9) COPEMAN, P. R. V. D. R.  
1924. AN INVESTIGATION INTO THE PHYSICAL AND CHEMICAL CHANGES OCCURRING IN GRAPES DURING RIPENING. *Union So. Africa Dept. Agr. Sci. Bul.* 30, 38 p.
- (10) ———  
1927. SOME CHANGES OCCURRING DURING THE RIPENING OF GRAPES. (THIRD PAPER.) *Union So. Africa Dept. Agr. Sci. Bul.* 60, 19 p.
- (11) ———  
1928. THE GROWTH OF GRAPES, IV. INITIAL CHANGES IN ACIDITY. *Royal Soc. So. Africa Trans.* 16 (pt. 2):103-120.
- (12) ——— and FRATER, G.  
1926. SOME PHYSICAL AND CHEMICAL CHANGES OCCURRING DURING THE RIPENING OF GRAPES. (SECOND PAPER.) *Union So. Africa Dept. Agr. Sci. Bul.* 50, 51 p.

- (13) DENNY, F. E., and YODEN, W. J.  
1927. ACIDIFICATION OF UNBUFFERED SALT SOLUTIONS OF PLANT TISSUE IN RELATION TO THE QUESTION OF TISSUE ISOELECTRIC POINTS. *Amer. Jour. Bot.* 14:395-414.
- (14) FURR, J. R., and MAGNESS, J. R.  
1931. PRELIMINARY REPORT ON RELATION OF SOIL MOISTURE TO STOMATAL ACTIVITY AND FRUIT GROWTH IN APPLE. *Amer. Soc. Hort. Sci. Proc.* (1930) 27:212-218, illus.
- (15) GUSTAFSON, F. G.  
1924. TOTAL ACIDITY COMPARED WITH ACTUAL ACIDITY OF PLANT JUICES. *Amer. Jour. Bot.* 11:365-369, illus.
- (16) ———  
1926. GROWTH STUDIES ON FRUITS. *Plant Physiol.* 1:265-272.
- (17) ———  
1927. GROWTH STUDIES ON FRUITS. AN EXPLANATION OF THE SHAPE OF THE GROWTH CURVE OF FRUITS. *Plant Physiol.* 2:153-161, illus.
- (18) ———  
1928. GROWTH STUDIES ON FRUITS. CHEMICAL ANALYSES OF TOMATO FRUITS. *Mich. Acad. Sci., Arts, and Letters, Papers* 8:121-127, illus.
- (19) ———  
1929. GROWTH STUDIES ON FRUITS. RESPIRATION OF TOMATO FRUITS. *Plant Physiol.* 4:349-356, illus.
- (20) HARTMAN, H., and BULLIS, D. E.  
1929. INVESTIGATIONS RELATING TO THE HANDLING OF SWEET CHERRIES WITH SPECIAL REFERENCE TO CHEMICAL AND PHYSIOLOGICAL ACTIVITIES DURING RIPENING. *Oreg. Agr. Expt. Sta. Bul.* 247, 38 p., illus.
- (21) HAWKINS, L. A.  
1921. A PHYSIOLOGICAL STUDY OF GRAPEFRUIT RIPENING AND STORAGE. *Jour. Agr. Research* 22:263-279, illus.
- (22) HOOKER H. D., JR.  
1920. SEASONAL CHANGES IN THE CHEMICAL COMPOSITION OF APPLE SPURS. *Mo. Agr. Expt. Sta. Research Bul.* 40, 51 p., illus.
- (23) MACGILLIVRAY, J. H., and FORD, O. W.  
1928. TOMATO QUALITY AS INFLUENCED BY THE RELATIVE AMOUNT OF OUTER AND INNER WALL REGION. *Iud. Agr. Expt. Sta. Bul.* 327, 28 p., illus.
- (24) NELLER, J. R., and OVERLEY, F. L.  
1926. PHYSICAL AND CHEMICAL CHARACTERISTICS OF MATURING APPLES AS RELATED TO TIME OF HARVEST. *Wash. Agr. Expt. Sta. Gen. Bul.* 205, 38 p., illus.
- (25) OPPENHEIM, J. D., and WINIK, L.  
1930. THE DETERMINATION OF THE SUGAR CONTENT AND THE pH VALUE OF THE JAFFA ORANGE. *Hadar (Palestine Citrogr.)* 3:170-173.
- (26) OVERHOLSER, E. L.  
1928. A STUDY OF THE CATALASE OF THE FRUITS OF PEAR VARIETIES. *Amer. Jour. Bot.* 15:285-306, illus.
- (27) REED, H. S.  
1930. THE SWELLING OF CITRUS FRUITS. *Amer. Jour. Bot.* 17:971-982; illus.
- (28) ——— and BARTHOLOMEW, E. T.  
1927. WATER TRANSLOCATION IN YOUNG FRUITS. *Science (n.s.)* 66:382.
- (29) ——— and HALMA, P. F.  
1926. FURTHER OBSERVATIONS ON THE RELATIONS BETWEEN GROWTH AND SAP CONCENTRATION IN CITRUS TREES. *Jour. Agr. Research* 32:1177-1194, illus.
- (30) ROBBINS, W. J.  
1923. AN ISOELECTRIC POINT FOR PLANT TISSUE AND ITS SIGNIFICANCE. *Amer. Jour. Bot.* 10:412-439, illus.
- (31) ——— and SCOTT, I. T.  
1925. FURTHER STUDIES ON ISOELECTRIC POINTS FOR PLANT TISSUE. *Jour. Agr. Research* 31:385-399, illus.
- (32) ROSA, J. T.  
1926. RIPENING OF TOMATOES. *Amer. Soc. Hort. Sci. Proc.* (1925) 22: 315-322.



- (33) ROSA, J. T.  
1927. RIPENING AND STORAGE OF TOMATOES. Amer. Soc. Hort. Sci. Proc. (1926) 23:233-242, illus.
- (34) ST. JOHN, J. L., and MORRIS, O. M.  
1929. STUDIES OF QUALITY AND MATURITY IN APPLES. Jour. Agr. Research 39:623-639, illus.
- (35) SANDO, C. E.  
1920. THE PROCESS OF RIPENING IN THE TOMATO CONSIDERED ESPECIALLY FROM THE COMMERCIAL STANDPOINT. U.S. Dept. Agr. Bul. 659, 38 p., illus.
- (36) TETLEY, U.  
1930. A STUDY OF THE ANATOMICAL DEVELOPMENT OF THE APPLE AND SOME OBSERVATIONS ON THE "PECTIC CONSTITUENTS" OF THE CELL-WALLS. Jour. Pomol. and Hort. Sci. 8:153-172, illus.
- (37) YOUNG, W. J., and DENNY, F. E.  
1926. FACTORS INFLUENCING THE PH EQUILIBRIUM KNOWN AS THE ISO-ELECTRIC POINT OF PLANT TISSUE. Amer. Jour. Bot. 13:743-753.

# ORGANIZATION OF THE UNITED STATES DEPARTMENT OF AGRICULTURE WHEN THIS PUBLICATION WAS LAST PRINTED

---

<i>Secretary of Agriculture</i> .....	HENRY A. WALLACE.
<i>Assistant Secretary</i> .....	REXFORD G. TUGWELL.
<i>Director of Scientific Work</i> .....	A. F. WOODS.
<i>Director of Extension Work</i> .....	C. W. WARBURTON.
<i>Director of Personnel and Business Administration.</i>	W. W. STOCKBERGER.
<i>Director of Information</i> .....	M. S. EISENHOWER.
<i>Solicitor</i> .....	SETH THOMAS.
<i>Bureau of Agricultural Economics</i> .....	NILS A. OLSEN, <i>Chief</i> .
<i>Bureau of Agricultural Engineering</i> .....	S. H. MCCORMY, <i>Chief</i> .
<i>Bureau of Animal Industry</i> .....	JOHN R. MOHLER, <i>Chief</i> .
<i>Bureau of Biological Survey</i> .....	PAUL G. REDINGTON, <i>Chief</i> .
<i>Bureau of Chemistry and Soils</i> .....	H. G. KNIGHT, <i>Chief</i> .
<i>Office of Cooperative Extension Work</i> .....	C. B. SMITH, <i>Chief</i> .
<i>Bureau of Dairy Industry</i> .....	O. E. REED, <i>Chief</i> .
<i>Bureau of Entomology</i> .....	LEE A. STRONG, <i>Chief</i> .
<i>Office of Experiment Stations</i> .....	JAMES T. JARDINE, <i>Chief</i> .
<i>Food and Drug Administration</i> .....	WALTER G. CAMPBELL, <i>Chief</i> .
<i>Forest Service</i> .....	FERDINAND A. SILCOX, <i>Chief</i> .
<i>Grain Futures Administration</i> .....	J. W. T. DUVEL, <i>Chief</i> .
<i>Bureau of Home Economics</i> .....	LOUISE STANLEY, <i>Chief</i> .
<i>Library</i> .....	CLARIBEL R. BARNETT, <i>Librarian</i> .
<i>Bureau of Plant Industry</i> .....	KNOWLES A. RYERSON, <i>Chief</i> .
<i>Bureau of Plant Quarantine</i> .....	A. S. HOYT, <i>Acting Chief</i> .
<i>Bureau of Public Roads</i> .....	THOMAS H. MACDONALD, <i>Chief</i> .
<i>Weather Bureau</i> .....	CHARLES F. MARVIN, <i>Chief</i> .

---

*Agricultural Adjustment Administration*.... CHESTER C. DAVIS, *Administrator*.

This bulletin is a contribution from

<i>Bureau of Plant Industry</i> .....	KNOWLES A. RYERSON, <i>Chief</i> .
<i>Division of Fruit and Vegetable Crops and Diseases.</i>	E. C. AUCHTER, <i>Principal Horticulturist, in Charge</i> .

**END**