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The Relationship Between the Internal Structure and Photosynthetic Behavior of Apple Leaves

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DISCUSSION

Livland apple leaves rank high in their rate of photosynthetic activity per unit of area. York leaves, under comparable environmental conditions, have shown a much lower rate. This ranking of these two varieties is in agreement with the relative amounts of internal leaf surface. Several other varieties were also studied and, in general, their rank as to photosynthetic activity and as to the extent of the intercellular space is similar.

Many factors influence the rate of photosynthesis. Important among these are: the chlorophyll content of the leaves, nitrate and moisture supply, temperature, and carbon dioxide content of the atmosphere. From the evidence here presented, the anatomical characteristics of apple leaves as expressed by measurements of the intercellular space may also be a factor which influences photosynthetic activity. This characteristic probably exerts its influence by governing the diffusive capacity of the leaves and determining the extent of the moist surface of the mesophyll cell walls bounding the intercellular space.

No attempt has been made in these studies to determine whether the characteristics of the intercellular space exert more or less influence on photosynthetic activity than the other factors listed above.

The Livland trees used in these studies were less vigorous than trees of the other varieties, and yet the Livland leaves were found to be the most active in the manufacture of photosynthate. However, when the total leaf area per tree is considered the Livland trees were larger per unit of leaf area than the other trees. A representative Winesap tree had 4.5 times as many leaves and more than twice the total leaf area than a typical Livland tree. A representative York tree had over twice as many leaves and nearly twice the leaf area of the Livland tree.

However, the Winesap and York trees are not so much larger than the Livland as the greater leaf area would indicate. The relative vigor was judged by making measurements of the spread of branches, height of tree, and trunk diameter. Apparently the relative photosynthetic activity per unit of leaf area becomes cumulative over a period of years when the entire tree is considered as a unit.

The low photosynthetic activity of York leaves may be one of several factors which are closely associated with biennial fruit production of this variety.

THE RELATIONSHIP BETWEEN THE INTERNAL STRUCTURE AND PHOTOSYNTHETIC BEHAVIOR OF APPLE LEAVES[1]

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INTRODUCTION

Several investigators have made studies of the photosynthetic behavior of the leaves of apple, *Malus sylvestris,* and a few studies have been made of the internal structure of leaves of several species of plants, but the literature does not record any attempt to determine whether the extent of the intercellular space in the spongy mesophyll of leaves is one of the factors which influences the rate of photosynthesis.

The purpose of the study herein reported was to determine whether varieties of the apple differ in the structure of the spongy leaf mesophyll, and if so, the extent of such differences and their relationship to variations in photosynthetic behavior of the leaves.

The problem had three distinct phases: (1) The anatomy of apple leaves, (2) stomatal characteristics and behavior, and (3) photosynthetic behavior. After the data on these three phases were assembled the influence of the mesophyll characteristics on photosynthetic activity was studied.

PART I. ANATOMICAL STUDY OF APPLE LEAVES

HISTORICAL

Pick (1882) and Stahl (1883) concluded that sun leaves are thicker than shade leaves, but that the air spaces of the shade leaves are larger.

De Lamarliere (1892) observed that for equal surfaces, sun leaves have greater intensity of respiration, assimilation, and transpiration than those grown in the shade, the well known structural differences thus having a corresponding physiological significance.

Bonnier (1894), comparing the same species of plants at various elevations in the Alps and Pyrenees, found that the Alpine leaves had a better developed palisade tissue, due to larger cells or an increase in the number of rows, and that there were more stomata per unit of leaf surface than on the leaves of plants grown in the lowland.

Eberhardt (1900) reported that humid air favored the production of larger leaves and greater amounts of chlorophyll and root development. In dry air the cuticle became thicker, more stomata were formed, and the palisade tissue was thicker.

Hesselman (1904) studied the influence of light on the leaf structure of forest trees. Leaves grown in the stronger light had more palisade cells than those in the poorer light. Shade leaves produced more starch than sun leaves of the same species when the light was equal.

Bergen (1904) found that sun leaves transpired more than shade leaves because the greater thickness of the former affords a larger evaporating surface.

Clements (1904) concluded that decreased light and increased water cause an increase in leaf surface and a decrease in thickness; decreased light causes a somewhat looser arrangement of the palisade; increased light and decreased water both cause a reduction in leaf surface and an increase in thickness; strong light causes a closer arrangement of the palisade; and, finally, that no laws can be laid down as to the exact amount of change taking place in the histology of the leaf in response to a definite difference in the physical factors.

Haller and Magness (1925) reported that under conditions in Virginia, from 30 to 40 leaves of medium size were necessary per apple for Grimes and Ben Davis, but for Delicious even more leaves were required in order to obtain apples of good size and quality.

Pfeiffer (1928) studied the influence of light of various wave lengths upon plant growth and found that full insolation produced thicker leaves than those in the limits of the visible spectrum.

Magness (1928) correlated leaf area and number of leaves with sugar content and size of apples and concluded that with smaller leaf area per fruit, the leaves seem to function more efficiently.

Heinicke and Hoffman (1933) judged that the internal conditions of the leaf and of the tree as a whole will have a profound influence on the efficiency of the foliage of apple shoots. Color is the only one of the internal conditions mentioned.

Vyvyan and Evans (1932) observed that the size of a leaf varies with the nature of the growth bearing it, with the number of leaves, and position of the leaves on the growth.

Turrell (1934) worked out formulae for the computation of the ratio of the internal exposed surface to the external exposed surface of mesomorphic, xeromorphic, and succulent leaves. Though this method may be satisfactory for comparative determinations for leaves which differ as much as xeromorphic and succulent leaves, it was found unsatisfactory for studies of varieties of apple leaves. The differences between the struc-

ture of apple leaves of several varieties are not sufficiently great to permit the use of this method.

Pickett (1934) reported that under Kansas conditions, 20 leaves per fruit on Delicious gave larger fruit than the largest of other varieties with 40 or even 50 leaves per fruit. The York ratio of 50 leaves per fruit produced apples which were larger than either Winesap or Jonathan, but smaller than Delicious at this ratio. The York trees, however, had not produced fruit the preceding year, while the other varieties had borne.

The weight of fruit produced per 100 square centimeters of leaf area was determined by Fisher (1934) for McIntosh, Delicious, Rome, and Newtown. This weight was least with McIntosh and greatest with Rome.

Chandler (1934) reported that fruiting does not reduce wood growth in proportion to leaf surface by as much as the dry matter of the fruit. One of the possible causes suggested was that the presence of the fruit accelerated photosynthesis by removal of the products which otherwise would accumulate in the leaves and inhibit photosynthesis.

Cowart (1935) reported that differences in photosynthetic and transpiration rates may be associated in some degree with differences in leaf structure in the apple.

Singh and Lal (1935) concluded that the variations in structural characteristics of leaves are negligible and that a chronological and morphological classification of leaves is no criterion of their assimilatory activity.

ANATOMY—PROCEDERE

Seven varieties of apples have been used in this study. The selection was based on the supposed efficiency of the leaves in promoting tree vigor and fruit production, rather than upon any previous knowledge of their internal structure. Livland and Wealthy were chosen because the fruit of these varieties ripens from early summer to mid-summer under Kansas conditions, and Livland is rather a dwarfish tree, while Wealthy trees are of standard size. Jonathan and Delicious trees are vigorous, and Jonathan is of major importance as a commercial variety in the Missouri river valley district. These varieties are usually harvested between September 1 and 15. Winesap, Gano, and York were the winter varieties studied. In central and eastern Kansas, Winesap is one of the most profitable varieties, especially in those orchards where adequate moisture and cross pollination are provided. Winesap trees are good in vigor on good sites but the fruit on the older trees is below medium in size and the leaves are smaller than those of most other varieties. Of the varieties selected, Gano is one of the most profitable for the commercial grower. It is an annual bearer and the fruit and leaves are usually of good size. York is distinctly biennial

in its fruit-bearing habit. The tree is above average in vigor.

The trees in the orchard of the Kansas Agricultural Experiment Station at Manhattan were used for this study. The average yearly rainfall at Manhattan is 31.49 inches. The soil on this site belongs to the Derby silt loam series. Considerable soil erosion has taken place and most of horizon A is gone. The trees are 18 to 20 years old and are fair to good in vigor. The soil management method for the past 14 years has been a combination clean-cultivation-cover-crop plan. Frequent scarcity of soil moisture is probably the greatest hazard in growing an orchard in this locality, and this factor becomes of major importance for a period varying from a few days to several weeks during most growing seasons. Drouth conditions are frequently aggravated by extremely hot weather and high, hot winds. During these periods the evaporating power of the air is great.

Leaves for the anatomical studies were selected from the middle portions of new shoots on the south side of the periphery of the trees. Pieces about 1 centimeter square were cut from near the midsection of the leaf blades, only one piece being removed from a leaf, and plunged into a chromo-acetic acid-killing solution containing 1 percent acetic acid. Dehydration of the samples was accomplished by using the series of water, ethyl, and N-butyl alcohols as reported by Zirkle (1930).

During the imbedding the leaf portions were arranged with the lower epidermis toward the bottom of the tray. A rotary microtome was used to cut the sections 8 to 10 microns in thickness. The imbedded material was so arranged on the microtome disc that the knife cut through the lower epidermis first; the palisade tissue and greater thickness of paraffin above the upper epidermis prevented tearing of the upper epidermis. Reversing the direction of the cut sometimes resulted in the tearing of the spongy mesophyll and lower epidermis. A weak mixture of powdered egg albumen suspended in water was used as the fixative. The sections were stained heavily in safranine O.

To permit a study of the looseness or compactness of the mesophyll, the slides were mounted on a microscope so arranged that it served as a microprojector. A spotlight was used as the source of light and the images from the projector were focused on a screen 43 inches from the outer end of the microscope barrel so that the leaf sections were magnified approximately 900 diameters.

Fifty tracings of representative samples of the mesophyll of each variety were made on paper, not more than five tracings being made of sections from any one leaf.

To secure mathematical descriptions of the relative compactness of the mesophyll, the cross sectional areas of the intercellular space, as traced an paper, were computed with a planim-

eter. By use of a chartometer the total linear perimeter measurement of each tracing was determined. These data are presented in Table I.

During the 1934 season for the orchard studies, only four varieties were used in contrast with seven varieties in 1933. The reduction in the number of varieties was feasible because of the great similarity between certain varieties; and the reduced number made it possible to determine photosynthetic activity more frequently and thereby secure more dependable records of the daily performance of the leaves. The varieties used in 1934 and 1935 were Jonathan, York, Delicious, and Livland. Delicious and Livland were selected because during 1933 they probably had the most compact and the most open mesophyll structure, respectively, of the varieties studied. Jonathan and York were retained because the leaves are large and hence better suited to photosynthetic studies by the modified Sachs punch method than the smaller leaves of Winesap.

In a study of the effect of certain environmental conditions on leaf structure, several 1-year-old whips of the Livland and Delicious varieties were planted in 12-inch clay pots in the greenhouse in January, 1933, and another similar planting was made in January, 1934. Data relative to the anatomical studies are found in Tables I, II, III and IV.

In Table I, data are presented showing the relative amounts of mesophyll tissue, as determined from cross sections of the leaves. In 1933, Delicious leaves possessed the most compact mesophyll, only 11.66 percent of the total cross sectional area of the mesophyll being intercellular space.

In 1934, the average amount of mesophyll tissue shown on the projected images was greatest with Delicious; Livland, Jonathan, and York followed in the order named. On a percentage basis, Livland possessed the greatest amount of mesophyll tissue, and York the least.

The measurements for 1935 show that Livland leaves possessed the greatest amount of mesophyll tissue and also the highest percentage of intercellular space. York ranked lowest in both these characteristics. With each variety the ratio of the total volume of the leaves occupied by intercellular space was lower in 1935 than in 1934.

The differences between measurements of the intercellular space in the mesophyll of some of these varieties are highly significant statistically. Between others, however, the differences are not significant.

The differences between the means of the intercellular area measurements for 1933 are presented in Table II and their perimeter differences in Table III. As shown by Table II, the differences between the cross sectional area measurements of orchard-grown Livland and those of orchard-grown Delicious,

TABLE I.—MEASUREMENTS OF APPLE LEAF MESOPHYLL.

Variety	Average cross sectional area of intercellular space, sq. cm.			Average perimeter measurements of intercellular space, cm.			Average cross sectional area of mesophyll, sq. cm.			Percentage of total cross sectional area occupied by intercellular space		
Orchard grown	**1933**	**1934**	**1935**	**1933**	**1934**	**1935**	**1933**	**1934**	**1935**	**1933**	**1934**	**1935**
Delicious............	56.76±5.03	86.96±9.67	68.84±7.87	148.31±12.88	205.74±19.30	169.93±19.05	429.95	414.09	395.31	11.66	17.35	13.96
Jonathan	61.15±8.64	77.85±11.74	60.45±8.96	159.80±15.42	202.51±26.03	165.86±16.25	381.58	369.96	413.89	13.81	17.38	12.74
Gano	67.27±7.67	....	....	154.43±11.45	....	....	418.74	......	......	13.84	.....	.....
Winesap.....	79.85±7.16	....	....	179.93±6.17	....	....	377.78	......	......	17.44	.....	.....
York	81.78±9.35	70.82±7.48	58.20±9.93	190.02±17.55	196.39±18.62	167.39±20.57	317.67	350.73	408.08	20.47	16.79	12.48
Wealthy	82.17±6.90	....	....	191.62±17.80	....	....	530.13	......	......	13.42	.....	.....
Livland	114.36±5.29	107.97±7.22	77.62±12.00	254.51±17.48	212.55±17.30	183.13±19.81	454.66	390.22	461.12	20.09	21.67	16.83
Greenhouse grown												
Delicious............	....	60.44±6.64	....	....	123.25±9.27	....	......	358.87	......	.....	14.41	.....
Livland	....	63.40±11.74	....	....	128.65±22.05	....	......	445.31	......	.....	12.46	.....

Note.—Measurements for each variety were made from 50 projected images, 11 inches long, at a magnification of 900.

Jonathan, Gano, and Winesap are significant to the extent that the differences are at least four times their probable errors. The differences between the means of Livland and the other varieties vary in terms of their own probable errors from 7.8 for the Livland-Delicious comparison, to 3.04 for the Livland-York comparison. (Pickett, 1933.)

TABLE II.—DIFFERENCE BETWEEN MEANS OF CROSS SECTIONAL AREA MEASUREMENTS OF INTERCELLULAR SPACE IN APPLE LEAF MESOPHYLL. SQUARE CENTIMETERS. 1933.

	Delicious	Jonathan	Gano	Winesap	York	Wealthy
Jonathan	4.39±9.99	....	....	....	....	....
Gano	10.51±9.17	6.12±11.55	....	....	....	....
Winesap	23.09±8.75	18.70±11.22	12.58±10.49	....	....	....
York	25.02±10.62	20.63±12.73	14.51±12.09	1.93±11.78	....	....
Wealthy	25.41±8.54	21.02±11.06	14.90±10.32	2.32±9.94	0.39±11.62	....
Livland	57.60±7.30	53.21±10.13	47.09±9.32	34.51±8.90	32.58±10.74	32.19±8.69
Greenhouse Delicious	Orchard Delicious 16.52±11.77	Orchard Livland	....	....	....	....
Greenhouse Livland	....	50.96±12.88	....	....	....	....

TABLE III.—DIFFERENCE BETWEEN MEANS OF PERIMETER MEASUREMENTS OF INTERCELLULAR SPACE IN APPLE LEAF MESOPHYLL. CENTIMETERS. 1933.

	Delicious	Jonathan	Gano	Winesap	York	Wealthy
Jonathan	10.49±20.09	....	....	....	....	....
Gano	6.12±17.23	4.37±19.21	....	....	....	....
Winesap	31.62±14.28	21.13±16.61	25.50±13.01	....	....	....
York	41.71±21.77	31.22±23.36	35.59±20.95	11.09±18.60	....	....
Wealthy	43.31±21.97	32.82±23.55	37.19±21.16	11.69±18.84	1.60±25.00	....
Livland	106.20±21.71	95.71±23.31	100.08±20.90	74.54±18.54	64.49±24.77	62.89±24.95
Greenhouse Delicious	Orchard Delicious 66.49±10.55	Orchard Livland	....	....	....	....
Greenhouse Livland	... .	14.29±22.68	....	....	....	....

Considering the 1934 data, when four varieties were used, no significant difference was shown in any comparison of orchard-grown Delicious, Jonathan, and York. (Table IV.) However, between orchard-grown Livland leaves and orchard leaves of the other three varieties, the differences in terms of their own probable errors vary from 3.57 for the Livland-York comparison, to 2.19 for the Livland-Jonathan comparison. The 1934 orchard data do not show so great differences in the cross sectional area measurements as those of 1933. There were no significant differences in the measurements for 1935.

TABLE IV—DIFFERENCES BETWEEN MEANS OF CROSS SECTIONAL AREA MEASUREMENTS OF INTERCELLULAR SPACE IN APPLE LEAF MESOPHYLL. SQUARE CENTIMETERS. 1934.

	Orchard Delicious	Greenhouse Delicious	Jonathan	York	Greenhouse Livland
Greenhouse Delicious	4.11 ± 1.82	. . . .	. . . .	. . . .	0.46 ± 2.08
Jonathan	1.41 ± 2.36	2.70 ± 2.09	. . . .	. . . .	. . . .
York	2.50 ± 1.84	1.61 ± 1.55	1.09 ± 2.15	. . . .	. . . .
Greenhouse Livland	3.65 ± 2.36	0.46 ± 2.09	2.24 ± 2.58	1.15 ± 2.15	. . . .
Orchard Livland	3.26 ± 1.93	7.37 ± 1.52	4.67 ± 2.13	5.76 ± 1.61	6.91 ± 2.13

When comparisons between greenhouse-grown and orchard-grown foliage are made the differences are greater. The difference between orchard-grown Livland and greenhouse-grown Delicious in terms of its own probable error is 4.85.

The environmental conditions present during the period when the apple leaves are in an active growing state have much influence on the character of the mesophyll. Leaves produced on potted trees in the greenhouse have less palisade development than the same varieties of leaves grown in the orchard. Within a variety, orchard-grown leaves possess the greater weight per unit of area in addition to having a more extensive development of intercellular space.

Immature leaves, those appearing just as a bud is beginning its vegetative growth, were found to possess no appreciable intercellular space in the mesophyll. When the leaves had grown to a width of 1 centimeter, the intercellular space had developed through the mesophyll cells, by splitting the middle lamella. This was determined by preparing microscopic cross sections of these small leaves and using ruthenium red or methyl blue stains. Pectic substances were observed on the cell walls which constituted the boundaries of the intercellular space. As the

leaves became older, less and less of the pectic substances were present. In mature leaves, no pectic substances could be detected by use of these stains.


FIG. 1.—Cross sections (X 200) of greenhouse-grown (A) Livland apple leaf and (B) Delicious apple leaf.

Photomicrographs of representative portions of cross sectional and tangential sections of the apple leaves are presented in figures 1 to 5, inclusive. The cross sections were prepared from the seven varieties used in 1933. The tangential views are from the four varieties studied in 1934. The most important feature of the tangential sections is the distinct looseness of the Livland mesophyll when contrasted with that of the York, Delicious, and Jonathan sections. The tangential illustrations show a portion of the lower epidermis with a few stomata clearly visible and the lower parts of some of the palisade cells, with the spongy tissue covering most of the field.

PART II. STOMATAL BEHAVIOR

INTRODUCTION

Stomata on apple leaves are found only on the lower surfaces, and are directly involved in the process of photosynthesis since the carbon dioxide enters the leaves, for the most part, through them. Cuticular absorption of carbon dioxide is probably not sufficient to be of importance in photosynthesis in apple leaves.
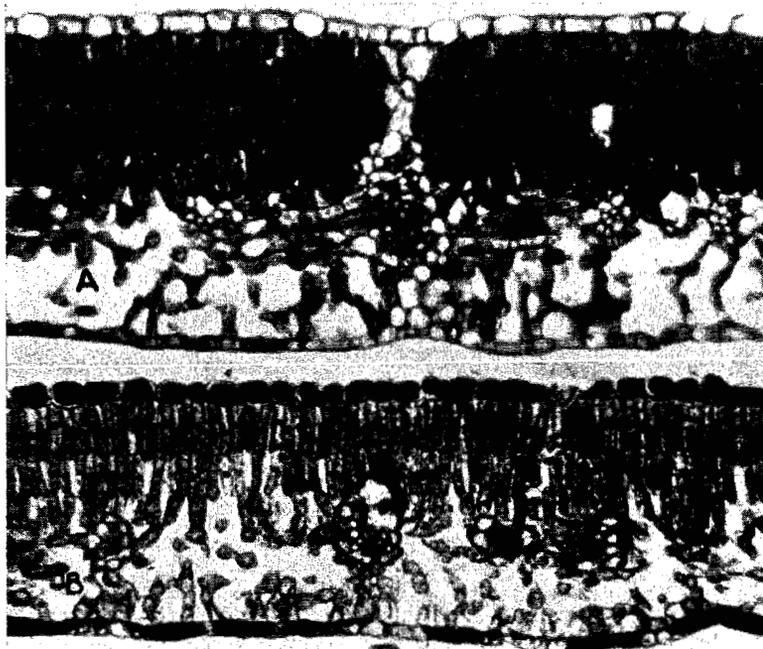
FIG. 2.—Cross sections (X 200) of orchard-grown (A) Jonathan apple leaf, and (B) York apple leaf.

HISTORICAL

No attempt is made here to give an extensive review of the literature on stomatal behavior or of methods for making these studies. A critical review of the latter together with a bibliography is given by Lloyd (1908). He concluded that, if a section of leaf epidermis be removed and plunged at once into absolute alcohol, the tissue is dehydrated so rapidly that no measurable change in the dimensions of the stomata takes place. Sachs had long before pointed this out to De Vries. The material thus treated may be studied in detail at a subsequent time. Lloyd,

working with *Fourquieria splendens* and *Verbena ciliata,* concluded that stomatal regulation of transpiration does not occur, except that conservation of the contained water follows on complete closure of the stomata. Lloyd believed that light was the most important of the environmental factors that cause stomata to open in the morning.
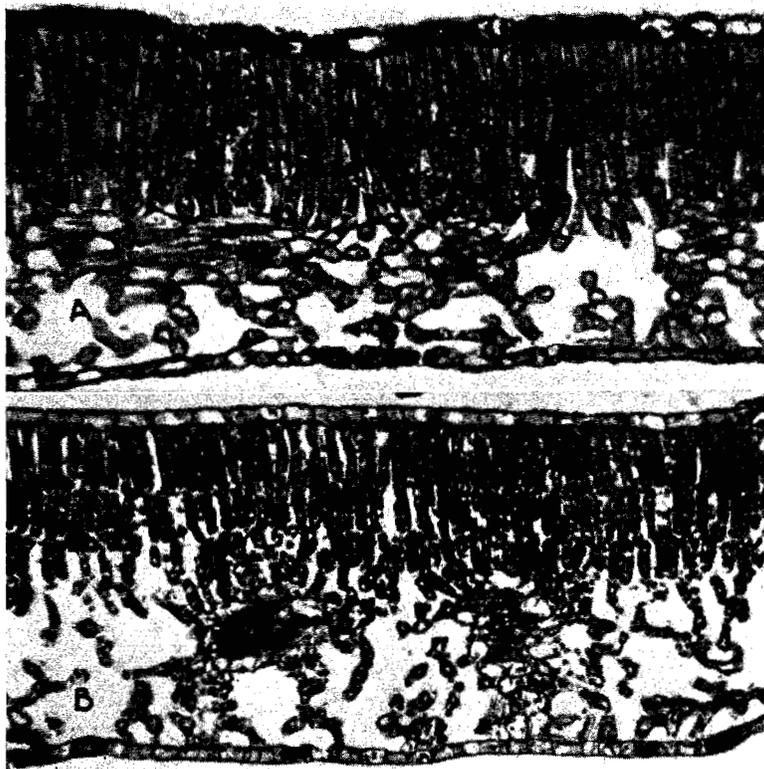
Fig. 3.—Cross sections (X 200) of orchard-grown (A) Delicious apple leaf, and (B) Livland apple leaf.

Loftfield (1921) studied the daily march of stomatal movement at Salt Lake City, Utah, Minneapolis, Minn., and Tucson, Ariz., and classified the apple with the group of plants, typified by alfalfa, in which the stomata are closed during the night and open from daybreak until midday or until nightfall. He presents data to show that stomata regulate the water loss from plants. The rate of transpiration is closely governed by stomata when they are nearly closed and by the factors affecting evaporation when they are wide open. He also gives a bibliography

on stomatal behavior, especially as it is involved in transpiration. The number and size of the stomata on any given area of leaf are influenced by the conditions under which they were formed. A leaf developed in the shade has fewer and larger stomata per unit area than one produced in light.
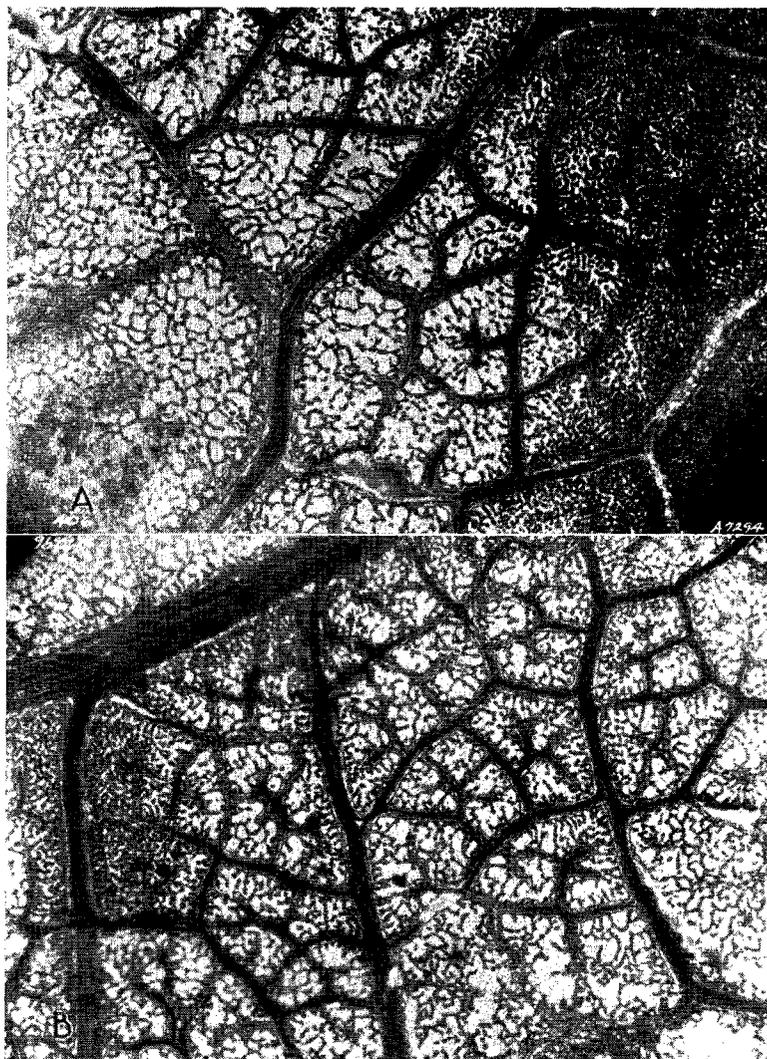
FIG. 4.—(A) Tangential section (X 45) of an orchard-grown Jonathan apple leaf. (Note stomata at lower left and palisade cells on right.)
(B) Tangential section (X 45) of an orchard-grown York apple leaf.

Maskell (1928) presented evidence to show that diurnal rhythm of assimilation is closely associated with the diurnal behavior of stomatal opening.

Furr and Magness (1930) found that the duration of stomatal opening was closely allied with soil moisture content
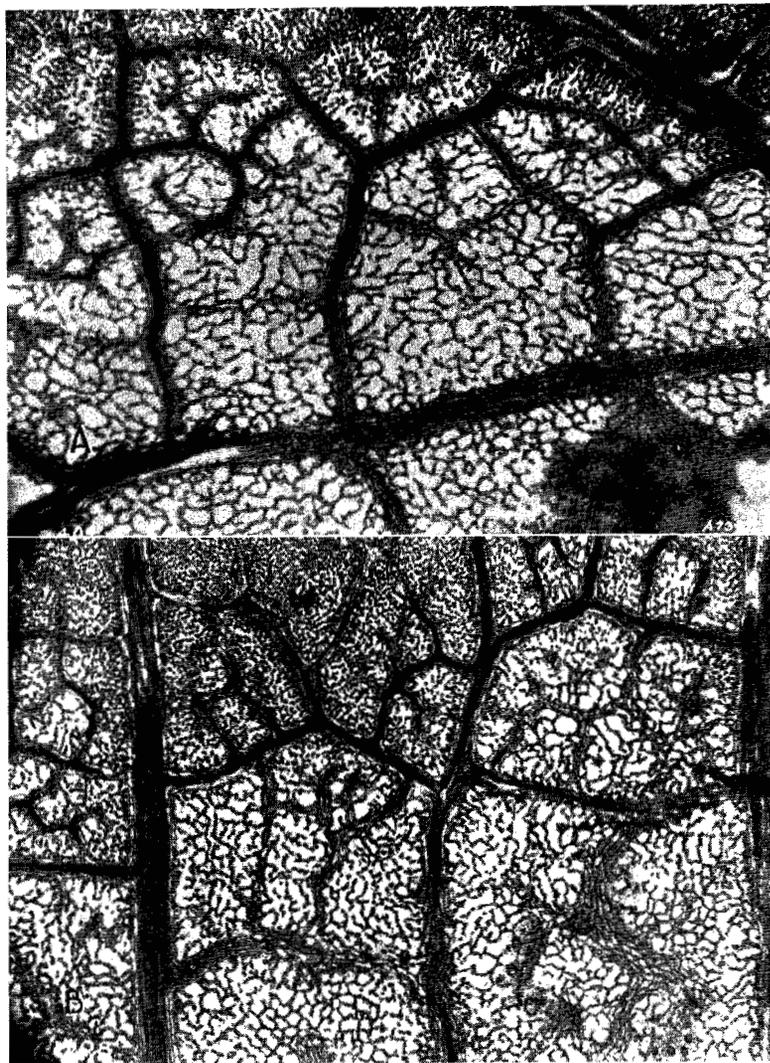

FIG. 5.—(A) Tangential section (X 45) of an orchard-grown Livland apple leaf. (Note stomata at lower right and lower parts of palisade illustrated at top. Compare intercellular space in the spongy mesophyll with that in figure 4, B.)

(B) Tangential section (X 45) of an orchard-grown Delicious apple leaf.

and the evaporating power of the air. Favorable soil moisture content caused the stomata to remain open longer than they did when the amount of moisture in the soil is low or near the wilting point. The period of daily opening was approximately twice as long on the irrigated plots as on the dry plots. These workers found that there was a close correlation between the daily period of stomatal opening and the growth of the fruit.

Penfound (1932), working with the castor bean, found that the number of stomata varied with the amount of light and indirectly with soil moisture content. Sawyer (1932) studied the stomatal apparatus of the cultivated cranberry, *Vaccinum macrocarpon,* and found no chloroplasts in the guard cells. The stomata never open widely and the apparatus seemed poorly adjusted to changes in light, temperature, and moisture. He reported that no differences of taxonomic or functional significance were found in four varieties.

PROCEDURE

Three items involving stomatal studies were investigated in this study; namely, the number of stomata per unit area of leaf surface for each variety of apple used, the size of the stomata as judged by the length of the stomatal slit or opening, and in a few instances the diurnal behavior in opening and closing.

In Table V are presented data on the number of stomata per square centimeter of leaf surface for the season of 1933 for both greenhouse-grown and orchard-grown trees. Livland, a Russian variety, has the smallest number of stomata per unit area of leaf surface for both the greenhouse and orchard trees, but has the longest stomatal opening of any variety studied. In measuring the length of the stomata (Table V) the aperture was measured and not the length of the adjacent guard cells.

TABLE V.—NUMBER AND SIZE OF STOMATA.

Variety	Orchard-grown foliage				Greenhouse-grown foliage			
	Average number of stomata per sq. cm. leaf area		Average length of stomata microns		Average number of stomata per sq. cm. leaf area			
					Cool house		Warm house	
	1933	1934	1933	1934	1933	1934	1933	1934
Livland	27,100	26,000	14.25	14.55	20,000	21,000	20,100	21,500
York	30,800	30,000	12.23	12.50	23,000	....	25,500	....
Gano	31,900	....	13.99	....	25,000	....	23,100	....
Jonathan	33,000	30,500	12.76	12.53	25,300	....	23,100	....
Winesap	33,000	....	12.16	....	22,200	....	23,000	....
Delicious	33,500	33,500	12.08	12.27	....	27,500	....	27,000
Wealthy	37,290	....	13.91	....	....	....	....	....

Stomatal counts and measurements were made from strips of the lower epidermis torn from the apple leaves and mounted in water. At least 26 counts and measurements were made for

each variety, representing one strip from each of 25 leaves located on the south side of the periphery of the trees. Only mature leaves were used. Later in this report data will be presented on the photosynthetic activity of orchard-grown leaves compared with that of greenhouse-grown leaves. It is of interest to note that greenhouse-grown leaves have fewer stomata per unit area than orchard-grown leaves of the same variety.

Opening and closing of stomata were studied for the seven apple varieties used in 1933 and for the four used in 1934. No attempt was made to determine the cause or causes of stomatal behavior, since the objective of this work was to determine whether there might be differences in this regard among the several varieties.

Two methods of studying stomatal behavior were employed. In one the microscope was taken to the orchard and the lower epidermis of the leaf was examined while still attached to the tree. This required a strong light to reflect against the leaf from the sub-stage mirror. There was much difficulty in using the higher power objectives for this purpose because of the uneven surface of the leaves and the presence of great amounts of pubescence on some varieties, especially Jonathan. Livland has little pubescence on the lower epidermis. The low power objective was not satisfactory because of insufficient magnification. This method was found to be too cumbersome. Too much time is required for each observation and no permanent material is on hand for confirmation of the data.

The second and more satisfactory method was to tear off strips of the lower epidermis and plunge them into absolute alcohol. Pieces of the lower epidermis of the leaves were taken by making a small cut with a safety-razor blade under the epidermis near the midrib, after which as much of the epidermis as would tear, was quickly stripped with a pair of tweezers. The section secured by starting near the midrib and tearing the epidermis laterally toward the leaf margin, was triangular in outline because the epidermis tore along the smaller veins. The epidermal strip was plunged immediately into absolute alcohol, the entire operation requiring only two or three seconds. Later the strips were stained in 2 percent safranine O in absolute alcohol, rinsed in absolute alcohol, and permanently mounted in euparal. The preparation of permanent slides was necessary because considerable time was required to determine which stomata were open, due to the fact that with most varieties the stomata were seldom more than partly open. It is probable that with any method of observing stomatal behavior there is sufficient error that it is practically impossible to determine whether a stoma is closed or only nearly so. The author has had extreme difficulty in making determinations of this kind.

On August 3 and 4, 1934, stomatal behavior was studied on a

King David apple tree at Manhattan, Kan. This 20-year-old tree was growing in a heavy clay soil and had been in a wilted condition for three weeks. During the few days preceding August 3, the foliage was wilted during the entire 24-hour period, while during the first part of the 3-week period the leaves wilted every day but recovered their turgidity over night. The condition of the stomata was determined by removing strips of the lower epidermis as described above. In addition the lower epidermis of the leaves was examined with a microscope without detaching the leaves from the tree. At every inspection all of the stomata were judged to be closed.

The same type of experiment was repeated on August 21 and 22, 1934, with a Jonathan tree. Here again all the stomata were judged to be closed at each inspection. The tree was badly wilted. The data for both the King David and Jonathan trees are presented in Table VI. The procedure of judging apparent photosynthesis according to the modified Sachs dry-weight method and of determining the total acid hydrolyzable carbohydrates is described later in this publication.

Although for the duration of the experiments there was a gain in combustible organic matter with the samples represented in Table VI, it is considered too small to represent any appreciable photosynthetic activity and probably falls within the limits of the error of sampling. Likewise, the variations in carbohydrate content are not significant.

Stomatal behavior of greenhouse-grown apple foliage was studied on May 22 and June 5, 1933, and May 2, 1934. Similar observations on orchard-grown leaves were made on June 12, July 6, and July 10, 1933, and on July 19, 1934. (Tables VII, VIII, and IX.) No experimental work was attempted to determine the factors governing stomatal opening and closing; neither were the trees subjected to any special treatment to prolong the period of stomatal opening. The primary purpose of this phase of the investigation was to determine whether there were any varietal differences in stomatal behavior. It is assumed that stomatal opening and closing largely govern the rate of photosynthesis in leaves, other environmental factors being favorable for this process. A few general statements summarize these studies:

a. Stomata on apple foliage in the greenhouse usually remain open longer each morning than those in the orchard.

b. With all varieties under observation, many stomata were partly open to wide open until noon in the greenhouse.

c. In the orchard, the stomata were seldom open after 8 or 9 o'clock in the morning and on some days they were closed during the entire 24-hour period. There is probably a certain amount of error in this last statement, because on one or two

TABLE VI—STOMATAL BEHAVIOR AND PHOTOSYNTHETIC ACTIVITY, WILTED APPLE FOLIAGE, 1934.

Variety	Date	Time	Tempera-ture, centigrade	Relative humidity, percent	Total dry weight per sq. m. leaf area, gm.	Ash percent	Ash per sq. m. leaf area, gm.	Combustible material per sq. m. leaf area, gm.	Acid hydrolyza-ble carbohy-drates as glucose per sq. m. leaf area, gm.
King David	Aug. 3	6:00 a. m.	22	42	81.01	......	......	......	11.72
	Aug. 3	2:00 p. m.	40	16	83.50	......	......	......	12.16
	Aug. 4	6:00 a. m.	29	76	84.47	......	......	......	12.14
Jonathan	Aug. 21	6:00 a. m.	15	89	82.72	5.74	4.75	77.97	13.01
	Aug. 21	2:00 p. m.	31	46	83.75	5.77	4.83	78.92	12.28
	Aug. 22	6:00 a. m.	21	85	89.25	5.66	5.05	84.20	11.78
	Aug. 22	2:00 p. m.	31	30	90.46	5.80	5.25	85.21	11.49

occasions the leaves were more active photosynthetically than shown in Table VI, although the stomata were judged to be closed. The author is of the opinion that it is impossible to determine with certainty by means of microscopic examination of

TABLE VII.—STOMATAL BEHAVIOR ORCHARD-GROWN FOLIAGE, JULY 18, 1934.

Time	5:00 a. m.	6:00 a. m.	7:00 a. m.	8:00 a. m.
Temperature, C.	28	29	30	31
Relative humidity, percent	42	40	37	35
Stomata Open, Percent				
Jonathan	19	20	....	....
York	16	18	....	....
Delicious	11	16	....	....
Livland	2	7	....	....

Note.—No stoma recorded as "open" in this table was open more than one fourth of full extent.

epidermal strips or of the attached leaves whether stomata are closed sufficiently to be gas-tight or only nearly closed.

d. Livland has the smallest number of stomata per unit of leaf area of any of the varieties observed, but the stomata are longer than any others.

e. Wealthy has the greatest number of stomata per unit of leaf area.

f. Fewer stomata are open in the morning in Livland and Wealthy than in the other varieties.

PART III. PHOTOSYNTHETIC ACTIVITY OF APPLELEAVES

INTRODUCTION

No entirely satisfactory method for determining the rate of photosynthesis has been devised. The reasons for this are obvious. Concomitant with the phenomenon of photosynthesis are the processes of respiration and translocation, making it difficult, if not impossible, to measure the first and exclude the effects of the latter two. There are several methods for measuring the apparent rate of photosynthesis, that is, the amount of photosynthetic material produced in excess of the amount of substances used in respiration and translocation. One of these methods considers the quantitative determination of the gaseous exchange. This method has two distinct types of study — in one the amount of oxygen liberated is measured and in the other the intake of carbon dioxide is determined. The second general method is based on the determination of organic substance formed or the dry matter accumulated.

TABLE VIII.—STOMATAL BEHAVIOR, ORCHARD-GROWN APPLE FOLIAGE, 1933.

Time	5:00 a. m.			9:00 a. m.			1:00 p. m.			3:30 p. m.			7:00 p. m.		
	June 12	July 6	July 10	June 12	July 6	July 10	June 12	July 6	July 10	June 12	July 6	July 10	June 12	July 6	July 10
Temperature, C.	22	20	24	29	27	29	31	33	32	36	38	34	32	37	32
Relative humidity percent	85	71	96	80	67	76	50	60	65	27	30	57	30	36	52
Stomata Open, Percent															
Delicious	15	19	20	6	2	10	0	0	0	0	0	1	0	0	1
Jonathan	12	8	10	10	5	96	0	0	0	0	0	0	0	0	0
Gano	20	21	55	8	0	23	0	0	2	0	0	1	0	0	1
Winesap	18	20	25	6	1	2	0	0	0	0	0	0	0	0	1
York	12	10	20	9	9	5	0	0	0	0	0	0	0	0	0
Wealthy	5	0	1	1	0	11	0	0	0	0	0	0	0	0	0
Livland	6	1	11	0	0	4	0	0	0	0	0	0	0	0	0

Note.—In compiling this table no distinction was made between the stomata which were only partly open and those open to a greater extent, both conditions were listed as being "open."

TABLE IX.—STOMATAL BEHAVIOR GREENHOUSE-GROWN FOLIAGE, MAY 2, MAY 22, AND JUNE 5, 1934.

Time	8:00 a. m.			9:30 a. m.			11:30 a. m.			1:30 p. m.			3:30 p. m.		
	May 2	May 22	June 5	May 2	May 22	June 5	May 2	May 22	June 5	May 2	May 22	June 5	May 2	May 22	June 5
Temperature, C.	22	21	20	24	20	19	24	20	24	23	25	27	23	23	31
Relative humidity, percent	77	75	70	66	72	67	76	68	65	69	69	62	69	65	60
Stomata Open, Percent															
Livland	90	75	77	100	90	89	100	76	72	10	5	10	....	....	....
Delicious	85	80	75	100	93	84	100	70	85	10	15	7	....	....	....

In the present study, apparent photosynthetic measurements were made in three ways: (1) By determining the amount of carbon dioxide absorbed by a known amount of leaf area; (2) by determining the weight of the dry matter accumulated per unit of leaf area during a definite period; and (3) by making comparisons of the total acid hydrolyzable carbohydrates at different periods of the day. Each of these methods will be discussed separately because the results are conflicting. No two of them measure the same plant activities. In each of the three methods the process of respiration complicates the photosynthetic determinations.

DETERMINATION OF THE AMOUNT OF CARBON DIOXIDE ABSORBED BY LEAF AREAS

HISTORICAL

The method of determining the absorption of carbon dioxide was first used by Kreusler (1885). Other investigators, including Matthaei (1905), Blackman and Matthaei (1905), Brown and Escombe (1905), Willstätter and Stoll (1918), Spoehr and McGee (1923), and Heinicke and Hoffman (1933), have modified and improved the method. Good bibliographies on this topic are found in the works of Stiles (1925), Spoehr (1926), Miller (1931), Gassner and Goeze (1932), and Heinicke and Hoffman (1933). Stiles (1925) expressed the opinion that the continuous current method is the most reliable of all methods that have been evolved for measuring photosynthesis. It involves drawing a stream of air past the plant part under test and through an absorbing solution where the remaining carbon dioxide is removed from the air.

Any leaf or group of leaves enclosed within a cellophane envelope, through which a stream of air is drawn, is not under entirely natural conditions. Miller (1931) and others have pointed out that the various methods of estimating apparent photosynthesis give conflicting results because different activities associated with this process are measured. It is considered that the intake of carbon dioxide is the first step in photosynthesis and the increase in dry matter is the last. Miller (1931) points out several details which must be very carefully manipulated if the results of the carbon dioxide absorption method are to be of value. Among these are: (1) The regulation of the air stream, (2) the constant temperature of this stream, (3) the carbon dioxide content, (4) the regularity of the illumination, and (5) the construction of forms of apparatus suitable for the collection of the gas, and at the same time placing the plant under favorable conditions for photosynthesis. Heinicke and Hoffman (1933) considered each of these details and stressed the necessity of using great skill and accuracy in manipulating

the apparatus. As perfected by Heinicke and Hoffman (1933), this method, with proper precautions, gives an index of relative amounts of apparent photosynthesis under the artificial conditions to which the leaves are subjected. These investigators have attempted to create natural environmental conditions for their studies.

PROCEDURE

The apparatus used in the series of experiments herein reported is essentially like that described by Heinicke and Hoffman (1933). In this procedure, the author used a series of three absorption towers for each day's run. One tower was used for a Livland leaf, one for Delicious, and the third as a blank, through which a stream of normal air was drawn.

The apple trees used in these tests were growing in a greenhouse and were planted in 12-inch clay pots as 1-year-old budded stock in January, 1934. The tests were made in August, 1934. The duration of the experiment was five hours on each of the three days.

At the beginning and at the conclusion of each experiment, leaf punches were taken from 50 leaves of each variety and used as an index of photosynthesis by the dry weight accumulation method. Also entire leaves were collected at these periods, killed by dry heat in an electric oven, and later analyzed for total acid hydrolyzable carbohydrates expressed as glucose. The procedure for these methods is described later. This plan makes it possible to compare these three methods of judging apparent photosynthetic activity of apple foliage under the same environmental conditions. The data thus derived are presented in Table X. There is no consistency in the results by the three methods, and it would be difficult to select one method as the standard of comparison by which to judge the accuracy of the other two. Heinicke and Hoffman (1933) found that there was great variation in the rate of photosynthesis shown by adjacent leaves on the same shoot, also on different shoots of the same variety. It seems justifiable, therefore, to expect to find different photosynthetic values for leaves on different shoots or even different trees of one variety as well as between leaves of different varieties.

The data in this table show a greater gain per square meter of leaf area for Delicious foliage with the dry weight increment method than with either the saccharification or the carbon dioxide absorption methods, With Livland leaves the dry weight increment indicated greater photosynthetic activity on two of the three days.

Heinicke and Hoffman's recent research with the carbon dioxide absorption method has shown the advantages of this method for studying photosynthetic activity of leaves when it is desirable not to destroy the leaves as is necessarily done with

TABLE X.—APPARENT PHOTOSYNTHETIC ACTIVITY OF GREENHOUSE-GROWN APPLE FOLIAGE LEAVES, AUGUST 15, 16, AND 17, 1934.

Date	Variety	Time, temperature, C., and relative humidity, percent				Gain per sq. m. leaf area—grams			
		At beginning of run		At end of run		Total dry weight	Combustible matter	Total acid hydrolyzable carbohydrates as glucose	Glucose measured by absorption of carbon dioxide
		9:45 a. m.		**2:45 p. m.**					
Aug. 15	Delicious...................	28°	63	39°	34	3.42	2.86	0.39	1.60
	Livland	....		....		5.54	5.13	.40	3.78
		8:45 a. m.		**1:45 p. m.**					
Aug. 16	Delicious...................	25°	87	30°	70	1.61	1.43	.23	1.14
	Livland	....		....		.59	.42	.42	2.49
		8:15 a. m.		**1:15 p. m.**					
Aug. 17	Delicious...................	24°	82	25°	55	2.30	2.22	.05	1.14
	Livland	....		....		3.26	2.88	.87	3.56
Average, three days	Delicious...................	....		....		2.44	2.30	.22	1.29
	Livland					3.12	2.81	.56	3.27

the other two methods. The carbon dioxide absorption method, however, gave values much greater than the saccharification methods but in general they were lower than the dry weight increment.

Each method is subject to criticism and all the results should be interpreted as being relative rather than absolute. The selection of the method to be used should depend upon the nature of the project, the number of leaves available, the equipment at hand, and whether or not the trees are grown in a greenhouse or in the orchard. The setting up outdoors of the equipment for using the continuous gas stream method is far more difficult and expensive than for indoor determinations. For many types of studies outdoor determinations are desirable.

The same two leaves were used for all the experiments measuring the carbon dioxide absorption. The area of the Delicious leaf was 39.49 square centimeters, and that of the Livland leaf, 40.09 square centimeters. At the conclusion of these experiments, the two leaves were removed from the trees and mounted sections for microscopic study were prepared, as described before. (Table XI.)

TABLE XI.—INTERCELLULAR MEASUREMENTS OF THE MESOPHYLL OF APPLE LEAVES USED WITH CARBON DIOXIDE ABSORPTION TOWERS IN GREENHOUSE, AUGUST 15 TO 17, 1934.

Variety	Average cross sectional area of intercellular space, sq. cm.	Average perimeter measurements of intercellular space, cm.
Delicious	87.01±7.01	179.78±14.21
Livland	107.71±12.19	192.79±16.06

Note.—Measurements for each variety were made from 50 projected images, 11 inches long, at a magnification of X 900.

All three methods give higher values for the Livland leaf than for the Delicious leaf, and it is significant that the intercellular space in the Livland leaves is more extensive than that of Delicious.

DETERMIXATION OF DRY MATTER ACCUMULATED BY LEAF AREAS

HISTORICAL

Sachs (1884) was the first to use the dry weight method of measuring the rate of formation of carbohydrates. He removed one half of a leaf blade at the beginning of an experiment and left the other half attached to the midrib. Portions of the severed half were measured for area and the dry weight determined. The half-leaf left on the plant was removed at the end

of the experiment, measured, and weighed as before, care being taken to avoid large veins in both cases. The gain in dry weight per unit area of leaf surface was attributed to the carbohydrates formed by photosynthesis. Sachs recognized that translocation and respiration should be measured, and discovered that detached leaves showed a greater gain when illuminated than leaves which remained attached to the plant. He attributed the smaller gain in the latter case to the translocation of the products of photosynthesis to other plant parts. In order to obtain the corrected photosynthetic value, therefore, he added the loss in dry weight per unit area during the night to the gain in dry weight per unit area found during the day.

The dry weight method has been criticized by several investigators. Brown and Escombe (1905) compared the results of measuring photosynthesis by the continuous gas stream method and the dry weight method. Working with *Catalpa bignonioides* they recorded values two and three times greater for the dry weight method than that calculated from the amount of carbon dioxide absorbed. They concluded that the great objection to Sachs' method is that all the errors accumulate in the final result.

Ganong (1908) was not convinced that the dry weight method gave results much too high. He designed (1905) a punch which could be used to remove circular discs having a diameter of 1.128 centimeters or an area of 1 square centimeter, from leaves. Since that date, most of the dry weight records have been made by using the punch, rather than the half-leaf method. Ganong (1908) concluded that the removal of the discs does not interfere seriously with the functioning of the leaves.

Too little is known of the composition of the products of assimilation to make possible an accurate calculation of the carbon dioxide absorbed from a given increase in dry weight. (Thoday, 1909.) Thoday recommends that the ash content of the leaf samples be determined and deducted from the increase in dry weight. According to this investigator there are two main errors in the dry weight method. These are: (1) The shrinkage of leaves in area during the experiment, and (2) their lack of symmetry in respect to dry weight per unit area. The latter objection may be overcome by avoiding large veins and using a large number of leaves for each experiment. Thoday concluded that if the dry weight gains are as great as 2 milligrams per square decimeter per hour, the method is capable of yielding useful results for comparative studies of assimilation. In 1910 he found that *Helianthus* leaves increased in dry weight by 17 milligrams per hour per 100 square centimeters of leaf area at a time when catalpa gained only 5 milligrams per hour per 100 square centimeters of leaf area, a fact which is cor-

related with the absence of stomata from the upper surface of catalpa leaves.

Spoehr (1926) sums up the merits of the dry weight method by stating that it offers the simplest means of estimating photosynthesis and that its very simplicity makes it highly desirable, but in its present form it is not reliable. He emphasizes the necessity of correcting the values for respiration and translocation.

Miller (1931) has used the dry weight method for making photosynthetic comparisons between corn, milo, and the sorghums under field conditions in the Great Plains.

The dry weight method was used more extensively than any other in these photosynthetic studies because it is the best suited to orchard conditions. Whatever may be said against this method, the fact remains that the results are comparable, and in the final analysis no method is accepted as absolutely accurate. Every possible precaution to avoid error was adopted in planning these experiments. Chief among these precautions were: (1) Many of the samples were corrected for variations in ash content; (2) large numbers, 50 or 100 leaves, were selected for sampling each variety for each experiment; (3) careful measurements showed that the leaves did not shrink in area during the daylight hours; (4) dust, spray residues, and similar material were washed from the leaves 24 hours before the beginning of each experiment; (5) in the removal of each disc with a Ganong punch, care was exercised to avoid the cutting of large veins; (6) comparable leaves were always selected, only mature leaves on new shoot growth being used; (7) no leaf showing injury caused by any fungus, insect, or other pest was sampled; (8) all leaves from which discs were cut were located on the south and southwest exposure of the periphery of the tree and at heights ranging from 4 to 6 feet from the surface of the groun; (9) none of these leaves was at any time between the hours of 5 a. m. and 2 p. m. shaded by the foliage of other trees; (10) all the trees were growing under practically the same method of soil management.

Figure 6 illustrates the relative sizes of representative leaves of the varieties under test. Most orchard-grown apple leaves are not sufficiently large to permit the removal of more than six discs, each having an area of 1 square centimeter, without severing large veins or the midrib. Accordingly many of these experiments were so planned that only four or six discs were removed from each leaf. Several preliminary tests revealed that apple leaves in the orchard ceased to gain in weight about mid-afternoon, that is, the processes of respiration and translocation then equaled or proceeded at a faster rate than did apparent photosynthesis.

In January, 1933, two lots of 1-year-old apple trees were planted in greenhouses in 12-inch clay pots. One lot was plunged into a ground bed in a house, designated as Plot A, where the temperatures were kept as high as the heating facilities permitted. The day temperatures usually ranged from 90° F. to 110° F. and the night temperatures were seldom below 70° F. Effort was made to keep the relative humidity high in this
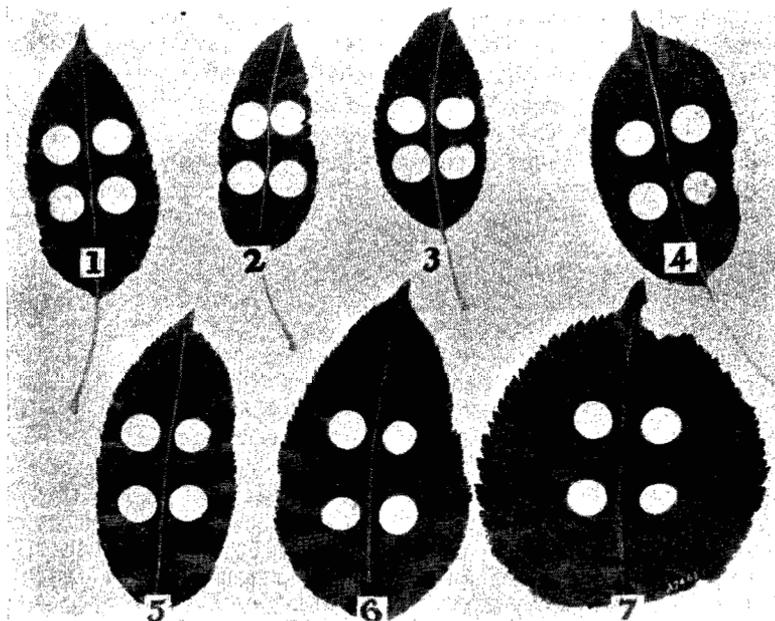

FIG. 6.—Representative leaves (X ⅓) with punches removed. (1) Jonathan, (2) Winesap, (3) York, (4) Gano, (5) Delicious, (6) Wealthy, and (7) Livland. The holes do not appear to be circular because the leaves were pressed between two pieces of glass to aid in securing a sharp focus.

house, by keeping one aisle flooded with water, and at times a small stream of water was directed on the steam heating pipes. The other lot of trees, Plot B, was plunged into a ground bed in a house largely devoted to the culture of lettuce. The day temperatures were kept at about 70° F., or slightly lower, and the night temperatures were in the upper 40's. The object of growing the trees under these two sets of environmental conditions was to attempt to produce, within a variety, leaves with variation in the extent of intercellular space in the spongy mesophyll. The two greenhouses were adjoining and on the days the leaf punches were collected the door between the houses was open, and the temperatures and relative humidity mere kept the same

TABLE XII.—INFLUENCE OF APPLE LEAF STRUCTURE ON DAILY INCREASE IN TOTAL DRY MATTER, IN GREENHOUSES, 1933.

Variety	Plot	Intercellular space (a)		Gain in total dry matter per sq. m. leaf area between 7:30 a. m. and 5:30 p. m.				
		Area sq. cm.	Perimeter, cm.	April 5	April 6	April 26	April 27	Mean
Livland	A	116.46	226.39	6.02	5.38	4.66	6.40	5.61
	B	94.59	196.92	5.96	4.08	3.12	6.34	4.87
Jonathan	A	•66.52	146.66	6.10	3.68	3.08	5.02	4.47
	B	62.52	124.01	2.82	2.24	2.98	2.28	3.34
Gano	A	60.46	142.90	4.46	3.16	....	....	3.81
	B	64.05	157.95	6.64	5.64	....	....	6.14
York	A	82.91	212.09	....	....	3.48	5.34	4.41
	B	72.78	189.74	....	....	2.52	3.50	3.01

(a) See Table I for explanation of measurements of intercellular space.

TABLE XIII.—PERCENTAGE OF WATER IN APPLE LEAVES.
(Greenhouse, April 5, 6, 26, and 27, 1933.)

Date	April 5				April 6				April 26				April 27			
Time	7:30 a. m.		5:30 p. m.		7:30 a. m.		5:30 p. m.		7:30 a. m.		5:30 p. m.		7:30 a. m.		5:30 p. m.	
Plot	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Livland	67.89	66.21	63.81	61.55	65.03	64.00	61.09	62.40	66.27	65.10	64.11	64.00	66.00	67.00	64.09	64.40
Jonathan	66.25	64.60	63.05	60.31	61.54	62.43	60.00	61.17	65.14	66.01	63.33	63.90	65.90	66.13	61.01	64.11
Gano	66.49	65.26	62.81	62.01	64.80	63.85	62.31	61.07	65.49	64.98	62.97	62.78	66.20	64.25	63.09	61.19
York	65.33	64.76	63.27	62.50	64.70	63.83	63.11	61.13	64.87	64.50	63.80	63.13	65.46	65.57	63.75	62.39

TABLE XIV.—TEMPERATURE AND RELATIVE HUMIDITY RECORDS IN GREENHOUSE. 1933.

Time		April 5	April 6	April 26	April 27
7:30 a. m.	Temperature, C.	15	8	10	16
	Relative humidity, percent	66	58	56	68
12:00 Noon	Temperature, C.	27	22	20	34
	Relative humidity, percent	45	45	42	39
5:30 p. m.	Temperature, C.	15	15	11	21
	Relative humidity, percent	61	63	58	50

in the two rooms. In Table XII are presented some data of anatomical and photosynthetic studies on leaves of these two groups of trees.

Many factors are blended in governing the rate of photosynthesis and in determining the quantity of photosynthate produced. It is extremely difficult to select any one of these factors and attempt to demonstrate the definite role it occupies in a process as complicated as this. As one variable is changed, its effect on the rate of photosynthesis is masked by the overlapping of influences of the other variables. Nevertheless, the data in Table XII indicate certain trends of behavior between the two variables of leaf structure and photosynthetic activity. These are: (a) The leaves of Livland, Jonathan, and York grown on trees in Plot A have a greater extent of intercellular space in the spongy mesophyll than leaves of the corresponding varieties grown in Plot B, where relatively low temperatures prevailed when the leaves were growing, while the reverse was true with Gano; (b) within each variety, the leaves possessing the more extensive intercellular space produced the greater gain in dry weight per square meter of leaf area between 8:30 a. m. and 5:30 p. m.; (c) the intercellular space in the Livland mesophyll from Plot A is larger than that of other varieties in the same plot (the same is true in Plot B); (d) Livland leaves accumulated a greater average weight of dry matter per square meter of leaf surface than the other varieties within each plot.

These records do not isolate leaf structure from the other factors which regulate photosynthesis, but it is likely that variations in intercellular space partly influence this activity or accompany it under the dominance of other more powerful factors.

In Table XIII the percentage of water in the apple leaves used in the photosynthetic studies on April 5, 6, 26, and 27, 1933, is given. Air temperature and relative humidity data in the greenhouse for these dates are presented in Table XIV.

Scarcity of available soil moisture accompanied by high temperatures constitutes one of the hazards of crop production

in the Great Plains. The 1933 season in Kansas was characterized by high temperatures and below normal rainfall. Soil moisture determinations were made on 10 days between June 14 and August 23. Between June 14 and July 7, the soil moisture content in non-irrigated plots ranged from 15 to 17 percent, which is not far above the wilting coefficient. Although the apple trees used in these studies did not exhibit wilted foliage, 1,400 gallons of water were used to irrigate each tree. Daily maximum temperatures exert a pronounced influence on the amount of dry matter gained per unit of leaf area, according to figure 7. Generally, the higher the daily maximum temperature, the lower the leaf gain in dry weight. Soil moisture data are not included in figure 7 because it was impossible to collect representative soil samples in the vicinity of the greatest root concentration, on account of the irrigation given each tree.
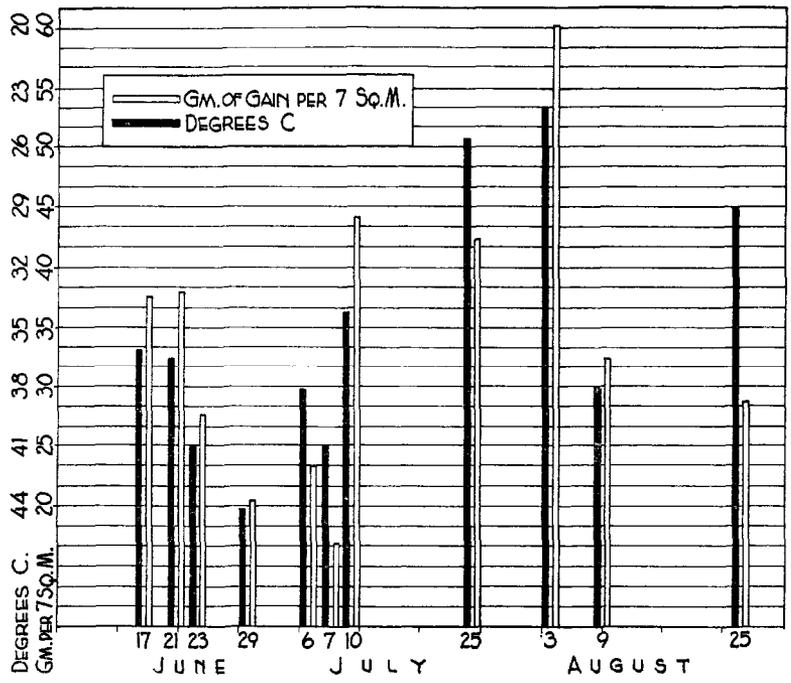
Fig. 7.—Relationship between maximum air temperature and total dry weight gain per square meter of leaf area for seven apple varieties, 1933.

Bose (1924) concluded that the rate of photosynthesis is the expression of the combined effect of light and temperature. Photosynthetic activity increased from 7:30 a. m. to 12:00 noon. After 2:00 p. m. both light and temperature underwent a decline, with resulting rapid fall of activity. His findings are in

accord with the relationship between temperature and photo-
synthetic activity as shown graphically in figure 7. Sunshine
prevailed on each day with the exception of August 25, which
was cloudy. No records of light intensity were made. Consider-
ing only the maximum air temperatures on the 11 days when
the dry weight determinations were made, these records show
the depressing effect of extremely high temperatures on photo-
synthetic activity.

An experiment was designed in 1934 to compare the photo-
synthetic efficiency of greenhouse-grown and orchard-grown
leaves of Livland and Delicious apple trees under orchard con-
ditions. (Pickett, 1934.) It has been shown in Table I that there
are marked differences in the extent of the intercellular space
in the spongy mesophyll of greenhouse-grown Delicious and
orchard-grown Delicious leaves. A similar condition exists with
Livland leaves. In January, 1934, several 1-year-old whips of
the two varieties were planted in 12-inch clay pots and placed
in a greenhouse. In July, 1934, these trees were taken to the
orchard, and the pots were plunged into the orchard soil for a
few days to bring the soil moisture in the pots to approximately
the same point as that in the soil outside the pots. The photo-
synthetic determinations of the greenhouse-grown trees could
then be made under the same environmental conditions as the
orchard trees.

TABLE XV.—VARIATION IN DRY MATTER OF APPLE LEAVES.
(6:00 a. m., July 31, to 6:00 a. m., August 1, 1934—24 hours.)

Variety	Place grown	Time	Grams per square meter of leaf area			Percent-age of water
			Dry weight	Gain or loss in dry matter	Total gain, dry matter	
Livland	Orchard	6:00 a. m.	91.60	....	....	55.12
		2.30 p. m.	97.53	+5.93	....	54.80
		6:00 a. m.	93.15	—4.38	10.31	57.31
Livland	Greenhouse	6:00 a. m.	85.24	....	....	55.17
		2:30 p. m.	88.72	+3.48	....	54.94
		6:00 a. m.	87.26	—1.46	4.94	57.09
Delicious	Orchard	6:00 a. m.	85.46	....	....	55.21
		2:30 p. m.	90.14	+4.68	....	53.48
		6:00 a. m.	87.70	—2.44 ·	7.12	54.80
Delicious	Greenhouse	6:00 a. m.	74.14	....	....	56.26
		2:30 p. m.	79.02	+1.88	....	54.05
		6:00 a. m.	76.72	—2.30	4.18	56.95

Temperatures: 6:00 a. m., July 31, 23 degrees C., relative humidity 42 percent.
2:30 p. m., July 31, 38 degrees C., relative humidity 21 percent.
6:00 a. m., Aug. 1, 28 degrees C., relative humidity 37 per cent.
July 31 was cloudy, practically no direct sunlight at any time
during the day.

This experiment was started on the last day of July, 1934,
a month which broke all records at Manhattan for the past 75
years for high temperatures. On 26 days the maximum tem-
perature was 100° F. or higher and during 11 consecutive days

the maximum reading was 111° F. or higher. The rainfall for the month was 0.86 of an inch, and at the time of this experiment the average moisture content of the top 3 feet of soil was 11.6 percent, dry weight basis. Many trees in the orchard were wilted but the ones used in this test of July 31 to August 1, were apparently turgid.

The rate of apparent photosynthesis was judged by Ganong's modification of the dry-weight method. Discs one square centimeter in area were punched from 50 mature leaves, one disc being removed from each leaf at 6:00 a. m., another at 2:30 p. m., and a third set at 6:00 a. m. the second day.

In Table XV, data are presented showing the gains and losses in dry weight per square meter of leaf area from 6:00 a. m., July 31, to 6:00 a. m., August 1, 1934. The orchard-grown Livland leaves made a net gain of 5.93 grams per square meter of leaf area while the greenhouse-grown Livland leaves gained 3.48 grams per square meter of leaf area. Likewise, the orchard-grown Delicious leaves gained more in dry matter than those grown in the greenhouse. These gains were 4.68 and 1.88 grams per square meter of leaf area, respectively. The four groups of leaves rank as follows in the net day gains in dry weight: (1) Orchard-grown Livland, (2) orchard-grown Delicious, (3) greenhouse-grown Livland, and (4) greenhouse-grown Delicious. The same ranking applies to the measurements of the intercellular space in the mesophyll as shown in Table I. Apparently the differences of the extent of the intercellular space

TABLE XVI.—ANALYSIS OF APPLE LEAVES. VARIATION IN TOTAL DRY MATTER, WATER CONTENT, AND ACID HYDROLYZABLE CARBOHYDRATES ESTIMATED AS GLUCOSE.
(July 16 to 17, 1935.)

Variety	Time	Grams per square meter of leaf area					Per-cent of water
		Dry matter	Gain or loss of dry matter	Total gain of dry matter	Carbo-hy-drates	Gain or loss of carbohydrates	
Orchard grown							
York	5:30 a. m.	81.02	....	....	13.10	....	53.85
York	2:30 p. m.	83.48	+2.46	5.10	14.75	+1.65	51.67
York	5:30 a. m.	80.84	—2.64	....	14.95	+ .20	56.51
York	2:30 p. m.	86.24	+5.40	8.04	14.20	— .75	52.69
Greenhouse grown							
York	5:30 a. m.	53.04	....	....	9.19	....	61.07
York	2:30 p. m.	55.16	+2.12	2.60	9.62	+ .43	52.64
York	5:30 a. m.	54.68	— .48	....	9.77	+ .15	57.53
York	2:30 p. m.	56.24	+1.56	2.04	9.09	— .68	53.30
Orchard grown							
Wealthy	5:30 a. m.	90.84	....	....	13.81	....	58.40
Wealthy	2:30 p. m.	94.58	+3.74	7.10	16.49	+2.68	55.11
Wealthy	5:30 a. m.	91.22	—3.36	....	15.51	— .98	59.72
Wealthy	2:30 p. m.	98.02	+6.80	10.16	14.28	—1.23	56.09
Greenhouse grown							
Wealthy	5:30 a. m.	78.74	....	....	11.89	....	56.84
Wealthy	2:30 p. m.	80.68	+1.94	4.12	12.96	+1.07	52.18
Wealthy	5:30 a. m.	78.50	—2.18	....	13.03	+ .07	54.12
Wealthy	2:30 p. m.	81.08	+2.58	4.76	13.03	.00	49.87

are reflected in the photosynthetic behavior of the two varieties. Several factors enter into and govern the rate of photosynthesis, and the extent of the surfaces of the exposed cell walls bordering the intercellular space is probably one of them.

On July 16 and 17, 1935, two lots of potted greenhouse-grown trees were transported to the orchard for the purpose of making photosynthetic comparisons between leaves grown indoors and those grown outdoors. The same general procedure was followed as was used in 1934 with the exception that York and Livland were the two varieties used, and that leaves were removed for chemical analysis. The data are presented in Table XVI.

Dry weight determinations of orchard-grown apple leaves were recorded on the following dates in 1933: June 7, 14, 17, 21, 23, and 29; July 1, 6, 7, 10, and 25; and August 3, 9, and 25.

Photosynthetic activity as measured by determining the amounts of total acid hydrolyzable carbohydrates expressed as glucose was determined on July 10 and 25, and August 3, 9, and 25, 1933.

In 1934, both dry weight and carbohydrate determinations were made from samples collected May 2, 16, and 23; June 5; July 2, 3, 9, 10, 18, and 19; and August 3, 6, 7, 15, 16, 17, 21, 22, 23, and 24. The data for the two seasons are presented in Tables XVII to XXII.

COMPARISONS OF TOTAL ACID HYDROLYZABLE CARBOHYDRATES

In this procedure the entire carbohydrate content is hydrolyzed to hexoses and the products thus formed are estimated as glucose by the reduction of Fehling's solution, according to Quisumbing and Thomas' (1921)-Shaffer and Hartmann (1920) method.

The leaves used in these analyses were killed by dry heat in an electric oven. They were placed in convenient trays made of hardware cloth and for the first hour the oven temperature was 70° C. During this hour the door was left open slightly to permit the ready escape of water vapor. The killing was completed at 98° C., after which the leaves were ground with a mortar and pestle until the powder would pass through a 40-mesh sieve. This method produced a powder which was a natural green. If samples of leaves were put in the oven at 98° without first going through the 70° step, generally the powder was somewhat darkened. No comparative analyses of the two methods were made. It was assumed that the bright green powder was the better.

None of the trees used in 1933 was bearing fruit. Trees not in bearing were selected because the presence of fruit probably influences the photosynthetic activity of nearby leaves. In 1934, the photosynthetic behavior of leaves on branches bearing ap-

TABLE XVII.—DAILY INCREASE IN TOTAL DRY MATTER AND ACID HYDROLYZABLE CARBOHYDRATES ESTIMATED AS GLUCOSE.

(Partial summary of Tables XX and XXI. Grams per square meter of leaf area. 1933.)

Date	Time A.M. P.M.	Wealthy Dry matter	Wealthy Carbo-hy-drates	Jonathan Dry matter	Jonathan Carbo-hy-drates	Livland Dry matter	Livland Carbo-hy-drates	Gano Dry matter	Gano Carbo-hy-drates	Winesap Dry matter	Winesap Carbo-hy-drates	Delicious Dry matter	Delicious Carbo-hy-drates	York Dry matter	York Carbo-hy-drates
June 17	6:00—6:00	5.38	....	2.40	....	6.54	....	5.46	....	3.78	....	4.44	....	3.54	....
June 21	6:00—6:00	6.02	....	3.20	....	7.52	....	4.80	....	5.60	....	5.04	....	3.56	....
June 23	6:00—6:00	5.92	....	3.56	....	5.38	....	3.46	....	2.50	....	3.42	....	2.44	....
June 29	6:00—6:00	3.04	....	2.08	....	3.94	....	2.26	....	4.50	....	2.88	....	2.24	....
July 6	5:00—7:00	2.50	....	4.14	....	4.32	....	3.48	....	3.30	....	3.10	....	2.14	....
July 7	5:00—7:00	2.26	....	3.42	....	3.18	....	3.00	....	2.04	....	1.66	....	1.04	....
July 10	5:00—1:00	7.42	2.96	5.32	1.56	5.32	2.25	3.56	0.47	8.68	1.03	5.38	—0.06	5.36	0.40
July 25	6:00—1:00	8.88	1.89	4.94	—2.07	6.38	.04	5.78	3.91	3.96	.25	8.18	.87	4.28	1.54
Aug. 3	7:00—4:30	9.88	1.34	9.16	.45	6.50	1.05	9.18	2.08	10.04	.63	7.32	2.82	8.14	2.36
Aug. 9	7:30—4:30	3.12	.41	5.30	.27	4.78	.57	6.66	1.42	5.12	.85	3.00	2.26	2.38	.17
Aug. 25	7:30—4:30	5.36	.40	7.22	.96	3.96	.34	4.20	.85	3.72	1.51	1.40	—.21	3.12	—.36
Total		59.78	6.20	50.74	1.17	57.82	4.25	51.84	8.73	53.24	4.27	45.82	5.68	38.24	4.11
Mean		5.43	1.24	4.61	.23	5.25	.85	4.71	1.74	4.84	.85	4.16	1.13	3.47	.82

TABLE XVIII.—DAILY INCREASE IN TOTAL DRY MATTER, COMBUSTIBLE MATTER, AND ACID HYDROLYZABLE CARBOHYDRATES ESTIMATED AS GLUCOSE.

(Partial summary of Table XXII. Grams per square meter of leaf area. 1934.)

Date	Time	JONATHAN No fruit Total dry matter	Combustible matter	Carbohydrates	JONATHAN With fruit Total dry matter	Combustible matter	Carbohydrates	YORK No fruit Total dry matter	Combustible matter	Carbohydrates	DELICIOUS No fruit Total dry matter	Combustible matter	Carbohydrates	DELICIOUS With fruit Total dry matter	Combustible matter	Carbohydrates	LIVLAND No fruit Total dry matter	Combustible matter	Carbohydrates
May 2	7:30 a. m. to 3:30 p. m.	Greenhouse									2.00	1.85	0.44				6.68	6.15	0.37
May 16	9:00 a. m. to 11:30 a. m.										1.36	1.30	.18				.64	.51	.17
July 31	6:00 a. m. to 2:30 p. m.										1.88						3.48		
Aug. 15	9:45 a. m. to 2:45 p. m.										3.42	2.86	.39				5.54	5.13	.40
Aug. 16	8:45 a. m. to 1:45 p. m.										1.61	1.43	.23				.58	.42	.42
Aug. 17	8:00 a. m. to 1:00 p. m.										2.30	2.22	—.05				3.26	2.88	.87
May 23	7:00 a. m. to 3:00 p. m.	0.80	0.53	0.17				3 00	2.70	—0.44	5.04	4.85	.46				5.66	5.22	.86
June 5	7:00 a. m. to 3:00 p. m.	5.36	4.91	—.17				2.12	2.09	1 17	3.88	3.56	.49				3.88	3.36	—.36
July 2	6:00 a. m. to 2:30 p. m.	2.50	2.34	.78				2.42	2.11	.54	1.54	1.53	.67				4.26	4.05	1.85
July 3	6:00 a. m. to 2:30 p. m.	1.56	1.62	.61				2.66	2.42	.25	1.62	1.61	.23				3.84	3.55	.56
July 9	6:00 a. m. to 2:30 p. m.	5.06	4.58	1.27				.96	1.46	.52	2.30	2.30	—1.33	3.42	3.39	0.50	.64	.23	—.47
July 10	6:00 a. m. to 2:30 p. m.	—.66	—.71	—.77				2.88	2.71	.12	.70	.60	—.20	2.74	2.67	—.04	4.12	3.82	.32
July 18	6:00 a. m. to 2:30 p. m.	1.10	.83	—.69	0.38	0.38	—0.23	—1.00	—.80	—.97	1.12	1.04	.18	2.16	2.05	—.32	.82	.76	1.39
July 19	6:00 a. m. to 2:30 p. m.	2.80	2.69	.41	5.42	4.86	.55	4.96	4.62	.46	1.76	1.59	.81	3.14	2.79	—.59	5.90	5.53	.65
July 31											4.68						5.93		
Aug. 6	6:00 a. m. to 2:30 p. m.	2.98	2.74	.82				2.88	2.72	.80	4.00	3.44	1.08				3.74	3.59	.55
Aug. 7	6:00 a. m. to 2:30 p. m.	.28	.18	.74				—1.94	—1.81	.06	—.22	.09	.15				6.16	5.77	.85
Aug. 23	6:00 a. m. to 2:30 p. m.	1.10	.96	—.82	2.56	2.17	—.01	.76	.69	—.96	1.94	1.73	.20	3.40	2.79	.51	.10	.19	.43
Aug. 24	6:00 a. m. to 2:30 p. m.	2.26	1.74	.94	1.42	1.40	.65	2.98	2.87	.35	3.32	3.29	.73	2.68	2.54	.22	1.78	1.74	1.13
T (1)		25.14	22.41	3.29				22.68	21.78	1.90	27.00	25.63	3.47				40.90	37.81	7.66
M (1)		2.09	1.86	.27				1.89	1.81	.158	2.25	2.13	.287				3.32	3.15	.638
T (2)											44.25	35.29	4.66				67.01	52.90	9.99
M (2)											2.33	2.07	.27				3.53	3.11	.58
T (3)		7.26	6.22	—.16	9.78	8.81	0.96				11.14	10.55	0.39	17.54	16.23	0.28			
M (3)		1.81	1.55	—.04	2.44	2.20	.24				1.85	1.79	.06	2.92	2.70	.047			

T (1) and M (1) indicate total and mean, respectively, for data from May 23 to August 24, inclusive, except July 31.

T (2) and M (2) indicate total and mean, respectively, for data from May 2 to August 24, inclusive.

T (3) and M (3) indicate total and mean, respectively, for data from Jonathan and Delicious on the days when photosynthetic activity of leaves on fruit bearing branches was compared with that of leaves on branches not bearing fruit.

ples was determined. For comparison, leaves on branches from which the fruit had been removed were used. The ratios given in Table XXII indicate the number of leaves per fruit on the branches from which the leaves were selected for study.

Partial summaries of the data for 1933, 1934, and 1935 are given in Tables XVII, XVIII, and XIX, respectively. These three tables summarize the data presented in Tables XX to XXIII, inclusive.

TABLE XIX.—DAILY INCREASE IN TOTAL DRY MATTER AND ACID HYDROLYZABLE CARBOHYDRATES ESTIMATED AS GLUCOSE.
(Partial summary of Table XXIII. Grams per square meter of leaf area. 1935.)

Date	Jonathan		York		Delicious		Livland	
	Total dry matter	Carbo-hy-drates	Total dry matter	Carbo-hy-drates	Total dry matter	Carbo-hy-drates	Total dry matter	Carbo-hy-drates
June 24	2.18	0.18	—0.24	0.09	7.26	0.88	3.90	0.61
June 25	5.82	.39	4.54	.27	7.82	.19	10.36	.26
July 5	5.86	1.21	4.52	.03	8.60	2.60	4.38	.23
July 6	6.08	.11	3.30	.06	6.88	.63	4.60	.21
July 24	3.90	1.43	—.28	.06	6.58	.16	2.42	.21
July 25	5.60	2.34	2.74	.22	3.94	—.10	3.50	.41
August 2	.14	.54	—.20	—.07	—.22	.21	1.38	.83
August 3	4.84	.39	1.10	.23	1.20	.86	3.76	.42
August 7	3.52	.34	3.94	1.08	5.96	·2.59	1.86	.96
August 8	4.94	—.11	4.16	.23	7.26	3.24	2.16	.64
Total	42.88	6.82	23.58	1.60	55.28	11.26	38.32	4.78
Av.	4.29	....	2.36	....	5.53	....	3.83	....

TABLE XX.—VARIATION IN DRY MATTER AND WATER CONTENT OF APPLE LEAVES.

Variety and Time		Gm. of dry matter per sq. m. of leaf area	Percent of water	Gm. of gain of dry matter per sq. m. of leaf area
June 7-8, 1933				
Jonathan	6:00 a. m.	71.02	61.55	....
	6:00 p. m.	73.60	59.64	2.58
	6:00 a. m.	73.02	61.01	— .58
Winesap	6:00 a. m.	68.80	62.72	....
	6:00 p. m.	71.04	61.58	2.24
	6:00 a. m.	71.42	61.23	.38
York	6:00 a. m.	65.70	61.04	....
	6:00 p. m.	65.82	61.10	.12
	6:00 a. m.	66.52	61.46	.70
Gano	6:00 a. m.	65.36	58.44	....
	6:00 p. m.	65.60	59.16	.24
	6:00 a. m.	66.52	60.26	.92
Delicious	6:00 a. m.	75.92	62.21	....
	6:00 p. m.	75.96	60.53	.04
	6:00 a. m.	74.16	63.55	—1.80
Livland	6:00 a. m.	66.46	66.74	....
	6:00 p. m.	69.26	66.52	2.80
	6:00 a. m.	67.18	66.05	—2.08
June 14-15, 1933				
Jonathan	6:00 p. m.	67.14	58.36	....
	6:00 a. m.	63.86	60.46	—3.28
	6:00 p. m.	67.06	59.25	3.20
Winesap	6:00 p. m.	74.40	57.79	....
	6:00 a. m.	72.66	58.99	—1.74
	6:00 p. m.	75.80	59.29	3.14
Delicious	6:00 p. m.	59.98	60.96	....
	6:00 a. m.	56.60	62.81	—3.38
	6:00 p. m.	58.98	62.02	2.38
Wealthy	6:00 p. m.	74.40	60.12	....
	6:00 a. m.	70.58	61.67	—3.82
	6:00 p. m.	75.60	60.62	5.02
Livland	6:00 p. m.	63.96	63.01	....
	6:00 a. m.	60.34	64.75	—3.62
	6:00 p. m.	64.74	64.00	4.40
June 16-17, 1933				
Jonathan	6:00 p. m.	72.80	59.19	....
	6:00 a. m.	71.44	58.80	—1.36
	6:00 p. m.	73.84	58.47	2.40
Winesap	6:00 p. m.	79.12	56.98	....
	6:00 a. m.	75.42	57.50	—3.70
	6:00 p. m.	79.20	55.46	3.78
York	6:00 p. m.	69.72	57.69	....
	6:00 a. m.	69.24	58.95	— .48
	6:00 p. m.	72.78	58.37	3.54
Gano	6:00 p. m.	67.16	55.98	....
	6:00 a. m.	66.04	56.60	—1.12
	6:00 p. m.	71.50	55.26	5.46
Delicious	6:00 p. m.	81.88	60.16	....
	6:00 a. m.	79.82	61.13	—2.06
	6:00 p. m.	84.26	60.55	4.44
Wealthy	6:00 p. m.	91.58	58.58	....
	6:00 a. m.	86.96	60.59	—4.62
	6:00 p. m.	92.34	59.18	5.38
Livland	6:00 p. m.	73.00	62.72	....
	6:00 a. m.	71.28	66.05	—1.72
	6:00 p. m.	77.82	63.84	6.54

TABLE XX.—Continued.

Variety and Time		Gm. of dry matter per sq. m. of leaf area	Percent of water	Gm. of gain of dry matter per sq. m. of leaf area
June 21-22, 1933				
Jonathan	6:00 a. m. 6:00 p. m. 6:00 a. m.	71.64 74.84 72.80	59.33 56.94 59.59	...... 3.20 —2.04
Winesap	6:00 a. m. 6:00 p. m. 6:00 a. m.	76.38 81.98 77.84	58.34 55.87 59.41	...... 5.60 —4.14
York	6:00 a. m. 6:00 p. m. 6:00 a. m.	68.14 71.70 71.26	59.12 56.99 59.26	...... 3.56 — .44
Gano	6:00 a. m. 6:00 p. m. 6:00 a. m.	66.44 71.24 69.66	57.85 56.54 58.31	...... 4.80 —1.58
Delicious	6:00 a. m. 6:00 p. m. 6:00 a. m.	75.38 80.42 75.58	61.60 59.23 62.20	...... 5.04 —4.84
Wealthy	6:00 a. m. 6:00 p. m. 6:00 a. m.	82.44 88.46 84.32	60.23 57.92 61.25	...... 6.02 —4.14
Livland	6:00 a. m. 6:00 p. m. 6:00 a. m.	69.12 76.64 69.74	62.62 61.24 63.36	...... 7.52 —6.90
June 23-24, 1933				
Jonathan	6:00 a. m. 6:00 p. m. 6:00 a. m.	72.34 75.90 73.40	60.13 57.51 59.96	...... 3.56 —2.50
Winesap	6:00 a. m. 6:00 p. m. 6:00 a. m.	77.12 79.62 77.92	57.76 56.14 58.00	...... 2.50 —1.70
York	6:00 a. m. 6:00 p. m. 6:00 a. m.	66.64 69.08 68.60	58.96 57.54 59.45	...... 2.44 — .48
Gano	6:00 a. m. 6:00 p. m. 6:00 a. m.	62.70 66.16 66.06	58.69 57.37 58.40	...... 3.46 — .10
Delicious	6:00 a. m. 6:00 p. m. 6:00 a. m.	79.48 82.90 80.44	60.80 59.07 60.43	...... 3.42 —2.46
Wealthy	6:00 a. m. 6:00 p. m. 6:00 a. m.	84.16 90.08 87.90	58.15 57.10 58.71	...... 5.92 —2.18
Livland	6:00 a. m. 6:00 p. m. 6:00 a. m.	72.30 77.68 72.70	62.46 61.82 62.46	...... 5.38 —4.98

TABLE XX.—Concluded.

Variety and Time		Gm. of dry matter per sq. m. of leaf area	Percent of water	Gm. of gain of dry matter per sq. m. of leaf area
June 29-30, 1933				
Jonathan	6:00 a. m. 6:00 p. m. 6:00 a. m.	67.02 69.10 69.96	59.41 57.90 59.36	.... 2.08 .86
Winesap	6:00 a. m. 6:00 p. m. 6:00 a. m.	75.40 79.90 78.70	57.86 56.00 56.73	.... 4.50 —1.20
York	6:00 a. m. 6:00 p. m. 6:00 a. m.	64.96 67.20 69.96	58.18 57.11 58.02	.... 2.24 2.76
Gano	6:00 a. m. 6:00 p. m. 6:00 a. m.	57.40 59.66 59.54	58.97 57.01 59.34	.... 2.26 — .12
Delicious	6:00 a. m. 6:00 p. m. 6:00 a. m.	69.80 72.68 70.78	61.26 59.92 62.24	.... 2.88 —1.90
Wealthy	6:00 a. m. 6:00 p. m. 6:00 a. m.	72.66 75.70 77.10	59.27 57.77 58.95	.... 3.04 1.40
Livland	6:00 a. m. 6:00 p. m. 6:00 a. m.	63.72 67.66 66.20	63.17 61.59 63.02	.... 3.94 —1.46
July 1, 1933 (a)				
York	6:00 a. m. 6:00 p. m.	71.14 74.34	56.33 54.72	.... 3.20
Livland	6:00 a. m. 6:00 p. m.	69.22 76.82	61.19 55.99	.... 7.60
July 6-7, 1933				
Jonathan	5:00 a. m. 7:00 p. m. 5:00 a. m. 7:00 p. m.	80.04 84.18 82.04 85.46	57.47 55.65 57.87 56.06	.... 4.14 —2.14 3.42
Winesap	5:00 a. m. 7:00 p. m. 5:00 a. m. 7:00 p. m.	85.14 88.44 85.70 87.74	55.55 54.16 56.68 54.59	.... 3.30 —2.74 2.04
York	5:00 a. m. 7:00 p. m. 5:00 a. m. 7:00 p. m.	69.70 71.84 70.78 71.82	57.83 56.80 58.84 57.49	.... 2.14 —1.06 1.04
Gano	5:00 a. m. 7:00 p. m. 5:00 a. m. 7:00 p. m.	68.60 72.08 70.12 73.12	56.64 54.48 57.60 55.44	.... 3.48 —1.96 3.00
Delicious	5:00 a. m. 7:00 p. m. 5:00 a. m. 7:00 p. m.	79.64 82.74 80.30 81.96	58.80 58.01 59.95 58.49	.... 3.10 —2.44 1.66
Wealthy	5:00 a. m. 7:00 p. m. 5:00 a. m. 7:00 p. m.	80.14 82.64 80.12 82.38	57.69 56.95 59.08 57.23	.... 2.50 —2.52 2.26
Livland	5:00 a. m. 7:00 p. m. 5:00 a. m. 7:00 p. m.	62.42 66.74 60.58 63.76	60.60 59.81 62.47 61.29	.... 4.32 —6.16 3.18

(a) Temperatures for July 1, 1933: 6:00 a. m., 85° F.; 3:00 p. m., 110° F.; 6:00 p. m., 90° F.

TABLE XXI.—ANALYSES OF APPLE LEAVES. VARIATION IN DRY MAT-
TER, WATER CONTENT, AND ACID HYDROLYZABLE CARBOHYDRATES
ESTIMATED AS GLUCOSE.

Variety and Time		Gm, per sq. m. of leaf area				Percent of water
		Dry matter	Gain of total dry matter	Carbohy-drates	Gain of carbohy-drates	
July 10-11, 1933						
Jonathan	5:00 a. m.	65.88	....	9.16	....	60.21
	10:00 a. m.	....	....	10.94	....	....
	1:00 p. m.	71.20	5.32	10.72	1.56	54.05
	4:00 p. m.	....	....	12.51	....	....
	7:00 p. m.	70.68	—.52	13.61	2.89	55.12
	5:00 a. m.	64.78	—5.90	11.47	—2.14	64.08
Winesap	5:00 a. m.	80.66	....	13.03	....	58.15
	10:00 a. m.	....	....	13.62	....	....
	1:00 p. m.	89.34	8.68	14.06	1.03	51.54
	4:00 p. m.	....	....	14.91	....	....
	7:00 p. m.	86.58	—2.76	13.75	— .31	53.55
	5:00 a. m.	83.48	—3.10	10.83	—2.92	63.83
York	5:00 a. m.	63.72	....	10.88	....	61.23
	10:00 a. m.	....	....	11.03	....	....
	1:00 p. m.	69.08	5.36	11.28	.40	55.93
	4:00 p. m.	....	....	14.66	....	....
	7:00 p. m.	69.60	.52	13.42	2.14	57.20
	5:00 a. m.	68.48	—1.12	11.05	—2.37	66.92
Gano	5:00 a. m.	70.60	....	11.40	....	57.14
	10:00 a. m.	....	....	14.52	....	....
	1:00 p. m.	74.16	3.56	11.87	.47	53.50
	4:00 p. m.	....	....	14.71	....	....
	7:00 p. m.	76.22	2.06	10.35	—1.52	54.64
	5:00 a. m.	73.60	—2.62	9.52	— .83	61.44
Delicious	5:00 a. m.	83.98	....	8.85	....	58.41
	10:00 a. m.	....	....	9.78	....	....
	1:00 p. m.	89.36	5.38	8.79	— .06	54.73
	4:00 p. m.	....	....	9.05	....	....
	7:00 p. m.	90.74	1.38	11.61	2.82	55.90
	5:00 a. m.	87.68	—3.06	10.80	— .81	61.28
Wealthy	5:00 a. m.	73.06	....	10.93	....	59.48
	10:00 a. m.	....	....	11.58	....	....
	1:00 p. m.	80.48	7.42	13.89	2.96	56.21
	4:00 p. m.	....	....	13.48	....	....
	7:00 p. m.	78.32	—2.16	12.44	—1.45	58.09
	5:00 a. m.	82.06	3.74	10.62	—1.82	60.78
Livland	5:00 a. m.	65.88	....	8.44	....	61.07
	10:00 a. m.	....	....	8.63	....	....
	1:00 p. m.	71.20	5.32	10.69	2.25	58.64
	4:00 p. m.	....	....	10.44	....	....
	7:00 p. m.	70.68	— .52	10.15	— .54	60.41
	5:00 a. m.	64.78	—5.90	9.49	— .66	.63.40
July 25-26, 1933						
Jonathan	6:00 a. m.	81.60	....	12.85	....	56.78
	10:00 a. m.	....	....	13.51	....	....
	1:00 p. m.	86.54	4.94	10.78	—2.07	53.20
	4:00 p. m.	....	....	10.67	....	....
	7:00 p. m.	86.20	— .34	11.74	.96	54.38
	6:00 a. m.	89.82	3.62	10.82	— .92	54.96

TABLE XXI.—Continued.

Time and Variety		Gm. per sq. m. of leaf area				Percent of water
		Dry matter	Gain of total dry matter	Carbohy-drates	Gain of carbohy-drates	
Winesap	6:00 a. m.	91.78	....	13.24	....	54.41
	10:00 a. m.	....	....	11.22	....	....
	1:00 p. m.	95.74	3.96	13.49	.25	51.20
	4:00 p. m.	....	....	9.80	....	....
	7:00 p. m.	96.70	.96	10.33	—3.16	52.78
	6:00 a. m.	94.12	—2.58	11.62	1.29	55.83
York	6:00 a. m.	71.16	....	10.83	....	57.44
	10:00 a. m.	....	....	9.89	....	....
	1:00 p. m.	75.44	4.28	12.37	1.54	53.93
	4:00 p. m.	....	....	9.99	....	....
	7:00 p. m.	75.14	— .30	11.61	— .76	55.41
	6:00 a. m.	76.00	.86	11.01	— .60	58.09
Gano	6:00 a. m.	79.42	....	12.10	....	55.74
	10:00 a. m.	....	....	12.26	....	....
	1:00 p. m.	85.20	5.78	16.01	3.91	53.32
	4:00 p. m.	....	....	13.25	....	....
	7:00 p. m.	84.86	— .34	10.46	—5.55	54.04
	6:00 a. m.	84.48	— .38	10.39	— .07	55.86
Delicious	6:00 a. m.	82.14	....	11.97	....	56.86
	10:00 a. m.	....	....	12.54	....	....
	1:00 p. m.	90.32	8.18	12.84	.87	53.72
	4:00 p. m.	....	....	14.45	....	....
	7:00 p. m.	86.56	—3.76	13.41	.57	55.54
	6:00 a. m.	87.76	1.20	11.26	—2.15	57.77
Wealthy	6:00 a. m.	89.04	....	9.52	....	57.32
	10:00 a. m.	....	....	9.01	....	....
	1:00 p. m.	97.92	8.88	11.41	1.89	53.75
	4:00 p. m.	....	....	13.31	....	....
	7:00 p. m.	97.06	— .86	10.68	— .73	55.61
	6:00 a. m.	95.22	—1.84	10.69	.01	58.05
Livland	6:00 a. m.	71.44	....	11.62	....	60.75
	10:00 a. m.	....	....	13.02	....	....
	1:00 p. m.	77.82	6.38	11.66	.04	57.46
	4:00 p. m.	....	....	12.09	....	....
	7:00 p. m.	76.44	—1.38	13.75	2.09	58.02
	6:00 a. m.	72.20	—4.24	10.08	—3.67	61.17
August 3-4, 1933						
Jonathan	7:00 a. m.	77.02	....	9.86	....	56.33
	4:30 p. m.	86.18	9.16	10.31	.45	52.88
	7:00 a. m.	81.76	—4.42	9.62	— .69	55.61
Winesap	7:00 a. m.	88.48	....	10.67	....	54.72
	4:30 p. m.	98.52	10.04	11.30	.63	51.92
	7:00 a. m.	93.34	—5.18	11.13	— .17	54.51
York	7:00 a. m.	72.46	....	9.06	....	56.18
	4:30 p. m.	80.60	8.14	11.42	2.36	52.84
	7:00 a. m.	78.66	—1.94	10.53	— .89	54.66
Gano	7:00 a. m.	72.30	....	11.82	....	56.12
	4:30 p. m.	81.48	9.18	13.90	2.08	52.90
	7:00 a. m.	78.80	—2.68	12.47	—1.43	54.61
Delicious	7:00 a. m.	71.22	....	8.38	....	58.39
	4:30 p. m.	78.54	7.32	11.20	2.82	56.34
	7:00 a. m.	75.72	2.82	10.45	— .75	58.13
Wealthy	7:00 a. m.	88.88	....	12.03	....	53.96
	4:30 p. m.	98.76	9.88	13.37	1.34	52.41
	7:00 a. m.	92.86	—5.90	12.38	— .99	54.60
Livland	7:00 a. m.	75.72	....	11.01	....	59.79
	4:30 p. m.	82.22	6.50	12.06	1.05	57.56
	7:00 a. m.	76.20	—6.02	10.62	—1.44	59.38

TABLE XXI.—Concluded.

Variety and Time		Gm. per sq. m. of leaf area				Percent of water
		Dry matter	Gain of total dry matter	Carbohydrates	Gain of carbohydrates	
August 9-10, 1933						
Jonathan	7:30 a. m.	86.92	....	11.25	....	54.05
	4:30 p. m.	92.22	5.30	11.52	.27	52.50
	7:30 a. m.	90.58	—1.64	11.86	.34	55.09
Winesap	7:30 a. m.	99.16	....	12.39	....	52.55
	4:30 p. m.	104.28	5.12	13.24	.85	50.50
	7:30 a. m.	98.44	—5.84	12.04	—1.20	54.12
York	7:30 a. m.	80.00	....	10.16	....	56.94
	4:30 p. m.	82.38	2.38	10.33	.17	53.34
	7:30 a. m.	81.08	—1.30	10.05	— .28	55.11
Gano	7:30 a. m.	80.70	....	10.41	....	53.57
	4:30 p. m.	87.36	6.66	11.83	1.42	52.66
	7:30 a. m.	84.42	—2.94	10.97	— .86	54.58
Delicious	7:30 a. m.	77.90	....	8.83	....	55.82
	4:30 p. m.	80.90	3.00	11.09	2.26	55.19
	7:30 a. m.	78.10	—2.80	10.42	— .67	56.00
Wealthy	7:30 a. m.	99.56	....	14.50	....	54.08
	4:30 p. m.	102.68	3.12	14.91	.41	52.46
	7:30 a. m.	100.00	—2.68	14.66	— .25	54.77
Livland	7:30 a. m.	75.18	....	10.57	....	58.25
	4:30 p. m.	79.96	4.78	11.14	.57	57.88
	7:30 a. m.	81.00	1.04	10.96	— .18	55.37
August 25-26, 1933						
Jonathan	7:30 a. m.	93.16	....	13.66	....	51.83
	4:30 p. m.	100.38	7.22	14.62	.96	49.76
	7:30 a. m.	91.44	—8.94	13.14	—1.48	55.62
Winesap	7:30 a. m.	99.10	....	14.53	....	50.08
	4:30 p. m.	102.82	3.72	16.04	1.51	50.39
	7:30 a. m.	98.48	—4.34	13.72	—2.32	54.08
York	7:30 a. m.	85.20	....	13.40	....	52.49
	4:30 p. m.	88.32	3.12	13.04	— .36	51.74
	7:30 a. m.	84.10	—4.22	12.25	— .79	53.95
Gano	7:30 a. m.	97.16	....	14.86	....	51.73
	4:30 p. m.	101.36	4.20	15.71	.85	50.25
	7:30 a. m.	94.30	—7.06	14.52	—1.19	54.00
Delicious	7:30 a. m.	89.84	....	15.78	....	52.80
	4:30 p. m.	91.24	1.40	15.57	— .21	53.16
	7:30 a. m.	86.92	—4.32	15.41	— .16	55.30
Wealthy	7:30 a. m.	109.88	....	20.91	....	49.50
	4:30 p. m.	115.24	5.36	20.51	— .40	50.11
	7:30 a. m.	105.98	—9.26	19.61	— .90	52.72
Livland	7:30 a. m.	84.56	....	14.69	....	54.62
	4:30 p. m.	88.52	3.96	15.03	.34	56.65
	7:30 a. m.	82.42	—6.10	13.46	—1.57	58.03

TABLE XXII.—ANALYSES OF APPLE LEAVES. VARIATION IN TOTAL DRY MATTER, COMBUSTIBLE MATTER, WATER CONTENT, AND ACID HYDROLYZABLE CARBOHYDRATES ESTIMATED AS GLUCOSE.

Variety and Time a	Gm. per sq. m. of leaf area						Percent of	
	Total dry matter	Combustible matter	Gain of Dry matter	Gain of Combustible matter	Carbohydrates	Gain of carbohydrates	Water	Ash
May 2, 1934								
D 7:30 a. m.	59.18	54.38	....	....	5.98	....	68.04	8.11
D 3:30 p. m.	61.18	56.23	2.00	1.85	6.42	0.44	67.46	8.09
L 7:30 a. m.	73.16	66.93	....	....	8.28	....	65.05	8.52
L 3:30 p. m.	79.84	73.08	6.68	6.15	8.65	.37	64.13	8.47
May 16, 1934								
D 9:00 a. m.	65.60	60.12	....	....	8.59	....	65.97	8.37
D 11:30 a. m.	66.96	61.42	1.36	1.30	8.77	.18	65.07	8.28
L 9:00 a. m.	82.76	75.72	....	....	11.12	....	62.56	8.51
L 11:30 a. m.	83.40	76.23	.64	.51	11.29	.17	62.20	8.60
May 23, 1934								
J 7:00 a. m.	67.88	62.25	....	....	8.35	....	61.53	8.30
J 3:00 p. m.	68.68	62.78	0.80	0.53	8.52	0.17	63.62	8.60
Y 7:00 a. m.	68.82	64.37	....	....	10.76	....	59.54	6.47
Y 3:00 p. m.	71.82	67.07	3.00	2.70	10.32	— .44	58.12	6.62
D 7:00 a. m.	66.52	61.56	....	....	10.04	....	63.44	7.46
D 3:00 p. m.	71.56	66.41	5.04	4.85	10.50	.46	60.81	7.20
L 7:00 a. m.	69.20	63.96	....	....	9.57	....	64.86	7.57
L 3:00 p. m.	74.86	69.18	5.66	5.22	10.43	.86	62.86	7.59
June 5, 1934								
J 7:00 a. m.	72.12	67.22	....	....	9.62	....	59.75	6.80
J 3:00 p. m.	77.48	72.13	5.36	4.91	9.45	—0.17	56.79	6.90
Y 7:00 a. m.	72.14	67.34	....	....	12.02	....	57.28	6.65
Y 3:00 p. m.	74.26	69.43	2.12	2.09	13.19	1.17	56.06	6.50
D 7:00 a. m.	75.92	70.57	....	....	10.98	....	62.90	7.05
D 3:00 p. m.	79.80	74.13	3.88	3.56	11.47	.49	60.67	7.10
L 7:00 a. m.	68.14	62.83	....	....	9.65	....	64.38	7.80
L 3:00 p. m.	72.02	66.19	3.88	3.36	9.29	— .36	62.83	8.10
July 2-3, 1934								
J 6:00 a. m.	77.38	72.46	....	....	10.78	....	57.56	6.36
J 2:30 p. m.	79.88	74.80	2.50	2.34	11.56	0.78	54.30	6.36
J 6:00 a. m.	79.14	73.92	— .74	— .88	10.55	—1.01	57.45	6.59
J 2:30 p. m.	80.70	75.54	1.56	1.62	11.16	.61	55.76	6.39
Y 6:00 a. m.	77.32	73.37	....	....	12.01	....	54.96	5.11
Y 2:30 p. m.	79.74	75.48	2.42	2.11	12.55	.54	52.52	5.34
Y 6:00 a. m.	79.88	75.59	.14	.11	12.30	— .25	54.62	5.37
Y 2:30 p. m.	82.54	78.01	2.66	2.42	12.55	.25	52.87	5.49
D 6:00 a. m.	82.46	77.35	....	....	11.62	....	60.25	6.20
D 2:30 p. m.	84.00	78.88	1.54	1.53	12.29	.67	58.28	6.19
D 6:00 a. m.	84.32	79.17	.32	.29	12.20	— .09	60.07	6.11
D 2:30 p. m.	85.94	80.78	1.62	1.61	12.43	.23	58.41	6.01
L 6:00 a. m.	80.84	74.80	....	....	8.08	....	60.24	7.47
L 2:30 p. m.	85.10	78.85	4.26	4.05	9.93	1.85	59.06	7.34
L 6:00 a. m.	80.08	74.34	—5.02	—4.51	9.00	— .93	58.41	7.17
L 2:30 p. m.	83.92	77.89	3.84	3.55	9.56	.56	59.68	7.18

TABLE XXII.—Continued.

Variety and Time a	Gm. per sq. m. of leaf area						Percent of	
	Total dry matter	Combustible matter	Gain of Dry matter	Gain of Combustible matter	Carbohydrates	Gain of carbohydrates	Water	Ash
July 9-10, 1934								
J b 6:00 a. m.	75.38	70.59	....	....	8.54	....	57.06	6.35
2:30 p. m.	80.44	75.17	5.06	4.58	9.81	1.27	54.23	6.55
6:00 a. m.	81.08	75.89	.64	.72	10.05	.24	56.65	6.40
2:30 p. m.	80.42	75.18	— .66	— .71	9.28	— .77	53.97	6.52
Y b 6:00 a. m.	70.02	65.89	....	....	10.06	....	55.00	5.95
2:30 p. m.	70.98	67.35	.96	1.46	10.58	.52	53.59	5.12
6:00 a. m.	73.80	69.71	2.82	2.36	10.82	.24	54.63	5.54
2:30 p. m.	76.68	72.42	2.88	2.71	10.94	.12	52.27	5.53
D b 6:00 a. m.	75.02	70.10	....	....	11.95	....	57.92	6.56
2:30 p. m.	77.32	72.40	2.30	2.30	10.62	—1.33	56.32	6.37
6:00 a. m.	78.06	73.34	.74	.94	11.94	1.32	57.59	6.05
2:30 p. m.	78.76	73.94	.70	.60	11.74	— .20	56.06	6.13
D c 6:00 a. m.	68.82	63.91	....	....	8.82	....	61.45	7.13
2:30 p. m.	72.24	67.30	3.42	3.39	9.32	.50	58.91	6.84
6:00 a. m.	71.92	67.06	— .32	— .24	11.24	1.92	61.09	6.75
2:30 p. m.	74.66	69.73	2.74	2.67	11.20	— .04	58.59	6.60
L b 6:00 a. m.	76.78	71.74	....	....	11.44	....	59.61	7.27
2:30 p. m.	77.42	71.97	.64	.23	10.97	— .47	60.00	7.04
6:00 a. m.	77.38	71.73	— .04	— .24	11.04	.07	58.95	7.30
2:30 p. m.	81.50	75.55	4.12	3.82	11.36	.32	57.93	7.30
July 18-19, 1934								
J b 6:00 a. m.	73.14	67.90	....	....	9.90	....	54.90	7.16
2:30 p. m.	72.24	68.73	1.10	0.83	9.21	—0.69	52.92	7.42
6:00 a. m.	75.94	70.43	1.70	1.70	11.14	1.93	53.73	7.25
2:30 p. m.	78.74	73.12	2.80	2.69	11.55	.41	52.13	7.14
J d 6:00 a. m.	68.50	63.50	....	....	11.14	....	57.01	7.30
2:30 p. m.	68.88	63.88	.38	.38	10.91	— .23	54.70	7.27
6:00 a. m.	68.70	63.77	— .18	— .11	11.11	.20	57.02	7.17
2:30 p. m.	74.12	68.63	5.42	4.86	11.66	.55	54.08	7.40
Y b 6:00 a. m.	76.06	71.89	....	....	12.63	....	51.90	5.48
2:30 p. m.	75.06	71.09	—1.00	— .80	11.66	— .97	49.84	5.29
6:00 a. m.	78.00	74.04	2.94	2.95	12.95	1.29	50.99	5.07
2:30 p. m.	82.96	78.66	4.96	4.62	13.41	.46	48.60	5.18
D b 6:00 a. m.	79.26	74.38	....	....	12.47	....	57.90	6.16
2:30 p. m.	80.38	75.42	1.12	1.04	12.65	.18	55.88	6.17
6:00 a. m.	80.32	75.16	— .06	— .26	11.30	—1.35	57.03	6.43
2:30 p. m.	82.08	76.75	1.76	1.59	12.11	.81	52.59	6.49
D c 6:00 a. m.	68.26	63.12	....	....	10.51	....	59.99	7.53
2:30 p. m.	70.42	65.17	2.16	2.05	10.19	— .32	58.03	7.46
6:00 a. m.	70.06	64.94	— .36	— .23	10.58	.39	60.22	7.31
2:30 p. m.	73.20	67.73	3.14	2.79	9.99	— .59	57.74	7.47
L b 6:00 a. m.	76.56	70.64	....	....	9.57	....	58.81	7.73
2:30 p. m.	77.38	71.40	.82	.76	10.96	1.39	57.27	7.60
6:00 a. m.	77.04	71.21	— .34	— .19	10.91	— .05	58.35	7.57
2:30 p. m.	82.94	76.74	5.90	5.53	11.56	.65	56.24	7.47
August 3-4, 1934								
K D 6:00 a. m.	81.01	76.61	....	....	11.72	....	50.50	5.43
2:30 p. m.	83.50	76.77	2.49	0.16	12.16	0.44	48.99	5.66
6:00 a. m.	84.47	79.85	.97	3.08	12.14	— .02	49.99	5.47

TABLE XXII.—Continued.

Variety and Time a		Total dry matter	Combustible matter	Gain of Dry matter	Gain of Combustible matter	Carbohydrates	Gain of carbohydrates	Water	Ash
August 6-7, 1934									
J	6:00 a. m.	90.72	85.00	....	....	13.52	....	52.17	6.30
	2:30 p. m.	93.70	87.74	2.98	2.74	14.34	.82	50.64	6.36
	6:00 a. m.	95.16	89.17	1.46	1.43	14.18	— .16	52.80	6.30
	2:30 p. m.	95.44	89.35	.28	.18	14.92	.74	50.40	6.38
Y	6:00 a. m.	75.04	71.39	....	....	12.13	....	50.43	4.87
	2:30 p. m.	77.92	74.11	2.88	2.72	12.93	.80	48.63	4.89
	6:00 a. m.	80.88	76.95	2.96	2.84	11.94	— .99	50.51	4.86
	2:30 p. m.	78.94	75.14	—1.94	—1.81	12.00	.06	48.17	4.80
D	6:00 a. m.	87.30	82.50	....	....	12.80	....	53.54	5.50
	2:30 p. m.	91.30	85.94	4.00	3.44	13.88	1.08	54.23	5.87
	6:00 a. m.	91.84	86.45	.54	.51	13.96	.08	54.15	5.87
	2:30 p. m.	91.62	86.54	— .22	.09	14.11	.15	51.92	5.55
L	6:00 a. m.	80.72	75.26	....	....	11.84	....	56.83	6.77
	2:30 p. m.	84.46	78.85	3.74	3.59	12.39	.55	54.51	6.64
	6:00 a. m.	83.00	77.46	—1.46	—1.39	11.48	—1.39	57.18	6.68
	2:30 p. m.	89.16	83.23	6.16	5.77	12.33	.85	54.75	6.65
August 15-17, 1934									
D	9:45 a. m.	66.96	61.50	....	....	9.06	....	62.70	8.16
	2:45 p. m.	70.38	64.36	3.42	2.86	9.45	0.39	60.63	8.56
	8:45 a. m.	66.05	61.01	—4.33	—3.35	9.49	.04	63.14	7.63
	1:45 p. m.	67.66	62.44	1.61	1.43	9.72	.23	62.09	7.71
	8:00 a. m.	64.04	58.94	—3.62	—3.50	10.35	.63	63.45	7.97
	1:00 p. m.	66.34	61.16	2.30	2.22	10.30	— .05	60.31	7.82
L	9:45 a. m.	76.20	69.88	....	....	11.18	....	59.98	8.30
	2:45 p. m.	81.74	75.01	5.54	5.13	11.58	.40	57.12	8.24
	8:45 a. m.	77.58	71.18	—4.16	—3.83	11.38	— .20	60.59	8.25
	1:45 p. m.	78.16	71.60	.58	.42	11.80	.42	59.10	8.40
	8:00 a. m.	76.76	70.40	—1.40	—1.20	12.23	.43	60.80	8.28
	1:00 p. m.	80.02	73.28	3.26	2.88	13.10	.87	58.50	8.42
August 21-22, 1934									
J	6:30 a. m.	82.72	78.03	....	....	13.01	....	52.15	5.70
	2:00 p. m.	83.75	78.93	1.03	0.90	12.28	—0.73	50.01	5.75
	6:30 a. m.	89.25	84.20	5.50	5.27	11.78	— .50	50.83	5.66
	2:00 p. m.	90.46	85.23	1.21	1.03	11.49	— .29	49.60	5.80

TABLE XXII.—Concluded.

Variety and Time a	Gm. per sq. m. of leaf area						Percent of	
	Total dry matter	Combustible matter	Gain of		Carbohydrates	Gain of carbohydrates	Water	Ash
			Dry matter	Combustible matter				
August 23-24, 1934								
J b 6:00 a. m.	84.12	79.33	....	....	13.40	....	52.47	5.70
2:30 p. m.	85.22	80.29	1.10	0.96	12.58	—0.82	50.60	5.79
6:00 a. m.	90.08	85.26	4.86	4.97	13.99	1.41	52.51	5.91
2:30 p. m.	92.34	87.00	2.26	1.74	14.93	.94	50.47	5.79
J e 6:00 a. m.	75.92	70.54	....	....	11.13	....	54.45	7.08
2:30 p. m.	78.48	72.71	2.56	2.17	11.12	— .01	52.25	7.33
6:00 a. m.	80.28	74.34	1.80	1.63	11.77	.65	54.53	7.40
2:30 p. m.	81.70	75.74	1.42	1.40	12.42	.65	51.62	7.30
Y b 6:00 a. m.	72.16	68.83	....	....	12.58	....	51.10	4.61
2:30 p. m.	72.92	69.52	.76	.69	11.62	— .96	48.60	4.66
6:00 a. m.	75.08	71.42	2.16	1.90	11.26	— .36	51.05	4.87
2:30 p. m.	78.06	74.29	2.98	2.87	11.61	.35	49.40	4.83
D b 6:00 a. m.	94.86	89.37	....	....	14.42	....	52.46	5.79
2:30 p. m.	96.80	91.10	1.94	1.73	14.62	.20	50.04	5.89
6:00 a. m.	95.96	90.36	— .16	— .74	15.93	1.31	52.88	5.84
2:30 p. m.	99.28	93.65	3.32	3.29	16.66	.73	51.32	5.67
D f 6:00 a. m.	87.20	81.81	....	....	13.08	....	53.47	6.18
2:30 p. m.	90.60	84.60	3.40	2.79	13.59	.51	51.26	6.63
6:00 a. m.	91.84	85.84	1.24	1.24	14.05	.46	53.30	6.50
2:30 p. m.	94.52	88.38	2.68	2.54	14.27	.22	51.29	6.50
L b 6:00 a. m.	91.14	84.94	....	....	14.04	....	55.30	6.80
2:30 p. m.	91.24	85.13	.10	.19	14.47	.43	53.26	6.70
6:00 a. m.	89.48	83.45	—1.76	—1.68	15.78	1.31	55.96	6.74
2:30 p. m.	91.26	85.19	1.78	1.74	16.91	1.13	54.36	6.65

a. The following abbreviations indicate the varieties used: D, Delicious; L, Livland; J, Jonathan; Y, York; KD, King David.
Leaf to fruit ratios: b, no fruit; c, 15:1; d, 20:1; e, 10:1; f, 40:1.

TABLE XXIII.—ANALYSES OF APPLE LEAVES. VARIATION IN TOTAL DRY MATTER, COMBUSTIBLE MATTER, WATER CONTENT, AND ACID HYDROLYZABLE CARBOHYDRATES ESTIMATED AS GLUCOSE.

Variety and Time		Gm. per sq. m. of leaf area				Percent of water
		Total dry matter	Gain of dry matter	Carbohydrates	Gain of carbohydrates	
June 24-25, 1935						
Jonathan	5:30 a. m.	77.76	....	13.48	....	60.41
	2:30 p. m.	79.94	2.18	13.66	0.18	57.89
	5:30 a. m.	81.06	1.12	13.19	— .47	Rain
	2:30 p. m.	86.88	5.82	13.58	.39	64.17
York	5:30 a. m.	65.84	....	11.98	....	61.35
	2:30 p. m.	65.60	— .24	12.07	.09	57.95
	5:30 a. m.	64.86	— .74	11.76	— .31	Rain
	2:30 p. m.	69.40	4.54	12.03	.27	58.02
Delicious	5:30 a. m.	79.80	....	13.83	....	63.74
	2:30 p. m.	87.06	7.26	14.71	.88	59.29
	5:30 a. m.	84.60	—2.46	14.75	.04	Rain
	2:30 p. m.	92.42	7.82	14.94	.19	59.03
Livland	5:30 a. m.	77.14	....	13.02	....	63.74
	2:30 p. m.	81.04	3.90	13.63	.61	52.11
	5:30 a. m.	77.76	—3.28	13.48	— .15	Rain
	2:30 p. m.	88.12	10.36	13.74	.26	53.81
July 5-6, 1935						
Jonathan	5:30 a. m.	81.34	....	13.15	....	58.89
	2:30 p. m.	87.20	5.86	14.36	1.21	54.88
	5:30 a. m.	82.68	—4.52	14.85	.49	59.16
	2:30 p. m.	88.76	6.08	14.96	.11	50.65
York	5:30 a. m.	62.46	....	11.22	....	59.89
	2:30 p. m.	66.98	4.52	11.25	.03	55.86
	5:30 a. m.	66.64	— .34	11.20	— .05	59.04
	2:30 p. m.	69.94	3.30	11.26	.06	56.17
Delicious	5:30 a. m.	86.04	....	15.00	....	64.47
	2:30 p. m.	94.64	8.60	17.60	2.60	57.63
	5:30 a. m.	88.64	—6.00	15.19	—2.41	61.97
	2:30 p. m.	95.52	6.88	15.82	.63	56.84
Livland	5:30 a. m.	59.20	....	10.63	....	66.68
	2:30 p. m.	63.58	4.38	10.86	.23	64.98
	5:30 a. m.	59.36	—4.22	10.55	— .31	65.76
	2:30 p. m.	63.96	4.60	10.76	.21	62.85
July 24-25, 1935						
Jonathan	5:30 a. m.	87.60	....	14.25	....	55.33
	2:30 p. m.	91.50	3.90	15.68	1.43	50.40
	5:30 a. m.	89.02	—2.48	14.57	—1.11	55.03
	2:30 p. m.	94.62	5.60	16.91	2.34	51.20
York	5:30 a. m.	85.10	....	14.92	....	51.66
	2:30 p. m.	84.82	— .28	14.98	.06	48.69
	5:30 a. m.	84.64	— .18	15.00	.02	52.12
	2:30 p. m.	87.38	2.74	15.22	.22	48.50
Delicious	5:30 a. m.	82.68	....	16.07	....	60.52
	2:30 p. m.	89.26	6.58	16.23	.16	54.22
	5:30 a. m.	85.50	—3.76	15.90	— .33	58.82
	2:30 p. m.	89.44	3.94	15.80	— .10	54.95
Livland	5:30 a. m.	65.92	....	11.50	....	64.36
	2:30 p. m.	68.34	2.42	11.71	.21	58.44
	5:30 a. m.	64.85	—3.76	11.32	— .39	62.47
	2:30 p. m.	68.08	3.50	11.73	.41	58.78

TABLE XXIII.—Concluded.

Variety and Time		Gm. per sq. m. of leaf area				Percent of water
		Total dry matter	Gain of dry matter	Carbohy-drates	Gain of carbohy-drates	
August 2-3, 1935						
Jonathan	7:00 a. m.	84.20	....	13.18	....	51.40
	2:30 p. m.	84.34	0.14	13.72	0.54	48.98
	7:00 a. m.	82.64	—1.70	13.46	— .26	55.12
	2:30 p. m.	87.48	4.84	13.85	.39	51.92
York	7:00 a. m.	73.48	....	12.77	....	46.17
	2:30 p. m.	73.28	— .20	12.70	— .07	45.27
	7:00 a. m.	75.08	1.80	12.61	— .09	48.17
	2:30 p. m.	76.18	1.10	12.84	.23	44.87
Delicious	7:00 a. m.	96.02	....	18.40	....	53.18
	2:30 p. m.	95.80	— .22	18.61	.21	52.63
	7:00 a. m.	96.78	.98	18.61	.00	55.47
	2:30 p. m.	97.98	1.20	19.47	.86	53.04
Livland	7:00 a. m.	77.36	....	12.66	....	56.27
	2:30 p. m.	78.74	1.38	13.49	.83	55.27
	7:00 a. m.	77.82	— .92	12.50	— .99	57.94
	2:30 p. m.	81.58	3.76	12.92	.42	55.13
August 7-8, 1935						
Jonathan	7:00 a. m.	90.44	....	15.85	....	52.01
	2:30 p. m.	93.96	3.52	16.19	0.34	48.49
	7:00 a. m.	92.14	—1.82	17.26	1.07	51.97
	2:30 p. m.	97.08	4.94	17.15	— .11	48.71
York	7:00 a. m.	86.30	....	17.43	....	52.20
	2:30 p. m.	90.24	2.94	18.51	1.08	48.12
	7:00 a. m.	88.78	—1.46	17.46	.95	52.44
	2:30 p. m.	92.94	4.16	17.69	.23	47.91
Delicious	7:00 a. m.	101.18	....	16.66	....	53.12
	2:30 p. m.	107.14	5.96	19.25	2.59	49.74
	7:00 a. m.	101.20	—5.94	19.90	.65	53.53
	2:30 p. m.	108.46	7.26	23.14	3.24	50.75
Livland	7:00 a. m.	74.40	....	11.85	....	59.18
	2:30 p. m.	76.26	1.86	12.81	0.96	55.86
	7:00 a. m.	74.54	—1.72	12.24	— .57	58.21
	2:30 p. m.	76.70	2.16	12.88	.64	56.01

SUMMARY

1. The leaves of apple varieties differ in their internal structure when the extent of the intercellular space in the spongy mesophyll is considered. The extent of the space was judged by measuring tracings of projected images with a planimeter and a chartometer. (Table I.)

2. Orchard-grown apple leaves possess more extensive intercellular space than greenhouse-grown leaves.

3. Livland, a Russian variety, has more extensive intercellular space than any other variety studied. In 1933 the Delicious mesophyll was the most compact, but in 1934 and 1936 the mesophyll in York leaves was the most compact.

4. In 1933 and 1935 the Livland foliage contained a greater amount of mesophyll tissue per unit of leaf area than the other varieties. In 1934 the Delicious leaves ranked first in this respect. On a percentage basis, the proportion of mesophyll tissue occupied by intercellular space was greater in 1933, 1934, and 1935 with the Livland orchard-grown leaves. The difference between the extremes in 1933 was greater than during the other two seasons. (Table I.)

5. During the abnormally dry and hot seasons of 1933 and 1934, the stomata on outdoor foliage were seldom open after 9:00 a. m. and frequently they were closed or nearly so by 7:00 a. m. or 8:00 a. m. No afternoon opening of the stomata was observed. Stomata on apple leaves in the greenhouse remained open longer each morning than those on outdoor foliage.

6. Extreme difficulty was encountered in attempting to determine whether stomata were closed or nearly closed. It is probable that the stomata which appeared to be closed were not gas tight.

7. Livland leaves had the fewest stomata per unit of leaf area and the longest pores.

8. Orchard-grown leaves have more stomata per unit of leaf area than greenhouse-grown leaves. In some instances this difference amounts to as much as 50 percent.

9. In January, 1933, some 1-year-old Livland, Jonathan, Gano, and York trees were divided into two groups. One group was planted in a greenhouse where the day temperatures were usually 15° to 20° C. higher than in the house where the second group was planted. The leaves of Livland, Jonathan, and York grown in the warmer house had a greater extent of intercellular space than those in the cooler house. The reverse was true with Gano.

(a) Within each variety, the leaves possessing the more extensive intercellular space produced the greater gain in total dry matter per square meter leaf area between 8:30 a. m. and 5:30 p. m.

(b) The intercellular space in the mesophyll of leaves from the warmer house was more extensive in the Livland than in the other varieties grown in the same house. The same was true in the cooler house.

(c) Livland leaves accumulated a greater gain of dry matter per unit of leaf area than the other varieties grown in each greenhouse.

(d) Leaves on potted trees in the greenhouse have a greater water content than orchard-grown foliage.

10. In January, 1934, Livland and Delicious trees were planted in 12-inch clay pots in the greenhouse. In July, 1934, these trees were transplanted to the orchard so that photosynthetic studies of the greenhouse-grown leaves could be made under the same environmental conditions as the orchard leaves. There were marked differences in the spongy mesophyll of the leaves of greenhouse-grown trees in contrast to orchard-grown leaves. The four groups of leaves ranked as follows in the measurements of the intercellular space in the mesophyll: (1) Orchard-grown Livland, (2) orchard-grown Delicious, (3) greenhouse-grown Livland, and (4) greenhouse-grown Delicious. The day gains in total dry matter per unit of leaf area were in the same relative order.

11. In 1933 the amount of total dry matter accumulated per square meter of leaf area of the seven varieties used was apparently markedly influenced by the maximum daily air temperature. On the days when the temperature was extremely high, the gain in dry matter was less than on days when the temperature was lower. In 1934, however, the inhibitory action of high temperatures did not become manifest, probably because of the great deficiency of soil moisture which became a limiting factor in leaf activity. On several days in 1934 dry matter determinations were made when the leaves were partially wilted.

12. Apparent photosynthetic determinations were made on three consecutive days in the greenhouse in 1934, by measuring the amount of carbon dioxide absorbed by a leaf on potted Delicious and Livland trees. Dry weight increments, ash determinations, and carbohydrate analyses were made from other leaves collected from these trees.

(a) On two of the three days the Livland foliage gained more in dry weight per unit of leaf area than the Delicious.

(b) The mean amount of carbon dioxide absorbed by the Livland leaf was greater than that absorbed by the Delicious leaf.

(c) Subsequently the two leaves used in these continuous gas stream studies were killed, dehydrated, and imbedded in paraffin, after which mounts on slides for microscopic study

were prepared. As described earlier, the intercellular space in the mesophyll was measured. The cross sectional area of the space for Livland was 107.71 square centimeters per unit area compared to 87.01 square centimeters for Delicious. (Table XI.)

13. York leaves possess the following distinguishing characteristics: (a) A lower percentage of ash than Jonathan, Delicious, or Livland; (b) usually a lower water content than Winesap, Jonathan, Delicious, Livland, Wealthy, or Gano; (c) a lower total dry weight per unit of leaf area than any of the other varieties, with the occasional exception of Gano; (d) a more compact mesophyll than any of the other varieties studied in 1934 and 1935.

14. During 1933, 1934, and 1935, York made lower daily gains in total dry matter per square meter of leaf area, and lower gains in total acid hydrolyzable carbohydrates estimated as glucose, per square meter of leaf area, than any of the other varieties included in these studies. The varieties used in addition to York were: In 1933, Livland, Gano, Wealthy, Jonathan, Winesap, and Delicious; in 1934 and 1935, Livland, Jonathan, and Delicious.

15. Livland leaves on the average weighed more per unit of leaf area, dry weight, than any of the other varieties used in 1934. In many instances during 1933, Wealthy leaves weighed the most per unit of leaf area. This is probably because of the extensive palisade tissue development of these two varieties. The water content of Livland leaves was usually higher than that of the other varieties. These two characteristics, in addition to the greater extent of the intercellular space in the mesophyll, probably account for the fact that Livland ranked first in average daily gains in total dry matter and total acid hydrolyzable carbohydrates estimated as glucose per unit of leaf area during 1934, and that Wealthy and Livland ranked first and second, respectively, in total dry matter gains per unit of leaf area in 1933. Of the varieties studied in 1935, Livland possessed the most open mesophyll. This was the first season that Livland did not rank first in photosynthetic activity. This is probably because of the fact the tree was in such low vigor that it died in the fall of 1935.

16. In 1934 the ranking of the varieties based on the extent of the intercellular space and the ranking based on photosynthetic activity, as judged by the average daily gains in total dry matter, in combustible matter, and in total acid hydrolyzable carbohydrates estimated as glucose, were identical. This ranking was Livland, Delicious, Jonathan, and York.

17. On six days during 1934 the total dry matter increase of Delicious leaves on branches bearing good crops of fruit was compared with that of leaves on branches bearing no fruit. On

five of these days the leaves on the fruiting branches gained more in total dry matter and combustible matter than the leaves on fruitless branches. The mean gain of total dry matter for the six days was 2.92 grams per square meter of leaf area on fruiting branches, and 1.85 grams per square meter of leaf area on fruitless branches. The mean gains of combustible matter were 2.70 grams per square meter of leaf area and 1.79 grams per square meter of leaf area, respectively.

18. On four days during 1934, the total dry matter increase of Jonathan leaves on branches bearing fruit was compared with that of leaves on fruitless branches. On two of these days the gain was greater for the leaves on fruiting branches, and on two days the leaves on fruitless branches made the greater gain. The mean gain of total dry matter for the four days was 2.44 grams per square meter of leaf area from branches with fruits and 1.81 grams per square meter of leaf area from branches from which the fruit had been removed. The ash and water content of leaves near fruits was in general higher than in leaves on fruitless branches. The carbohydrate concentration was usually lower in leaves on fruiting branches than in leaves on branches from which the fruit had been removed.

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