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SEASONAL CHANGES AND TRANSLOCATION OF CARBOHYDRATE MATERIALS IN FRUIT SPURS AND TWO-YEAR-OLD SEEDLINGS OF APPLE.*†

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At the suggestion of Prof. W. Paddock, of the Department of Horticulture of the Ohio State University, the writer undertook the work of determining the changes in carbohydrate content of fruit spurs and two-year-old seedlings of apple throughout the year. The work was done under the direction of Dr. H. C. Sampson, of the Department of Botny, and with the assistance of Dr. T. G. Phillips and Dr. J. F. Lyman, of the Department of Agricultural Chemistry.

This is a part of the larger problem of determining what effect the carbohydrate content of fruit spurs has upon vegetative growth and reproduction, and to what extent it should be considered in handling fruit trees.

The methods used in the analysis of plant materials were as follows: The samples were collected from the campus orchard and nursery every two weeks and a quantitative analysis was made in every case to determine the percentage of starch and the sugars, sucrose, glucose, and maltose. For the determination of starch the method described by Abderhalden[5] was followed, and for sugars, that described by Darwin and Acton[4], with a slight modification. In both cases the quantity of dextrose was determined by Fehling's solution, titrating against a standard potassium permanganate solution, as has been approved by the Association of Official Agricultural Chemists.[3] In the case of two-year-old seedl ngs, separate analyses were made on the one-year-old stem segments, two-year-old stem segments, and roots. All percentages are expressed on a dry weight basis.

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†Papers from the Department of Botany, Onio State University, No. 121.

The earliest work on the study of translocation of starch is that of Mer.[1] This investigator made a thorough study of the changes of starch content throughout the growing and dormant periods of the year in different parts of the tissues, both in ordinary and girdled stems of various plants, such as beech, oak, pine, etc. Similar investigations were made by Rosenberg.[2] The most recent work is that of Butler, et al,[7] who made a thorough analytical study of the carbohydrate, nitrogen, fats, phosphorus, and potassium of different parts of bearing

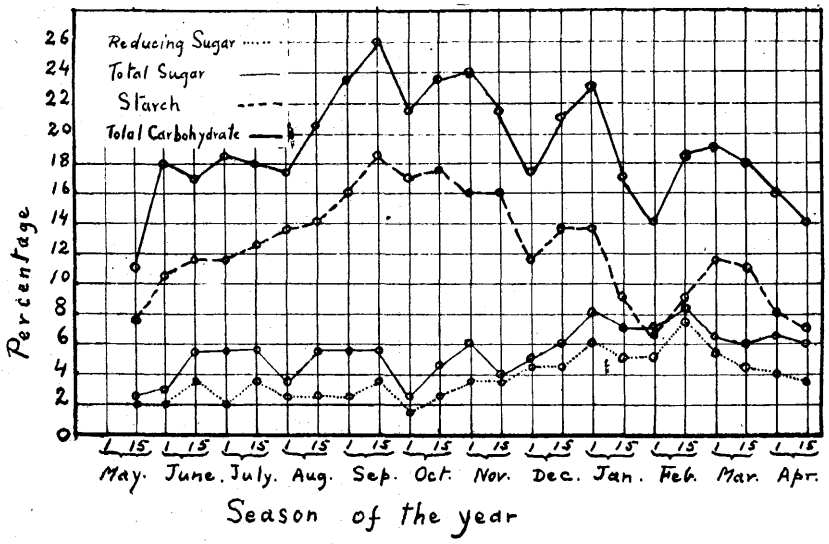

Fig. 1. Curves showing changes in carbohydrates in fruit spurs of apple from May to April, 1919–1920. The ordinates represent the percentage of carbohydrates and the abscissae, the season of the year.

apple trees. The writer's work is similar to that of the latter investigators, so far as the carbohydrate materials are concerned. There is, however, some disagreement in the data obtained in the two cases. This is, perhaps, due to the difference in age and in location of the trees in different climatic conditions. The data presented in this report show a seasonal periodicity in the changes of the carbohydrate materials, i. e., starch to sugar and vice versa, and a partial explanation of the factors that bring about these changes. The data also show that changes in temperature play a very important part in the changes of carbohydrates in plant tissues. The fluctuations

of temperature during the growing and dormant periods are accompanied by changes in acidity in the plant, which in turn affect the activity of the enzymes which have always been found by actual experiment to be present at all seasons of the year.

The data of the analyses are presented under three headings: First, curves showing changes in carbohydrates in fruit spurs; second, curves showing changes in carbohydrates in two-year-old seedlings; third, curves showing acidity in both the fruit spurs and seedlings. The curves in each case are followed by a brief summary and discussion.

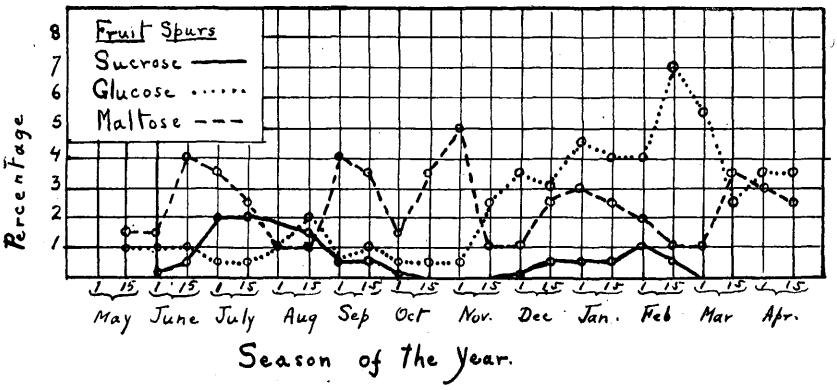

Fig. 2. Curves showing the percentage of sucrose, glucose and maltose in fruit spurs of apple from May to April, 1919–1920. The ordinates represent the percentage of sugars and the abscissae, the season of the year.

The Fruit Spurs.

1. Change of temperature has a marked bearing on the translocation of carbohydrate materials in fruit spurs of apple.

2. The accumulation of both total carbohydrate and starch shows marked increase during August and September, the maximum accumulation occurring in September.

3. As the temperature decreases in autumn the starch content decreases without any marked increase in either the total or reducing sugars. This decrease of starch continues until February, when it reaches its maximum for the dormant season. The total carbohydrate content of the fruit spurs follows a similar course.

4. Most of the hydrolysed starch is either utilized in metabolic processes or transferred to the adjacent parts of the stem, as is evidenced by the change in the total carbohydrate content of fruit spurs. This occurs during the dormant period when metabolic processes are at a minimum. There is also a possibility that some of the carbohydrates are used in fat synthesis or other syntheses at this time, but no data were obtained on this point.

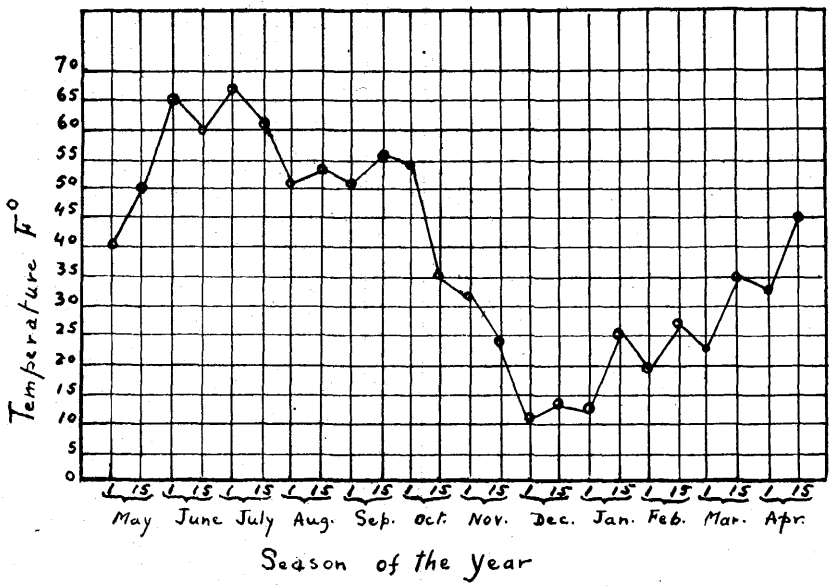

Fig. 3. A curve showing the average minimum temperature of the campus (Ohio State University) from May to April, 1919–1920. The ordinate represents the temperature in F° and the abscissa, the season of the year.

5. In the early spring, especially in March and April, during the swelling of buds and the early growth of leaves and flowers, the starch and sugars disappear very rapidly, apparently being utilised in the formation of new growth and the respiration of the growing cells.

6. The total sugar, especially reducing sugars, increases in December and is at its maximum during December, January and February. This increase of total sugar does not account quantitatively for the decrease of starch during the dormant period.

7. The translocation of sugars in apple spurs is largely in the form of glucose and maltose. Glucose appears to be the most important sugar of translocation during the dormant period.

8. Maltose appears to be the most important sugar of translocation during starch accumulation in autumn. To sum up, the upward translocation of sugar in spring is largely in the form of glucose, while the translocation of sugar from leaves to stem in autumn is largely in the form of maltose.

9. The quantity of sucrose is very small in comparison to glucose and maltose. In fruit spurs it is found in the early growing and dormant period and is almost lacking at other times.

10. The process of downward translocation of sugar is very slow in comparison to the upward translocation, the latter of which is influenced by the transpiration stream during the early spring.

11. The correlation between the changes in acidity and the resultant effect upon the enzymes involved and the changes in carbohydrates in fruit spurs will be discussed later.

The Two-year-old Apple Seedlings.

1. The effect of temperature upon the changes and translocation of carbohydrates in apple seedlings is similar to its effect on carbohydrates in the fruit spurs of apple.

2. Total carbohydrate accumulation increases rapidly in both stems and roots at the close of the growing period in August, September and October, followed by a slight increase in roots and two-year-old stems, the maximum being reached in October, after which a gradual decrease follows.

3. After December there is a marked decrease in total carbohydrate both in roots and stems, which reaches its minimum in January, February and March. This decrease is perhaps due to slow metabolic processes, such as respiration, and also to a change of carbohydrates to non-carbohydrate materials, such as fats. There is also a marked development of latex-like material in the roots during January and February. Butler, et. al.* have found a slight increase of fats in roots and two-year-old branches during the dormant period. The latex material

*Loc. Cit.

was not analysed. It disappears by the middle of February, at which time the total carbohydrate material increases slightly. A marked decrease of carbohydrate occurs during the growing period of April, May and June.

4. The starch content of roots and stems increases rapidly with the decrease of growth in autumn, following a course

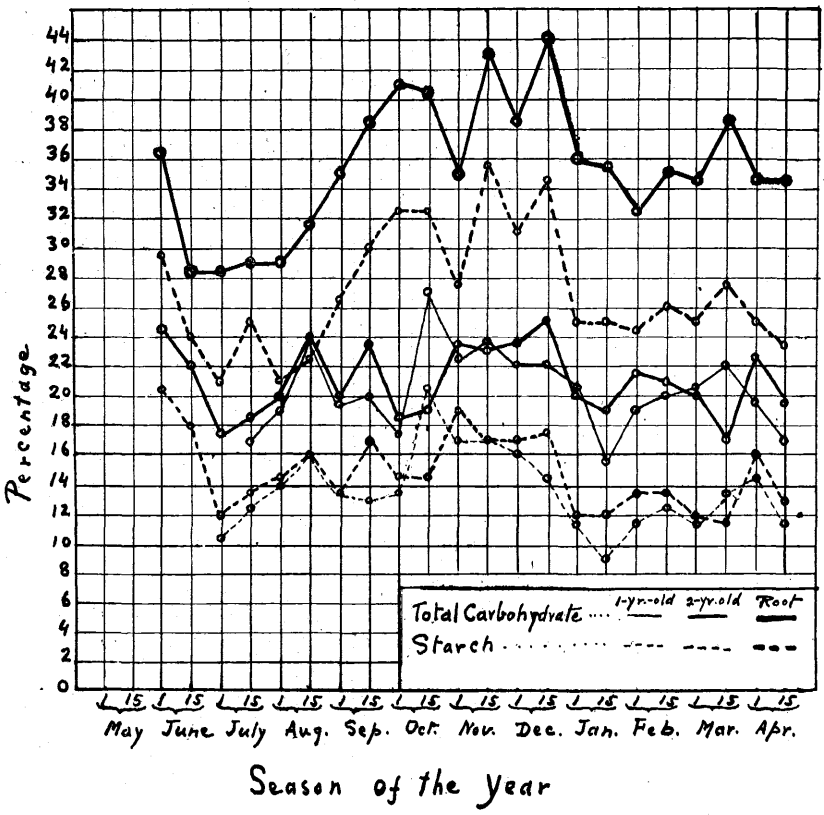

Fig. 4. Curves showing the changes in carbohydrates in two-year-old seedlings of apple from June to April, 1919–1920. The ordinates represents the percentage of carbohydrates and the abscissae, the season of the year.

parallel to that of total carbohydrate in each case. The increase of starch in roots is much greater than that in stems. In one- and two-year-old stems the maximum is reached in October and November, followed by a gradual decrease, while in the case of roots the maximum accumulation of starch occurs in December, after which there is a rapid fall. The minimum

starch content during the dormant period in stems and roots occurs from January to March, after which there is a gradual increase until the inception of growth in spring.

5. This decrease of starch during the dormant period is due partly to hydrolyzation to sugar and probably to slow respiration, and in the case of roots to the formation of latex-like material, as already mentioned. There is a possibility of some

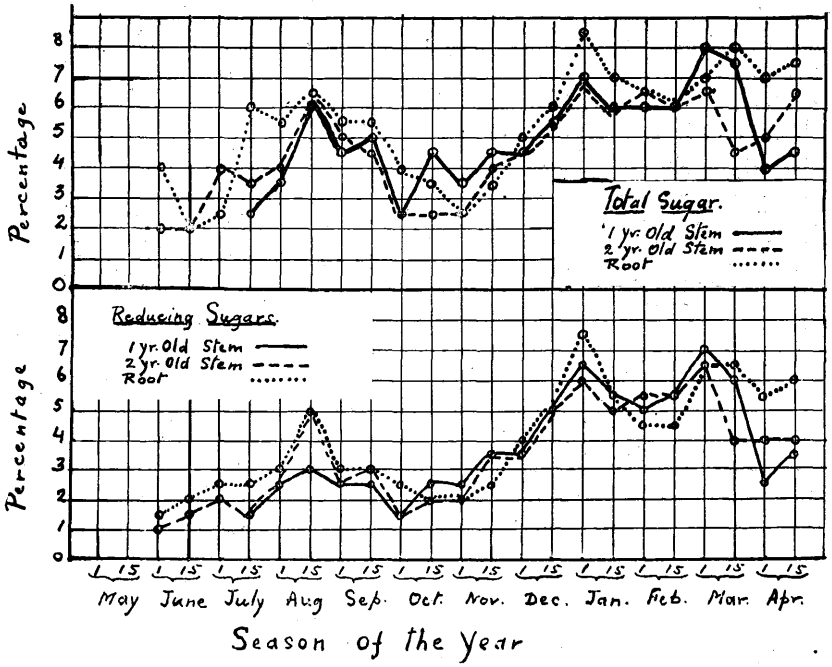

Fig. 5. Curves showing the percentage of total sugar and reducing sugars in two-year-old seedlings of apple from June to April, 1919–1920. The ordinates represent the percentage of carbohydrates and the abscissae, the season of the year.

fat or other synthesis. With the swelling of buds in the spring a general decrease of starch and total carbohydrate occurs in all parts of the plant.

6. The role played by the different sugars is similar to that described in the case of fruit spurs. Glucose and maltose are the principal sugars of translocation. Glucose reaches its maximum during the dormant period in all parts of the plant. It decreases in stems very rapidly during the early spring and increases in roots until April and then decreases owing to its

upward translocation and root growth. It is apparently the most important sugar of upward translocation in spring.

7. Maltose reaches its maximum in both stems and roots during summer and autumn at the time of translocation of

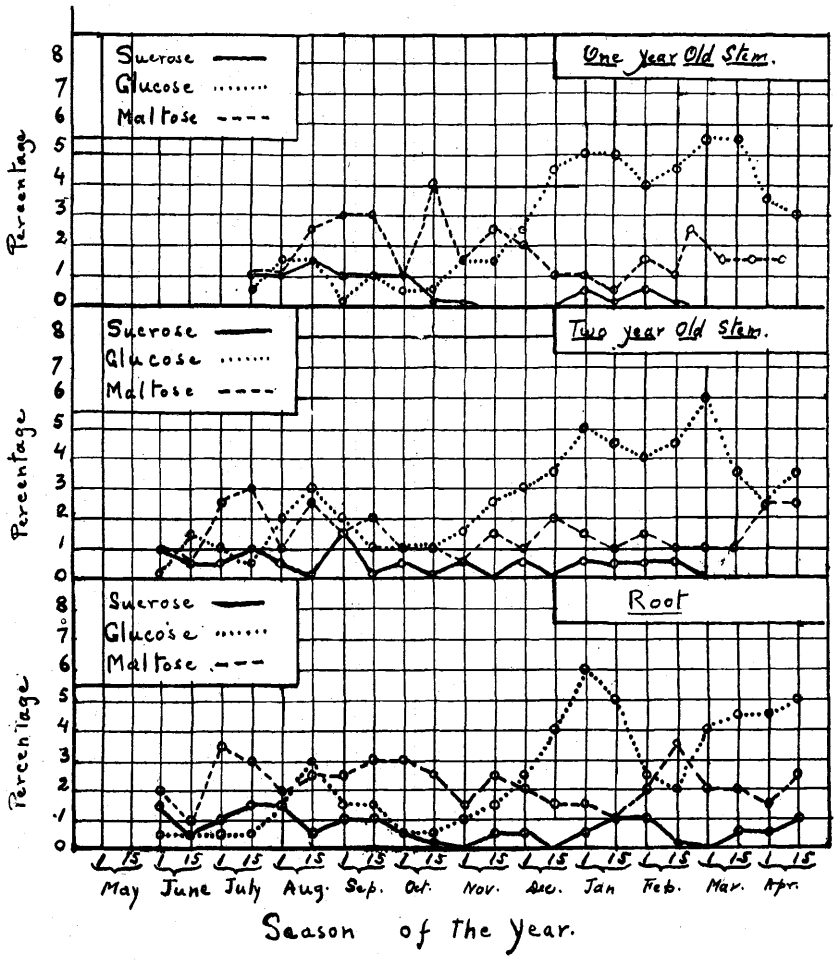

Fig. 6. Curves showing the percentage of sucrose, glucose and maltose in two-year-old seedlings of apple from June to April, 1919–1920. The ordinates represent the percentage of carbohydrates and the abscissae, the season of the year.

sugars from the leaves. It is very low in stems during the dormant period, but increases slightly with the rise of sap in spring.

8. Sucrose is very low in comparison to glucose and maltose. Its maximum occurs in all parts of the plants during summer and autumn. Its presence in roots is more pronounced than in the stems, which has also been shown by Butler et al. It is not an important storage sugar in seedlings.

9. It is interesting to note that the amount of sugars in both stems and roots runs a close parallel throughout the year, with the exception of a greater content in roots during early spring.

10. The total sugar and the reducing sugars in both stems and roots show parallel curves. There is a marked increase at the beginning of the dormant season, which reaches its maximum from January to March, when the starch content is at a minimum. During the dormant period there is a marked hydrolysis of starch to sugar and a partial resynthesis of this sugar to non-carbohydrate compounds.

11. Total carbohydrate in roots is twice as much as that found in one and two-year-old stems, which are almost identical in their carbohydrate content.

The Acidity of Fruit Spurs and Two-year-old Seedlings of Apple.

1. Acidity is high in summer and low in winter. In general during the growing period all parts of the seedlings are distinctly acid, while during the dormant period they approach close to neutrality. The roots and two-year-old stems become slightly alkaline during February and March, after which there is a rapid rise in acidity.

2. Acidity is highest in the leaves and lowest in the roots. The acidity of the leaves is on the decline at the time of abscission.

3. Acidity of the one-year-old stems and the fruit spurs used in the experiments is identical.

4. There is an approximate correlation between the optimum hydrogen ion concentration for the hydrolytic action of plant diastases (about $10^{-4.5}$, Sherman et al.)[8] and maltase ($10^{-6.6}$, Hober[6]) and the time of the most active hydrolyzation of starch in the fruit spurs and stems, i. e., during the dormant period beginning with November. The correlation is not so clear in the case of hydrolysis in roots. Further data on this point are needed.

5. There is also a general correlation between the H ion concentration and the relative activity of diastase and maltase and the consequent concentration of glucose and maltose in the tissues. The optimum H ion concentration for diastase is somewhat more acid than for maltase.

6. Maltose is most abundant and glucose is least abundant in summer and autumn, when acidity is highest and nearer the optimum for diastase than for maltase. On the other

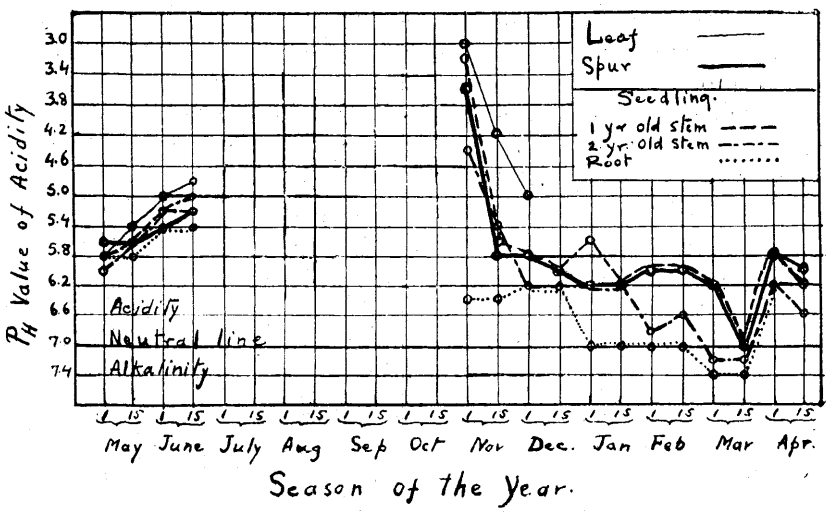

Fig. 7. Curves showing the seasonal changes in PH value of acidity in fruit spurs and two-year-old seedlings of apple from November to June, 1919–1920. The ordinates represent the acidity in PH and the abscissae, the season of the year. Unfortunately, no data were obtained from July to October.

hand, maltose is lowest and glucose is highest during the dormant period, when acidity is lowest and nearer the optimum for maltase than for diastase. The maltose is thus hydrolyzed to glucose at this time almost as rapidly as it is formed from starch. These facts suggest an explanation of why maltose is the most important sugar of translocation from leaves to stem in summer, while glucose is the most important sugar of translocation from root to stem at the close of the dormant period.

7. The presence of invertase has been found by experiment to be much more in abundance in the tissues of fruit spurs and seedlings than either diastase or maltase. It is for this reason that sucrose is rapidly hydrolysed in October and November,

when the acidity is nearer to the optimum activity of invertase (about 10^{4511}, Hober). Sucrose is mostly at its highest during the growing period and early dormant period, when the acidity is rather below the optimum for sucrase. In fact, the data on acidity show in general a correlation of acidity to the activity of enzymes that are involved in the changes of the carbohydrate materials and their accumulation in plant tissues.

The writer is indebted to Professors J. F. Lyman and T. G. Phillips for helpful suggestions in analytical work and especially to Prof. H. C. Sampson for numerous suggestions on problems and interpretation of results.

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ANALYSIS OF FRUIT SPURS OF APPLE (DRY BASIS).

Date	Starch	Sucrose	Maltose	Glucose	Total Sugar
May 15.....	7.470	.....	1.438	1.214	2.720
June 1.....	10.580	.190	1.531	1.152	2.960
" 15.....	11.439	.252	3.960	.905	5.333
July 1.....	11.459	2.166	3.258	.378	5.533
" 15.....	12.459	2.052	2.628	.349	5.266
Aug. 1.....	13.500	.....	1.234	1.218	3.086
" 15.....	13.815	1.531	1.073	1.871	5.266
Sept. 1.....	16.214	.502	4.020	.508	5.266
" 15.....	18.599	.507	3.401	1.258	5.266
Oct. 1.....	17.100	.126	1.700	.636	2.543
" 15.....	17.399	.....	3.403	.558	4.400
Nov. 1.....	16.200	.....	4.950	.597	5.800
" 15.....	15.899	.....	1.328	2.696	4.066
Dec. 1.....	11.459	.127	.928	3.696	4.800
" 15.....	13.500	.443	2.628	2.909	6.133
Jan. 1.....	13.500	.696	2.939	4.317	8.133
" 15.....	8.879	.468	2.541	4.092	7.233
Feb. 1.....	6.300	.950	2.011	3.887	6.933
" 15.....	8.879	.443	.928	6.963	8.400
Mar. 1.....	11.459	.....	.772	5.323	6.533
" 15.....	10.899	.....	3.387	2.571	6.133
April 1.....	8.259	.....	2.996	3.492	6.568
" 15.....	6.899	.....	2.560	3.688	6.091

ANALYSIS OF TWO-YEAR-OLD SEEDLINGS OF APPLE (DRY BASIS).

Date	Starch	Sucrose	Maltose	Glucose	Total Sugar
June 1-1*.....	.....	.....	.....	.....	.....
" 1-2.....	20.279	.772	1.111	.152	2.213
" 1-2.....	29.399	1.342	2.041	.389	3.920
" 15-1.....	.....	.....	.....	.....	.....
" 15-2.....	17.759	.253	.679	1.238	2.213
" 15-3.....	23.999	.251	.752	.608	1.653
July 1-1.....	10.399	.....	.....	.....	.....
" 1-2.....	11.999	.393	2.628	.963	4.133
" 1-3.....	29.999	1.077	3.401	.558	5.266
" 15-1.....	12.699	.840	.958	.526	2.666
" 15-2.....	13.500	.822	2.889	.267	3.533
" 15-3.....	24.899	1.647	3.248	.658	5.800
Aug. 1-1.....	14.088	.750	1.236	1.491	3.533
" 1-2.....	14.699	.570	1.238	1.904	3.800
" 1-3.....	20.999	1.648	2.320	1.362	5.533
" 15-1.....	16.204	1.582	2.630	1.370	5.800
" 15-2.....	15.899	.190	2.628	3.042	6.133
" 15-3.....	22.500	.442	2.630	3.170	6.400

* 1=One-year-old stem. 2=Two-year-old stem. 3=Root.

ANALYSIS OF TWO-YEAR-OLD SEEDLINGS OF APPLE (DRY BASIS).
(Continued.)

Date	Starch	Sucrose	Maltose	Glucose	Total Sugar
Sept. 1–1.....	13.500	.750	3.248	.235	4.400
" 1–2.....	13.699	1.647	1.392	1.805	5.000
" 1–3.....	26.450	1.077	2.628	1.642	5.533
" 15–1.....	13.299	1.077	2.784	.943	5.000
" 15–2.....	17.100	.253	2.011	1.178	4.400
" 15–3.....	29.800	.823	3.248	1.258	5.433
Oct. 1–1.....	13.500	.823	.958	.517	2.386
" 1–2.....	14.699	.409	.958	.944	2.386
" 1–3.....	32.699	.278	2.909	.455	3.800
" 15–1.....	20.250	.228	3.804	.366	4.500
" 15–2.....	14.699	.126	1.020	1.045	2.546
" 15–3.....	32.699	.236	2.350	.516	3.266
Nov. 1–1.....	17.100	.152	1.670	1.355	3.266
" 1–2.....	18.900	.705	.308	1.630	2.386
" 1–3.....	27.299	....	1.331	1.182	2.680
" 15–1.....	17.100	....	2.320	1.438	4.533
" 15–2.....	17.100	....	1.392	2.672	4.133
" 15–3.....	35.399	.266	2.626	1.384	3.666
Dec. 1–1.....	15.899	....	2.011	2.287	4.400
" 1–2.....	17.100	.316	1.236	3.038	4.652
" 1–3.....	29.999	.316	2.011	2.554	5.000
" 15–1.....	14.699	....	1.160	4.281	5.500
" 15–2.....	17.739	....	1.934	3.470	5.500
" 15–3.....	34.538	....	1.547	4.179	5.800
Jan. 1–1.....	11.469	.570	1.236	4.771	6.866
" 1–2.....	11.999	.396	1.545	4.892	6.916
" 1–3.....	24.899	.712	1.547	5.989	8.333
" 15–1.....	8.879	.127	.467	5.235	5.833
" 15–2.....	11.999	.571	.772	4.409	5.833
" 15–3.....	24.899	.905	.765	5.162	6.916
Feb. 1–1.....	11.469	.348	1.468	3.790	6.133
" 1–2.....	13.500	.507	1.392	3.988	6.400
" 1–3.....	23.599	1.076	2.011	2.551	6.400
" 15–1.....	12.638	.127	.928	4.696	5.800
" 15–2.....	13.500	.507	.772	4.709	6.133
" 15–3.....	26.100	.126	3.712	2.100	6.133
Mar. 1–1.....	11.459	....	2.591	5.378	8.000
" 1–2.....	11.999	....	.772	5.943	6.733
" 1–3.....	24.899	....	2.532	4.202	6.916
" 15–1.....	13.500	....	1.530	5.320	6.916
" 15–2.....	11.459	....	.772	3.656	4.400
" 15–3.....	27.599	.627	2.514	4.696	8.000
April 1–1.....	14.699	....	1.663	3.434	4.183
" 1–2.....	15.899	....	2.320	2.312	4.750
" 1–3.....	24.899	.712	1.531	4.552	6.916
" 15–1.....	11.455	....	2.624	3.562	6.390
" 15–2.....	12.860	....	2.624	3.560	6.390
" 15–3.....	23.599	.876	2.610	4.806	7.668

PERCENTAGE OF REDUCING SUGARS IN FRUIT SPURS AND TWO-YEAR-OLD SEEDLINGS OF APPLE (DRY BASIS).

Date	Spurs	Seedlings		
		1-Yr.-Old Stem	2-Yr.-Old Stem	Roots
May 15	2.100	.....	.....	.....
June 1	.....	.820	.820	1.635
" 15	3.360	.....	1.653	1.866
July 1	2.100	.....	2.253	2.666
" 15	3.360	1.400	1.686	2.666
Aug. 1	2.386	2.253	2.666	2.800
" 15	2.546	3.000	4.800	4.800
Sept. 1	2.666	2.253	2.666	3.233
" 15	3.266	2.666	3.233	3.233
Oct. 1	1.680	1.660	1.533	2.253
" 15	2.666	2.720	1.973	1.813
Nov. 1	3.666	2.386	1.813	2.106
" 15	3.400	3.533	3.533	2.253
Dec. 1	4.266	3.533	3.533	3.800
" 15	4.533	5.000	5.000	5.000
Jan. 1	6.133	6.616	5.833	7.250
" 15	5.000	5.500	4.750	5.666
Feb. 1	4.800	5.000	5.266	4.400
" 15	7.533	5.266	5.266	4.400
Mar. 1	5.500	6.983	6.400	5.833
" 15	4.666	6.150	4.183	6.250
April 1	3.950	2.466	3.750	5.500
" 15	3.450	3.012	4.183	6.000

PERCENTAGE OF TOTAL CARBOHYDRATE IN TERMS OF GLUCOSE.

Date	Spurs	Seedlings		
		1-Yr.-Old Stem	2-Yr.-Old Stem	Root
May 15	11.042	.....	.....	.....
June 1	17.900	.....	24.743	36.525
" 15	16.975	.....	21.945	28.318
July 1	18.265	.....	17.465	28.598
" 15	17.998	16.776	18.533	28.198
Aug. 1	17.386	19.186	20.132	28.865
" 15	20.616	23.804	23.798	31.400
Sept. 1	23.281	19.400	20.201	34.921
" 15	25.931	19.776	23.400	38.644
Oct. 1	21.543	17.386	18.718	40.132
" 15	23.732	27.000	18.876	39.598
Nov. 1	23.800	22.266	23.386	33.012
" 15	21.331	23.533	23.133	42.999
Dce. 1	17.532	22.065	23.652	38.332
" 15	21.133	21.832	25.210	44.175
Jan. 1	23.133	20.552	20.248	35.988
" 15	17.098	15.698	19.165	35.581
Feb. 1	13.933	18.876	21.400	32.621
" 15	18.265	19.842	21.133	35.133
Mar. 1	19.230	20.732	20.065	34.581
" 15	18.245	21.916	17.132	38.665
April 1	15.854	19.515	22.415	34.581
" 15	13.756	17.191	20.486	34.603

DETERMINATION OF ACIDITY IN FRUIT SPURS AND TWO-YEAR-OLD SEEDLINGS OF APPLE, EXPRESSED IN VALUES OF PH.

DATE	SPURS	SEEDLINGS			
		1-Yr.-Old Stem	2-Yr.-Old Stem	ROOT	LEAF
	PH	PH	PH	PH	PH
Nov. 1.....	3.6	3.2	4.4	6.4	3.0
" 15.....	5.8	5.6	5.4	6.4	4.2
Dec. 1.....	5.8	5.8	6.2	6.2	5.0
" 15.....	6.0	6.0	6.2	6.2	...
Jan. 1.....	6.2	5.6	6.2	7.0	...
" 15.....	6.2	6.2	6.2	7.0	...
Feb. 1.....	6.0	6.0	6.8	7.0	...
" 15.....	6.0	6.0	6.6	7.0	...
Mar. 1.....	6.2	6.2	7.2	7.4	...
" 15.....	7.0	7.0	7.2	7.4	...
April 1.....	5.8	5.8	6.2	6.2	...
" 15.....	6.0	6.2	6.6	6.2	...
May 1.....	5.6	5.8	6.0	5.8	5.8
" 15.....	5.6	5.6	5.6	5.8	5.4
June 1.....	5.4	5.2	5.2	5.4	5.0
" 15.....	5.2	5.2	5.0	5.4	4.8

N. B.—The data from July to October were not obtained.