ABSORPTION OF CARBON DIOXIDE BY MAIZE¹

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(WITH SIX FIGURES)

Zea mays is the most important crop plant in North America and one of the more efficient plants of the world in dry matter production. In spite of the economic importance of the plant and its adaptability to physiological experimentation, the authors have been unable to locate any published studies of photosynthesis in the plant beyond those of MILLER (13), in which the indirect methods of leaf-punch weights and chemical analyses were used. In the present study a modification of HEINICKE's method (7) was employed, which the recent work of SMITH (18) has shown to be a direct measure of carbohydrate synthesis as well as convenient and free from errors of leaf shrinkage and carbohydrate translocation.

Although little has been published on photosynthesis in the maize plant, many papers on the effect of environmental factors on photosynthesis are available. EMERSON (3) has worked on the effect of light intensity and temperature. HOOVER, JOHNSTON and BRACKETT (8) have shown the interdependence of light intensities and CO_2 concentrations. GABRIELSEN (4) found the saturation intensity for single, exposed leaves to be about onethird of full sunlight. Tests with entire large plants, such as apple trees (6), or with compact groups of plants (21), however, indicate increased CO_2 absorption up to maximum sunlight intensities. Increased illumination and assimilation in shaded portions of the plants affect the light response in these experiments.

The temperature curve for CO_2 absorption under controlled conditions (3, 11) indicates that chemical reactions limit the over-all rate of the process. Results are complicated by side reactions and secondary effects, however, particularly under field conditions (5, 9, 17, 19).

Wilting is assumed to check or stop photosynthesis although the data on the problem are variable. SCHNEIDER and CHILDERS (16) observed that CO_2 absorption dropped to 13 per cent. of normal when apple trees were held in soil at the wilting percentage. MITCHELL (14) found that stomata of Cineraria apparently were closed before wilting occurred, but a rapid drop in CO_2 absorption was obtained only after the onset of visible wilting of the leaves. Pelargonium and Lycopersicon were not studied in the wilted condition, but apparent stomatal closing without wilting did not markedly decrease CO_2 absorption. DASTUR (2) found that CO_2 absorption decreased with a drop in the water content of leaves, and NUTMAN (15) observed that stomata of unwilted coffee leaves closed in full sunlight, reducing CO_2 absorption.

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Methods

The apparatus used for measuring rates of CO_2 absorption was essentially that of HEINICKE and HOFFMAN (7) with small modifications in equipment and technique. Three units were operated simultaneously; one measuring the CO_2 content of a stream of normal air, and two measuring the CO_2 content of air streams which had been drawn over enclosed maize leaves.

A unit of apparatus is diagrammed in figure 1. The cellophane envelope A encloses a measured area near the center of a leaf which is in contact with the moving air stream. The CO_2 remaining in the air is absorbed as the stream bubbles through a column of NaOH solution in the glass tower D. A Jena G_1 fritted glass filter C serves to break the air stream into small bubbles rendering CO_2 absorption 97 + per cent. complete. The flow meters H were calibrated to pass 95.09 liters of air per hour at 19.5° C., and all tests were

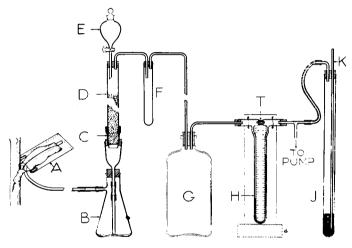


FIG. 1. Diagram of apparatus. See text for description.

made at this rate of air flow. The air reservoir G prevents sudden changes in suction, and the safety tube F catches any alkali which may be accidentally drawn over. Suction for the system was provided by a rotary pump and regulated by means of the mercury by-pass J.

Before beginning a test the pump was started and a funnel, E, of distilled water was let down into each tower. Connections were inspected for leakage, flow meters adjusted, cellophane envelopes fitted over test leaves, and the enclosed areas measured. Fifty ml. of 0.1 N NaOH was pipetted into each funnel, the alkali let down into the towers, and the time recorded as the beginning of the test. The funnels were then rinsed with distilled water, making a volume of about 250 ml. or a twenty-four-inch column in each tower. During the test period, usually of one hour's duration, the apparatus was carefully watched to maintain constant air flow through each tower and to guard against other errors in manipulation. Routine checks of the CO_2 content of free air were run to insure a variation among towers of less than 5 per cent.

At the end of a test the pump was shut down and the envelopes removed from the leaves. The NaOH solutions ran into the flasks B at the base of each tower and were transferred, with hot water rinsing of tower and flask, to 500-ml. Erlenmeyer flasks. The absorbed CO_2 was then precipitated by adding 30 ml. of 0.2 N BaCl₂, and the remaining alkali was titrated with standard HCl, using phenolphthalein as indicator. CO_2 absorption was calculated from the titration differences between test and control towers.

Light intensities were measured with a Weston photometer exposed in the plane of the leaf. Readings for light and temperature were taken at the beginning and end of each one-hour test period. With fluctuating conditions several readings were taken during the hour and their average used.

Results

VARIATION IN RATES OF CO_2 Absorption

The rates of CO_2 absorption observed in laboratory experiments under controlled conditions usually have been fairly uniform and have shown rather characteristic responses to variations in temperature, CO_2 supply, and light intensity. But studies under more nearly natural conditions have

PAIRED LEAVES (700- 2500 fc)	PERCENT- AGE VARIATION	PAIRED LEAVES (7000- 10000 fc)	PERCENT- AGE VARIATION	PAIRED LEAVES (7000- 10000 fc)	PERCENT- AGE VARIATION
	1 %		%		%
$0.993 \\ 1.403$	41	$1.297 \\ 1.261$	3	$\begin{array}{c} 2.022\\ 3.204 \end{array}$	58
$\begin{array}{c} 0.418 \\ 0.503 \end{array}$	20	$\begin{array}{c} 2.231 \\ 1.451 \end{array}$	54	$\begin{array}{c} 1.423 \\ 2.710 \end{array}$	90
$\substack{0.431\\0.572}$	33	$2.188 \\ 2.209$	1	$\begin{array}{c} 1.157 \\ 1.498 \end{array}$	29
$\begin{array}{c} 1.019 \\ 0.828 \end{array}$	23	$1.121 \\ 1.547$	38	$\begin{array}{c} 1.994 \\ 2.175 \end{array}$	9
$\begin{array}{c} 1.131 \\ 1.325 \end{array}$	17	$\begin{array}{c} 1.322 \\ 1.455 \end{array}$	10	$2.386 \\ 1.789$	33
$1.298 \\ 1.183$	10	$\begin{array}{c} 1.904 \\ 1.329 \end{array}$	43	$\begin{array}{c} 2.703 \\ 2.080 \end{array}$	30
$\begin{array}{c} 1.751 \\ 2.314 \end{array}$	32	$1.906 \\ 1.529$	25	$\begin{array}{c} 2.080\\ 2.327\end{array}$	12
$\begin{array}{c} 0.509 \\ 0.514 \end{array}$	1	$\begin{array}{c} 1.763 \\ 1.798 \end{array}$	2	$\begin{array}{c} 2.441 \\ 2.488 \end{array}$	2
$\begin{array}{c} 0.927\\ 0.904 \end{array}$	3	$\begin{array}{c} 2.493 \\ 2.008 \end{array}$	24	$2.546 \\ 2.165$	18
$\begin{array}{c} 0.697 \\ 0.452 \end{array}$	54	$\begin{array}{c} 1.641 \\ 2.047 \end{array}$	25	$2.158 \\ 1.657$	30
$1.467 \\ 1.519$	4	$1.473 \\ 1.781$	21	$2.670 \\ 2.587$	3
$\begin{array}{c} 1.180 \\ 1.507 \end{array}$	28	$\begin{array}{c} 1.694 \\ 1.574 \end{array}$	8	$\begin{array}{c} 1.879 \\ 1.153 \end{array}$	63

$\mathbf{T}\mathbf{A}$	BL	\mathbf{E}	I

VARIATIONS IN CO₂ Absorption under similar conditions. Data are gm. CO₂/m²/hr.

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frequently yielded widely variable responses that could not always be attributed to changing external factors. MAXIMOV (12) found tests under apparently identical conditions varying as much as 139 per cent. HEINICKE

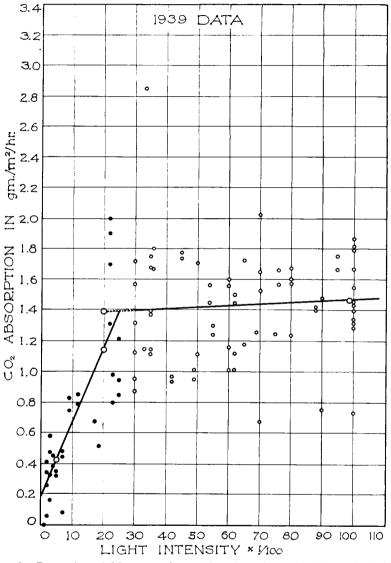


FIG. 2. Regression of CO₂ absorption on light intensity—1939 data. Left, intensities below 2500 fc; r = 0.82. Right, intensities above 3000 fc; r = 0.06. A light saturation value of about 2500 fc is indicated.

and HOFFMAN (7) found similar variations of as much as 500 per cent. KOSTYCHEV *et al.* (9), SCHODER (17), and HEINICKE and HOFFMAN all report instances of CO_2 evolution under conditions apparently favorable for photosynthesis.

In the studies reported here two leaves were tested simultaneously. These were treated alike in every respect; they were on plants of the same hybrid variety; frequently they were on the same plant. Results obtained from such paired leaves would normally be regarded as tests under similar conditions. Table I shows a number of such paired observations taken at random from our data. Variations of 10 to 30 per cent. were the rule, with an average of 25 per cent. for the 36 pairs of observations; variations of 50 per cent. were frequent, and variations approaching 100 per cent. were observed. Variations were as frequent and as large between leaves of the same plant as between leaves on different plants; on the same plant, leaves below the ear shoot yielded higher values than upper leaves as frequently as not. During two summers, however, CO_2 evolution under light intensities favorable for photosynthesis was never observed.

LIGHT INTENSITY AND CO_2 Absorption

Light intensities varied normally with the time of day and with cloudiness. Additional data were obtained with shades of varying density. All determinations in which the light intensity for a one-hour period was nearly constant are thrown together in figures 2 and 3. The scatter diagrams, particularly of the 1939 data, suggested a sharp break in the correlation between light intensity and CO_2 absorption near 3000 fc. The data were accordingly arbitrarily divided into a group with light intensities of less than 2500 fc and a second group with intensities of more than 3000 fc. A few intermediate readings were discarded. Regression and correlation coefficients were then determined for the groups separately.

The correlations between light intensity and CO_2 absorption were highly significant in both seasons for light intensities below 2500 fc, with r values of 0.82 and 0.78. At the higher light values, however, the correlations of 0.06 and 0.11 were not statistically significant. The regression coefficients, b = 0.048 and 0.068, show the gains of CO₂ absorption in gm./m.²/hr. from each added 100 fc of light. At the higher light intensities the corresponding gains were 0.001 and 0.003, with no statistical significance. The artificial division of our data must be emphasized. If all data points were plotted together they would give a curvilinear regression with less resemblance to a so-called limiting factor curve (1). The figures do indicate, however, that light intensities above 3000 fc are of questionable value in CO_2 absorption by fully exposed leaves of maize. Similarly, if the regression coefficients for the lower light range are divided into the average readings for the higher range they give values of 2600 to 2900 for the calculated maxima. Data obtained by LEONARD in 1938 showed the same light response. It is significant in this comparison that ground-level light intensities under fully grown maize are 30 to 40 per cent. At normal planting distances and full sunlight, we may expect, therefore, that photosynthesis will not be limited by light intensity in any of the leaves of the plants.

The higher average value of 1940, 1.74 gm./m.²/hr. against 1.42 gm. in 1939, is attributed to a greater number of readings on younger leaves with their higher rates of assimilation. For comparison with published rates of

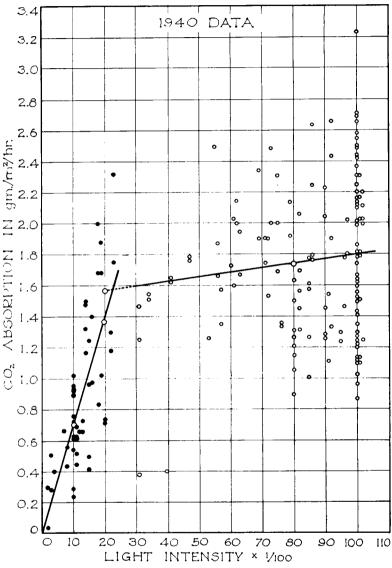


FIG. 3. Regression of CO₂ absorption on light intensity—1940 data. Left, intensities below 2500 fc; r = 0.78. Right, intensities above 3000 fc; r = 0.11 and not statistically significant.

photosynthesis in other plants, the average glucose produced was 0.97 and 1.19 gm./m.²/hr. The first figure is identical with the value obtained by MILLER (13) for maize.

TEMPERATURE AND CO_2 Absorption

Under controlled conditions and at median temperatures, photosynthesis commonly shows a temperature coefficient of $2 \pm$, characteristic of a chemical reaction (**3**, **11**). Under more natural conditions temperature effects tend to be obscured by other factors and complicated by the rapidly changing temperatures of insolated leaves. All readings for the two seasons obtained with more than 4000 fc of light were thrown together for a study of the effect of air temperature on CO₂ absorption by maize. Outside air temperatures ranged from 18.5 to 33.6° C., but temperatures within the cellophane envelopes were 5 to 10° C. higher, and leaf blade temperatures were prob-

ΓА	BL	\mathbf{E}	Π

Turgid	Wilted	DIFFERENCE	WILTED AS A PERCENTAGE OF TURGID
1.28	0.97	0.31	76.0
1.28	0.17	1.82	8.5
1.86	0.00	1.86	0.0
1.48	0.65	0.83	44.0
1.46	1.27	0.19	87.0
1.36	0.78	0.58	57.0
1.52	0.27	1.25	18.0
1.46	0.24	1.22	16.0
1.80	0.87	0.93	48.0
1.90	0.52	1.38	27.0
1.82	0.35	1.47	19.0
1.29	0.06	1.23	4.6
1.72	0.69	1.03	40.0
1.64	0.93	0.71	57.0
1.75	0.52	1.23	30.0
1.25	0.58	0.67	46.0
2.08	1.39	0.69	67.0
1.66	0.82	0.84	49,0
1.70	0.77	0.93	45.0
1.93	0.63	1.30	33.0
2.08	0.62	1.46	30.0
$\vec{x} = 1.67$	$\overline{\mathbf{x}} = 0.62$	$\bar{x} = 1.04$	x = 37.1

Absorption of CO_2 by turgid and wilted leaves. Data are gm. CO_2/M .²/Hr.

ably higher still. Correlation between air temperature and rate of CO_2 absorption was not significant. When the data were divided into three groups, 18.5 to 25, 25 to 30, and 30 to 33.6° C., the mean CO_2 absorption rate for 73 tests below 25° C. was 1.63; the mean for 85 tests between 25 and 30° C. was 1.81, and for 46 tests above 30° C. was 1.62 gm./m.²/hr. The rates at the medium temperatures were highest, suggesting possible retarding influences of low and high temperatures, but statistical analyses did not indicate that any of the differences were significant. Considering the fact that leaves in the above-30° group were subjected to temperatures near 40°, it seems surprising that no significant reduction in CO_2 absorption was evident.

The effect of wilting on CO_2 absorption

Tests were made to determine the effect of visible wilting on the rate of CO_2 absorption. In these experiments plants were grown in large wooden boxes standing in the center of the experimental plot. The soil in these boxes dried more rapidly than field soil, and thus wilted plants could be obtained for comparison with turgid plants in the field. The only criterion used to determine wilting was outward appearance, and in each test a visibly wilted leaf was paired with an apparently turgid leaf. No attempt was made to judge degrees of wilting although differences were evident.

The data from twenty-one such tests, with differences between paired leaves, are included in table II. There were wide variations in the rates exhibited by visibly wilted leaves. Some showed rates of CO_2 absorption as

TIME	WATERED	DRY PLANT	DRY AS A PERCENT AGE OF WATERED
July 4th	1		
7:30 A.M.*	1.46	1.27	87
9:00	1.36	0.78	57
10:30	1.52	0.27	18
1:30 P.M.	1.46	0.24	16
4:45	1.90	0.52	27
July 5th			
8:30 A.M.	1.82	0.35	19
10:00	1.29	0.06†	5†
11:30	1.72	0.69	40
2:00 P.M.	1.20	1.21	101

TABLE III	FABL	E II	Ι
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Adsorption of CO_2 during wilting and recovery. Data are gm. $CO_2/M.^2/HR$.

* Times noted are beginnings of one-hour test periods.

+ Plant watered at beginning of this test.

high as 1.27 and 1.39 gm. per square meter per hour; while one showed no CO_2 absorption. The mean value for twenty-one turgid leaves was 1.67 gm. and for twenty-one wilted leaves was 0.62 gm., or 37 per cent. of the controls.

The course of CO_2 absorption in a wilted leaf during two days is shown in table III. The "dry plant" data are all observations on the same leaf. At 7:30 A.M. on July 4th this leaf appeared turgid and the test showed little reduction in rate. Visible loss of turgor was accompanied by increasingly serious reduction. The box was watered at 10:00 A.M. on July 5th to observe recovery, which was apparently complete within four hours. The data of table III are presented graphically in figure 4.

Relation of porosity of leaves to CO_2 absorption

In an attempt to determine whether the drop in CO_2 absorption with wilting was caused by stomatal closing or by internal changes within the leaf, porosity tests with a conventional porometer were compared with CO_2 absorption rates. A rubber tube with an internal area of 0.32 sq. cm. was

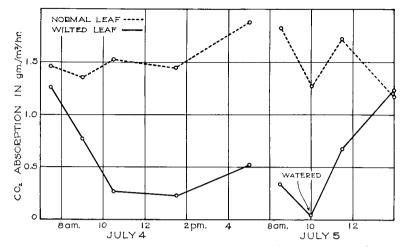


FIG. 4. Carbon dioxide absorption by normal and wilted leaves, showing recovery after watering.

sealed with a plastic wax to the lower surface of the leaf to be tested, and the time recorded for 1.22 cu. cm. of air to pass through the leaf under a pressure drop of 12 to 7 inches of water.

The porosity of apparently turgid leaves varied widely and changed rapidly, especially under changing light conditions. For example, the time for a 5-inch drop changed from 1.8 seconds to 36.1 seconds during a fiveminute period when a cloud hid the sun; frequently the test taken before a one-hour photosynthesis test period varied from that taken immediately after the period by 20 to 40 seconds. Time differences ranging from 20 to 40 seconds were not associated with corresponding differences in CO_2 absorp-

LEAF	WILTING	Porosity	CO_2
		sec.	<i>gm</i> .
la 1b	3 2	∞ 54	$0.17 \\ 0.93$
2a 2b	$\frac{2}{1}$	$\begin{array}{c} 380 \\ 65 \end{array}$	$0.18 \\ 0.60$
3a 3b	$\frac{2}{0}$	600 4	$\begin{array}{c} 0.56 \\ 1.81 \end{array}$
4a 4b	$\frac{2}{0}$	125 6	$\begin{array}{c} 0.62 \\ 2.08 \end{array}$
5a 5b	2+ 0	$\frac{182}{57}$	$0.82 \\ 1.25$
6a 6b	$2 \\ 0$	∞ 15	$\begin{array}{c} 1.23 \\ 2.21 \end{array}$
7a 7b	0	$\begin{array}{c} 158\\ 38\end{array}$	$\begin{array}{c} 1.63 \\ 1.64 \end{array}$

TABLE	IV
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Porosity and CO_2 absorption of paired maize leaves

tion rate. Time for a 5-inch drop usually was less than 15 seconds for apparently turgid leaves in sunlight.

In visibly wilted leaves a distinct decrease in porosity was noted as well as the decreased absorption rate previously discussed, but the decrease in CO_2 absorption was not proportional to the decrease in porosity. Table IV, comparing porosity and CO_2 absorption, shows seven pairs of leaves having widely different porosities. All tests were made under good light conditions, and the two leaves of the pairs were tested simultaneously. Porometers were attached to the same leaves, and near but not on the area enclosed for CO_2 absorption. Degree of wilting, obtained by appearance and by the amount of water vapor collecting on the cellophane envelopes, is indicated by 0 for none and 1 to 3 for moderate to severe. Porosity is given as seconds for the water column to drop 5 inches (1.22 cu. cm.), except nos. 1a and 6a in which no drop was observed in 100 seconds.

The leaves of the (a) group showed the most wilting, the least porosity, and the lowest rate of CO_2 absorption. The correlation between porosity and CO_2 absorption, however, obviously was not close; results such as those obtained with leaf 6a, which showed no porosity but a good rate of CO_2 absorption, suggest that the measured porosities may have varied from those on the absorbing area of the leaves. Insofar as the tests are valid, they indicate the action of internal factors, as well as stomatal closure, in wilted leaves.

The effect of sugar accumulations on CO_2 absorption

If photosynthesis is a partially reversible process, as has sometimes been assumed, the accumulation of the end products in the leaves should reduce CO₂ absorption. Such accumulation is easily obtained in maize by bagging the developing ears to prevent pollination. With this treatment, leaf-blade sugar concentrations of more than 10 per cent., three or four times normal, were obtained. Surprisingly the effect of the treatment seemed to be to increase rather than to decrease net CO₂ absorption. At no time was the average absorption by the high sugar leaves less than that of the controls; two to four weeks after silking the thriftier, darker, green leaves of the nonfruiting plants showed significantly higher absorption than the controls. One of the authors (10) has shown that bagged, non-fruiting plants do not accumulate as much dry matter in the tops as do the fruiting controls (grain Several field tests failed to show markedly higher respiration included). rates for the high carbohydrate plants, and with photosynthesis rates equal to or better than the controls, only translocation to the roots seems to be available as a means of disposing of the surplus photosynthate.

The CO_2 content of Air

The CO_2 content of the air is not a static value, as is shown by analyses made at different times and places, but the figure now generally accepted as an approximate average is 0.03 per cent. by volume, or 0.594 mg. of CO_2

per liter of air. HEINICKE and HOFFMAN (7) found an average CO_2 content of about 0.50 mg./l. They observed marked fluctuations from day to day and usually found lower values in the afternoon than in the morning. They obtained exceptional values as high as 0.81 and as low as 0.35 mg. per liter. Their data show a decrease in CO_2 content during summer months, but they do not comment on this trend. Since their tests usually were of four hours' duration, their data contain no information on hourly fluctuations. HARDER *et al.* (5) report that CO_2 content of air in the Sahara desert was constant between 0.029 and 0.030 per cent. They also report that soil respiration was negligible. STOCKER (20), studying CO_2 content of air in the Buitenzorg gardens (West Java), found daily trends similar to those shown in the present report, but averages usually were above 0.594 mg. per liter.

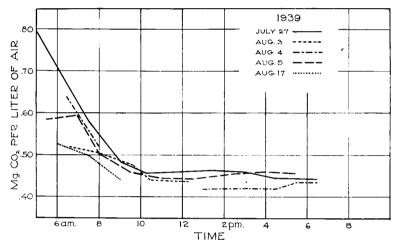
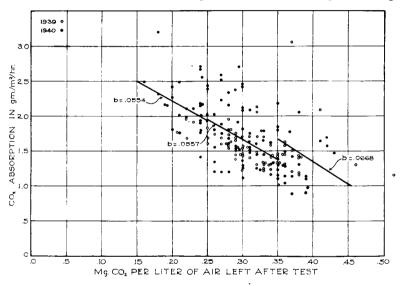


FIG. 5. Diurnal variations in the CO_2 content of field air. Midday values in a field of maize were 75 per cent. of the normal 0.59 mg./l.

The experiments here presented were not designed to study this problem specifically, but the control tower, sampling air from the field at a height of about 1 meter during each test, measured its CO₂ content for that hour. The data thus obtained indicated that the 0.594 mg./l. (0.03 volume per cent.) value was seldom obtained during daylight hours in air taken from among large maize plants. The mean value for fifty-three tests calculated from the 1939 data was 0.488 mg. of CO₂ per liter of air. The mean value for 203 tests made during the 1940 season was 0.482 mg. Fluctuations from day to day also were observed, but they were less striking than the fluctuations from hour to hour. Figure 5 presents graphically the trend of such fluctuations. The points on each curve represent tests made on successive hours of the same day. The downward trend during early morning hours was a common occurrence. The 0.80 mg, value of August 27th was the highest obtained in the two years, and the 10:15 A.M. test for that day was down to 0.455 mg. The levelling of the curve in late morning and afternoon was the most constant characteristic of these data. Erratic fluctuations were sometimes obtained, particularly during and after rain storms when the CO_2 content dropped to a low value during the storm and rose, usually to above normal, a few hours afterward. Normal air movement was surprisingly ineffective in raising the CO_2 content of air among the plants, possibly because of insufficient turbulence to mix surface air with higher strata.

The effect of CO_2 depletion upon absorption

The assumption is generally made that the CO_2 content of air is too low by several times for maximum rates of photosynthesis (8). If the normal content is low, the mid-day field level of 20 to 40 per cent. below normal shown in our analyses might be an important factor limiting rates of photo-



F16. 6. Regression of carbon dioxide absorption on residual CO_2 content of air sample. The data indicate efficient absorption, even with residual CO_2 contents one-third of normal.

synthesis. HEINICKE and HOFFMAN (7) found evidence that CO_2 absorption of apple was decreased by depletions of as little as 10 per cent.; they recommended an aeration rate of not less than 2 l/cm.²/hr. to insure maximum rates of photosynthesis. This is double the rate usually recommended (9) and four times the rate found limiting by LEONARD in preliminary tests on maize.

In the tests reported here leaf areas of 70 to 130 sq. cm., averaging 90 sq. cm., were used with an air flow of 95 l. per hour. Under these conditions depletions of as much as 70 per cent. were obtained, and with 4000 fc or more the average depletion was 35 per cent. Attempts to determine the effect of such depletion on absorption rate are complicated by the fact that CO_2 depletion was not an independent variable. If leaf area tested remained constant;

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depletion was a linear function of absorption. Since, however, leaf areas did vary by nearly 100 per cent., and initial CO_2 content of the air by a like figure, it is possible, by comparing CO_2 absorption per unit area with the weight of CO_2 remaining unabsorbed, to make depletion take on some of the aspects of an independent variable.

In figure 6 the CO₂ absorption rates of all 1939 and 1940 tests in which the light intensity was 4000 fc or more are plotted against mg. of CO_2 per liter of air after absorption. The data were divided arbitrarily into three groups: plus 0.25; 0.25 to 0.35; and 0.15 to 0.25 mg. CO₂ per liter. The dependence of CO₂ depletion on absorption rate is reflected in the negative slope of the regression lines. The greater regression (b = 0.067 against 0.056) with the higher residual CO₂ values is evidence that maximum rates of photosynthesis were not obtained with the greater depletions. On the other hand, the differences were small, and the regressions for the two lower groups were identical (0.0554 and 0.0557). Two absorption values above 3.0 gm. are interesting. The 1939 determination had a low depletion by virtue of an initial CO₂ content of 0.64 mg./l. A fully mature leaf with an area of 81 sq. cm. was used on August 4th. The 1940 reading was made with a young leaf on June 20th. Area was 85 sq. cm., and initial CO₂ content of air 0.49 mg./l. With a depletion to 0.18 mg., the average CO₂ content of the air passing over the leaf was less than 60 per cent. of normal, and the final CO₂ value was 30 per cent. of normal. The rate of photosynthesis in this leaf was more than double the usual "good" rate. Taken together, the data of figure 6 indicate that maize leaves are able to absorb CO₂ rapidly from badly depleted air, and that the low regressions with the high light intensities in figures 2 and 3 were not evidence of limiting CO₂ but of light saturation.

Discussion and summary

The gas stream method of measuring photosynthesis by CO_2 absorption has the advantages of eliminating translocation errors and of permitting the use of the same leaf segment for successive experiments. The principal difficulties encountered were in the accurate metering of the air flow through the several trains and the uniform subdivision of the stream in the absorption towers. These difficulties plus natural variation gave an average difference of 20 to 30 per cent. between duplicate determinations and obscured small experimental differences.

With large numbers of determinations, however, it was not difficult to show that the light saturation value for fully exposed maize leaves was in the neighborhood of 2500 fc, or 25 per cent. of full sunlight. This light intensity may be obtained on the ground under well-grown maize, suggesting that mid-day light intensities with full sun are fully adequate for all leaves of this plant.

Air temperatures between 18 and 34° C. were not significantly correlated with rate of CO₂ absorption. Only determinations with light intensities above 4000 fc were used for this correlation, but other factors were uncontrolled. There was a suggestion in the data that air temperatures of 25 to 30° C. gave the highest rate with decreases at both higher and lower temperatures, the differences being largely masked by variability of the data. The recorded temperatures were air temperatures. Thermometers within the cellophane envelopes with the leaves showed temperatures 5 to 10° C. higher than the air, and it is probable that thermocouples inserted within the mesophyll would have shown still higher readings. Under such conditions it is worthy to note: first, that an indication of decreased rates with air temperatures of less than 25° C. was obtained; and second, that a more serious drop was not obtained with the higher air temperatures. One might postulate that optimum leaf temperature for photosynthesis in maize over one-hour periods is above 35° C.

When visibly wilted and unwilted leaves were compared, the wilted leaves always gave the lower CO_2 absorption values. A range of 0 to 87 per cent. of the controls was obtained in wilted leaves, with an average for 21 experiments of 37 per cent. The drop in rate of absorption with wilting was gradual, and readings of less than 10 per cent. of normal were obtained only with badly desiccated leaves.

Porometer readings on the same leaf, but not on the area enclosed for CO_2 absorption, indicated low porosity for wilted leaves. The correlation between porosity measurements and CO_2 absorption rates was not close, however, and the action of factors other than stomatal closure in wilting leaves was indicated.

Bagging the silking ear shoots of maize plants to prevent pollination resulted in increases of 200 to 400 per cent. in the sugar content of the leaf blade tissue, but did not decrease rates of CO_2 absorption. These results indicate that photosynthesis in maize is not inhibited by the accumulation of end products.

The CO_2 content of the air in a small area of maize at a level of 10 to 12 dm. showed a characteristic and rapid drop during photosynthesis from a night value of 0.55 to 0.80 mg. per liter to a day time level close to 0.45 mg. Air movement and soil moisture had some effect upon the CO_2 content of the air, but photosynthesis appeared to be the most important factor at these altitudes.

With free air around the plants depleted 25 per cent. below its average CO_2 content, depletion within the cellophane envelopes covering test sections of the leaves reached 70 per cent. of normal. Photosynthesis was affected surprisingly little by these low values. The highest rate of CO_2 absorption observed was obtained with a residual CO_2 content of less than 0.2 mg. CO_2 per liter of air.

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