

PHOTOSYNTHESIS IN THE POTATO UNDER FIELD CONDITIONS¹

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Received December 30, 1952

In spite of the importance of the potato as a food, little is known about the effect of environmental factors on photosynthesis in the plant. Studies with several other crops (1, 12, 16, 23, 24) have not only added to the knowledge of photosynthesis but have aided in understanding certain responses of these crops to environmental variations. VERDUIN and LOOMIS (24) and GABRIELSON (10) have shown that saturation light intensity for single, fully exposed leaves is reached at about one-fourth of full sunlight (10,000 + f.c.). THOMAS and HILL (23), working under field conditions, found directly proportional increases in CO₂ absorption with up to ten times normal (0.03%) CO₂ in the air. HOOVER, JOHNSTON, and BRACKETT (14) found increases in photosynthesis at light intensities less than 2,000 f.c. as the CO₂ content of the air was increased, with indications that both light and CO₂ supply may limit photosynthesis at low light intensities.

The temperature curve for CO₂ absorption under laboratory conditions indicates that the enzymatic reactions ($Q_{10} = 2$ or more) may limit the overall rate of the process (9, 17). In the field, however, Q_{10} values near 1.0 have been demonstrated for photosynthesis within the range of 2° to 40° C (1, 6, 8, 23, 24). Reduction in leaf hydration is assumed to check photosynthesis. SCHNEIDER and CHILDERS (21) found that CO₂ absorption of apple trees held in soil at the wilting percentage dropped to 13% of optimum. Recovery of optimum rates of CO₂ absorption occurred after a period of several days. VERDUIN and LOOMIS, (24) observed reduction to 5% of optimum in temporarily wilted maize leaves. Recovery occurred within a few hours after rewatering. MITCHELL (18) found that changes in humidity of surrounding air had little or no effect on photosynthesis. Stomatal closure without wilting did not markedly decrease CO₂ absorption. DASTUR (7) observed reductions in photosynthesis with a drop in water content of leaves.

The study reported here was planned to measure the effects of physiological and environmental factors on photosynthesis in the potato (*Solanum tuberosum* L.) under dry-land and irrigation conditions in western Nebraska. Data from earlier experiments have been reported by CHAPMAN (6).

Methods

Rates of CO₂ absorption were measured by determining the difference in CO₂ content between a measured stream of air and an equal volume of simi-

¹ Published with the approval of the Director as paper no. 595, Journal Series, Nebraska Agricultural Experiment Station.

lar air that had been drawn over an enclosed potato leaf. The apparatus was a modification of that described by HEINICKE and HOFFMAN (12, 13). Six units were operated simultaneously; two units measuring the CO₂ content of normal air streams, and four of air drawn over enclosed leaves.

A unit of the apparatus is diagrammed in figure 1. The leaf chamber (A, B, or C) enclosed a leaf in contact with the air stream. The CO₂ remaining in the air was absorbed in a column, H, of KOH solution containing 0.2 per cent. *n*-butanol. A coarse grade, fritted glass filter, G, served to break the air stream into small bubbles which gave CO₂ absorptions of 99 + per cent.

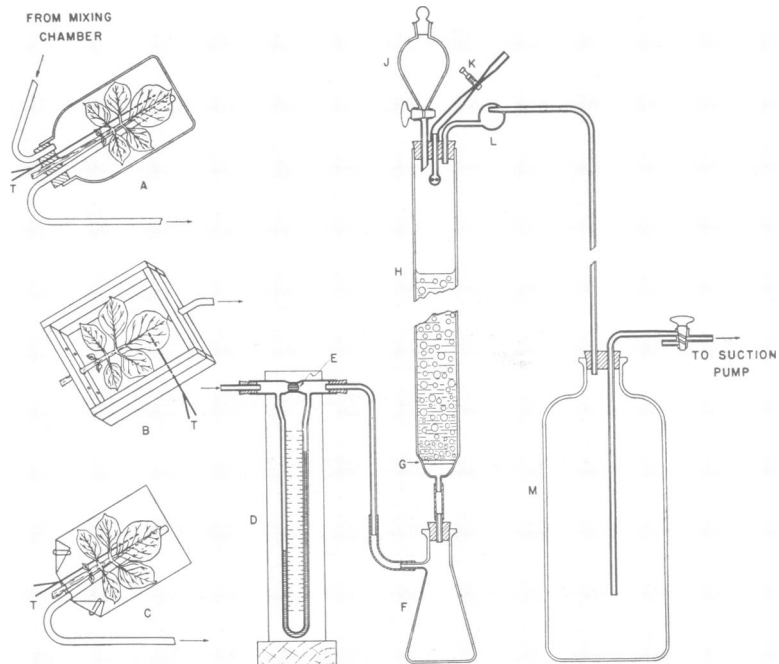


FIG. 1. Apparatus for measurement of CO₂ absorption. A, B, and C, leaf chambers used in different experiments; D, flowmeter; G, fritted glass disc to insure absorption of CO₂ in tower H.

Cellophane envelopes, C, were used as leaf chambers for the 1950 tests and for the soil moisture and wilting studies in 1951. Thin wooden frames, B, covered with cellophane, were used as leaf chambers for the 1949 tests. Two-liter clear glass, wide-mouth jars, A, were used as leaf chambers for the studies of varying CO₂ concentration. The system was made air-tight by sealing the leaf petiole into a split stopper with modeling clay.

During a test period, usually one hour, the flowmeters, D, were watched carefully to insure uniform movement of air through each tower. At the end of the period the absorbent solution was washed into the basal flask, F, an excess of BaCl₂ solution added, and the residual alkali titrated with stand-

ard HCl. Following the final test period for the day, the leaf chambers were removed, the leaves detached from the plants, and their areas determined with a planimeter from contact prints.

The apparatus diagrammed in figure 2 was used in conjunction with leaf chamber A (fig. 1) when higher than normal CO_2 in the air was to be used. Compressed CO_2 , A, was reduced to low pressure, bubbled through concentrated H_2SO_4 in flask C and through water in flask D. Flowmeters, F, fitted with thermometer tubing were calibrated to pass sufficient CO_2 to raise the content of the air stream to the desired level. From the flowmeter the CO_2 was fed into the air stream inlet G, through the mixing chamber H, and then to the leaf chambers or control towers. The level of CO_2 supplied to any

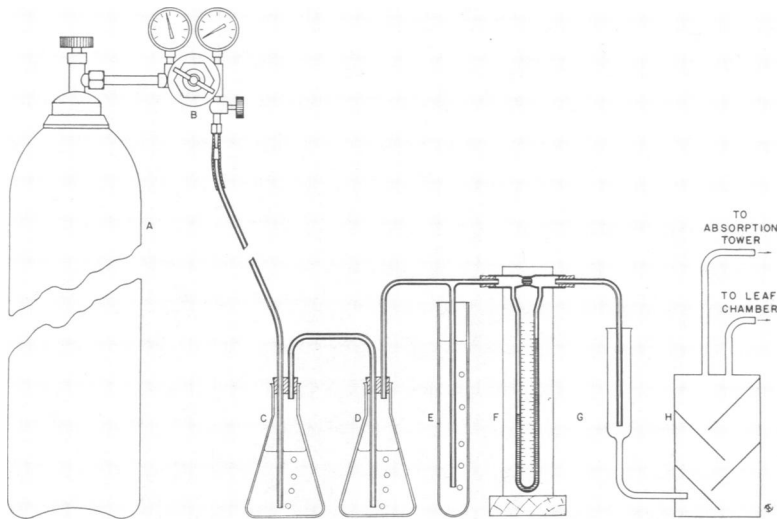


FIG. 2. Apparatus for enriching air with CO_2 . Washed CO_2 from the cylinder, A, is metered into the air inlet, G, where 200 l. of air an hour is taken up for one control and one leaf-chamber air stream.

particular leaf was changed after each test period. Approximately ten minutes was allowed between tests for equilibration of the CO_2 level in the leaf chambers.

Light intensities were measured with a Weston photometer, the target of which was placed inside an empty leaf chamber held near the leaves and in the same plane in relation to the sun. Temperatures were determined with copper-constantan thermocouples (T, fig. 1) placed in the shade inside the leaf chambers.

All determinations were made near Alliance, Nebraska (elevation slightly over 1220 meters). The potatoes were planted about June 15th each year on summer fallowed land. A small number of plants were irrigated and fertilized with NH_4NO_3 in 1951 for the irrigation vs. dry-land comparisons.

Experimental results

VARIABILITY IN RATES OF PHOTOSYNTHESIS

Under controlled laboratory conditions other workers have observed fairly uniform rates of CO₂ absorption and have demonstrated rather characteristic responses of photosynthesis to variations in temperature, CO₂ supply, and light intensity. However, studies under more nearly natural conditions have frequently yielded widely variable responses not clearly attributable to changing external factors (6, 12, 15). VERDUIN and LOOMIS

TABLE I

VARIATIONS IN CO₂ ABSORPTION BY PAIRED LEAVES UNDER SIMILAR CONDITIONS IN 1949. DATA ARE MILLIGRAMS OF CO₂ ABSORBED PER SQUARE DECIMETER OF LEAF AREA PER HOUR.

Third leaf ²		Per cent. variation ¹	Fourth leaf ²		Per cent. variation ¹
Plant A	Plant B		Plant A	Plant B	
15.2	17.2	13	15.5	12.9	20
13.1	19.7	50	11.6	11.6	0
14.8	22.8	54	17.9	17.9	0
16.8	26.0	55	21.5	23.4	9
19.9	26.1	31	17.7	25.9	46
15.9	17.8	12	8.2	16.6	102
19.7	16.1	22	15.4	16.2	5
16.1	19.0	18	15.5	14.6	6
18.9	25.6	35	17.4	20.0	15
7.5	13.6	81	12.5	10.8	16
22.6	23.2	3	26.9	17.3	55
22.6	23.7	5	26.7	18.7	43
10.8	16.8	6	17.1	12.2	40
18.4	17.7	4	15.6	16.7	7
15.4	12.5	23	10.4	20.6	98
16.7	15.9	5	9.8	14.8	51
14.1	18.0	4	13.8	18.2	32
<i>Mean</i>					
16.4	19.5		16.1	17.0	

¹Calculated by dividing the difference between A and B by the smaller of the two numbers and multiplying by 100.

²Coefficient of variability 95%.

(24) found variations of as much as 90%, averaging 25%, with paired maize leaves on the same or adjacent plants.

In these studies, the third and fourth leaves below the terminal leaf cluster on two similar plants were selected for determinations, and conditions were maintained as nearly identical as possible in all four leaf chambers. The results from several such paired observations are shown in table I. A maximum variation of 102% was recorded, variations of 40% or more were frequent, and a mean variation of 28% was found. Differences were as large between leaves on the same plant as between leaves on different plants, and

the coefficient of variability was 95%. The need for large numbers of observations from which to draw conclusions about even gross differences in photosynthesis under field conditions is clearly evident (cf. fig. 4).

THE CO₂ CONTENT OF NORMAL AIR

The generally accepted average CO₂ content of the air is 0.03% by volume, or 0.594 mg. of CO₂ per liter of air. Analyses made at many different times and places have shown that this is not a fixed value but varies with a variety of factors. Since the quantity of CO₂ diffusing into the leaf cells may limit the rate of photosynthesis under field conditions, the importance of these variations in CO₂ content of the air is apparent. BÖHNING (3), for example, found that the rate of CO₂ absorption of apple leaves varied directly with the normal changes in CO₂ content of the atmosphere.

HEINICKE and HOFFMAN (12) observed marked fluctuations in normal CO₂ from day to day, and state that the level was usually less in the afternoon than in the morning. They report an average value of 0.50 mg. of CO₂/l. of air. VERDUIN and LOOMIS (24) made hourly control-tower determinations of the CO₂ content of the air. They concluded that the usually accepted 0.03% is seldom reached during daylight hours at a height of 1 meter in an Iowa cornfield. Day to day as well as pronounced hourly fluctuations were also observed. They reported a maximum value of 0.80 mg./l. and a low value of 0.36 mg. of CO₂/l. of air. Graphs of their data showed a distinct downward trend during the early morning and a leveling of CO₂ content during the remainder of the daylight hours. Their means of 53 tests in 1939 and of 203 tests in 1940 were 0.488 mg. and 0.482 mg. CO₂/l. of air respectively. Typical, midday readings were 25% below readings made at dawn.

Although not designed to measure CO₂ content of the air specifically, the control-tower, sampling air usually 4 to 12 inches above the tops of the plants, measured its CO₂ content for the test period. In these tests the average CO₂ content of the air (mean of 222 tests) was 0.497 mg./l. in 1949, 0.484 mg./l. (148 tests) in 1950, and 0.482 mg./l. (177 tests) in 1951. These values indicate that the expected 0.03% by volume or 0.594 mg./l. was seldom obtained during daylight hours in a western Nebraska potato field.

A downward trend in CO₂ content of the air during the early daylight hours was clearly evident in most of our experiments. There was usually a gradual increase during the afternoon, when, as will be shown later, photosynthesis tended to drop with incipient or actual wilting. After sundown the CO₂ content generally rose rapidly to levels somewhat below 0.03%.

CO₂ CONCENTRATION AND CO₂ ABSORPTION

Increasing the CO₂ content of the air has been shown to increase photosynthesis when other factors are not seriously limiting (4, 5, 14, 23). For experiments with CO₂ concentration, a set of three leaves was selected on each of a number of days, and allowed to carry on photosynthesis with nor-

mal, twice normal, and five times normal CO_2 concentrations. The CO_2 level of the air moving to each leaf was changed after each one-hour test period; thus "fatigue," accumulation of photosynthate, and other effects were avoided or equalized among the test leaves. Each increment of 1.0 mg. CO_2 /l. gave an increase of 14.2 mg. of CO_2 absorbed per dm^2 per hr. on July 31, a typical day (fig. 3). This regression coefficient is significant at the 1% level. Excellent correlation of these factors is indicated by the large coefficient of 0.89.

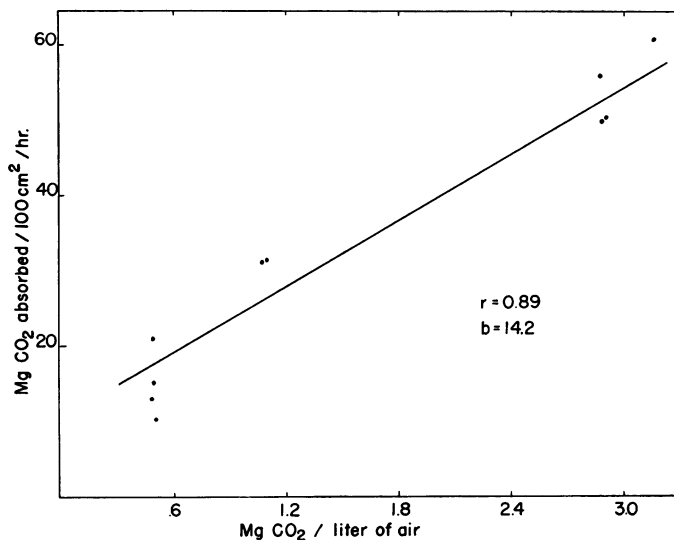


FIG. 3. Regression of CO_2 absorption by potato leaves on the CO_2 concentration in the air.

As shown in table II, the over-all average rates of CO_2 absorption increased directly with increased CO_2 content of the air. With normal CO_2 , the higher average value in 1949, 18.2 mg./ $\text{dm}^2 \times \text{hr.}$ against 14.9 mg. in 1950 and 13.6 mg. in 1951, can be attributed to a large number of readings made on leaves of younger plants with their higher assimilation rates.

LIGHT INTENSITY AND PHOTOSYNTHESIS

Light intensities varied with the time of day and with cloudiness. Additional data at intermediate intensities were obtained by use of shades. Scatter diagrams of photosynthesis against light intensity suggested a break in correlation near 3000 f.c. with normal CO_2 ; near 4500 f.c. with twice normal CO_2 , and near 6000 f.c. with five times normal CO_2 . The data were accordingly arranged into groups ranging above and below these light intensity values, and regression and correlation coefficients were determined for the separate groups.

With normal CO_2 , close correlation was found between light intensities below 3000 f.c. and CO_2 absorption, with highly significant r values of 0.80,

TABLE II
AVERAGE RATES OF CO₂ ABSORPTION WHEN LIGHT
INTENSITIES WERE ABOVE SATURATION.

Year	CO ₂ level	Mg./dm ² × hr.
1949	Normal (ca. 0.25%)	18.2 ± .66
1950	Normal "	14.9 ± .87
1951	Normal "	13.6 ± .98
"	2 × normal (0.06%)	32.2 ± 2.63
"	5 × normal (0.15%)	50.0 ± 2.59

0.52, and 0.71 for data of three seasons representing 684 individual measurements. For light values over 3000 f.c. the corresponding r values were 0.04, -0.04, and 0.09. The regression coefficients, $b = 0.527$, 0.347 , and 0.351 , show the gains of CO₂ absorption in mg. per dm.² per hr. for each added 100 f.c. of light up to 3000 f.c. In the groups with more than 3000 f.c. of light, the corresponding gains for the three seasons were 0.011, -0.039, and 0.09, with no statistical significance. A scatter diagram of 1951 data with regression lines is shown in figure 4.

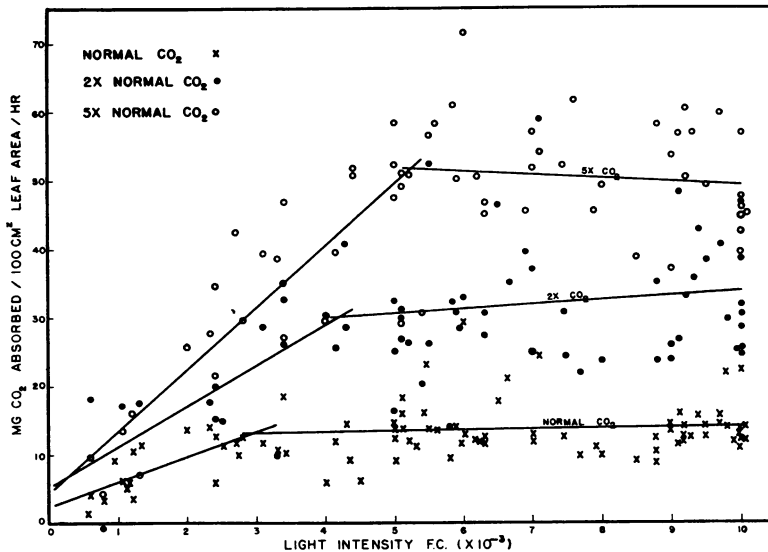


FIG. 4. Scatter diagrams and regressions for photosynthesis at varying light intensities and three levels of CO₂ in 1951.

With twice normal CO₂, the correlation values for the above and below 4500 f.c. groups were 0.139 and 0.745 respectively. The regression coefficients were 0.064 and 0.581 mg./dm.² × hr. × 100 f.c., only the latter, from the below 4500 f.c. group, was statistically significant.

The correlation values for the above and below 6000 f.c. groups (5 × normal CO₂) were 0.097 and 0.886. The regression coefficients were -0.050 and 0.901 mg./dm.² × hr. × 100 f.c.; again only the values from the below 6000 f.c. group of data were statistically significant.

Light saturation of photosynthesis, as indicated by the intersection of these regression lines (fig. 4), was reached at about 3000 f.c. with normal CO₂; at about 4200 f.c. with twice normal, and near 5200 f.c. with five times normal CO₂. These intercepts are considered to be the best available estimates of light saturation for our experiments. In the 1949 data, for example, with 315 determinations, the intercept for normal CO₂ was at 2950 f.c., the same as for 1951. It is significant that even at light intensities below saturation, photosynthesis was increased by increasing the CO₂ content of the air, as indicated by the steadily increasing slope of the regression lines in figure 4.

The artificial division of our data must be emphasized. If all data points were plotted together they would give a curvilinear regression, as pointed out by SPOEHR (22), with less resemblance to a so-called limiting factor curve (2). Likewise, abscissa intercepts would approach values near zero in such a curvilinear plot.

The wide variations observed at similar light intensities indicate an interaction of factors influencing CO₂ absorption. At low light intensities, rate of CO₂ absorption was plainly retarded both by insufficient light and low CO₂ supply, with other factors causing the remainder of the observed variation. At light intensities above saturation the process was limited primarily by the CO₂ supply, and was influenced directly or indirectly by other factors to cause the observed wide variation. Among these other factors, protoplasmic hydration may be important.

THE TEMPERATURE COEFFICIENT OF PHOTOSYNTHESIS UNDER FIELD CONDITIONS

Photosynthesis is commonly reported to show a temperature coefficient of 2.0 or more, characteristic of enzymatically controlled reactions, under controlled laboratory conditions (9, 17). Temperature effects under more nearly field conditions tend to be obscured by other factors and complicated by the rapidly changing temperature of insolated leaves.

DECKER (8) found that temperature had no effect on photosynthesis in some conifers. VERDUIN and LOOMIS (24), working with maize leaves in the field, observed no correlation between moderately high temperatures and photosynthesis. THOMAS and HILL (23) also observed that the Q_{10} of photosynthesis was near 1.0 for several field crops over the range 16° to 28° C. ANDERSON (1) found a Q_{10} of 1.2 for photosynthesis in cereals over the range 2° to 12° C.

Our data have been divided into four groups on the basis of temperature for the three seasons (table III); all temperatures were measured with thermocouples inside the leaf chambers. Differences among the means for any one year or CO₂ level are not statistically significant. Although the highest rates of CO₂ absorption with normal air were recorded in the 27° to 32° C range, the data indicate that temperature did not significantly influence the trend of CO₂ absorption.

With the exception of Anderson's work, observations on the effect of temperature under field conditions are lacking at lower temperatures. We can say, however, that the range of temperatures usually encountered during the growing season does not appear to have a significant effect on photosynthesis, even with CO₂ increased to 5 × normal. This response is considered to indicate that CO₂ limits photosynthesis in the field.

HYDRATION AND CO₂ ABSORPTION

Changes in hydration of cells and leaves are influenced both by the surrounding atmospheric conditions and by the availability of soil moisture. In general, the effects of hydration on photosynthesis have received less attention than the factors of temperature, CO₂ supply, and light, yet under field conditions the water factor must be considered of primary importance.

The mean rate of CO₂ absorption by wilted potato leaves in 1949 was 8.9 mg./dm.² × hr., while the mean for turgid leaves under otherwise similar

TABLE III
MEAN RATES OF CO₂ ABSORPTION IN MG. PER DM² PER HR.
WITHIN VARIOUS TEMPERATURE RANGES.

Year	18 to 27°	27 to 32°	32 to 38°	over 38°
1949	14.7	16.1	15.3	
1950	14.2	15.1	14.8	
1951		16.1	12.7	13.2
		2 × normal CO ₂		
1951		30.3	29.6	33.3
		5 × normal CO ₂		
1951		53.5	48.0	58.6

conditions was 16.5 mg. In 1951, irrigated and dry-land plants (16.3 inches average rainfall) were grown in adjacent plots. The mean rate of CO₂ absorption for the leaves from dry-land plants was 9.2 mg./dm.² × hr., while the mean rate for the irrigated leaves was 14.0 mg. Test plants were within 25 feet or less of each other and leaves of similar age and size were selected. Representative data showed a more rapid diurnal decline in the absorption by dry-land leaves, following nearly equal early morning values. On cloudy or cool days this decline began several hours later, or on some days did not occur at all.

Also, in 1951, single plants were grown in cans 9 by 15 by 30 inches deep, which were buried in the ground to within about 2 inches of the top. The soil in a number of these cans was allowed to dry to the wilting percentage and rewatered following various periods of permanent wilting of the potato plants. Leaf turgidity was always regained within one hour after watering, while CO₂ absorption returned to normal more slowly. Following approximately 24 hours of permanent wilting, CO₂ absorption by leaves was 75%

of controls within one and one-half hours after rewatering (fig. 5). Complete recovery had occurred within four hours. The rate of CO_2 absorption by leaves which had been permanently wilted for approximately 72 hours had not returned to normal 6 hours after rewatering, when tests were terminated for the day. Some 48 hours later CO_2 absorption by different leaves from these same plants was equal to the unwilted controls.

Our results are in agreement with those of VERDUIN and LOOMIS (24) and also with those reported by SCHNEIDER and CHILDERS (21). Rate of recovery of photosynthesis by potato leaves following watering was dependent upon the duration of the period of moisture stress.

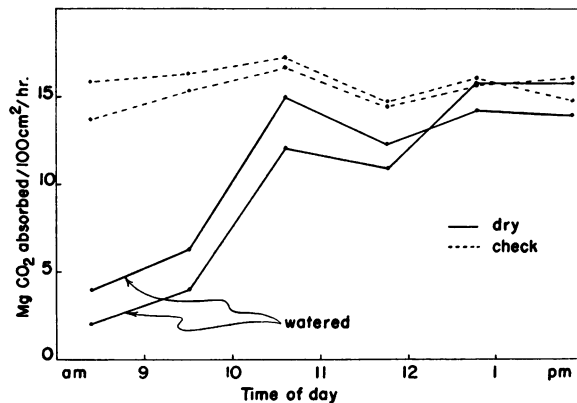


FIG. 5. Recovery of CO_2 absorption by potato leaves following 24 hours of permanent wilting.

VARIETAL DIFFERENCES IN CO_2 ABSORPTION

Data compiled by RABINOWITCH (20) indicate wide variation among plant species in rates of CO_2 absorption. However, most workers have been unsuccessful in measuring differences between varieties within a species with the techniques now available (6, 19).

In 1949 and 1951, the mean rate of CO_2 absorption by Triumph was significantly lower than for Cobbler, Progress, White Cloud, or Neb. 85.41-1. In 1950, the means were not significantly different. Although the mean for Triumph was lower in all three years, these values may be associated with its tendency to wilt more readily and for longer periods during midday than the other varieties tested. Since no significant differences appeared among the other varieties, it seems likely that nearly equal rates of CO_2 absorption per unit area of leaf might be expected under conditions of optimum hydration. Perhaps this optimum hydration is higher for Triumph, or perhaps moisture is lost more rapidly from Triumph leaves than from leaves of the other varieties tested.

Discussion

The CO_2 absorption method of measuring net photosynthesis has the advantage of eliminating translocation errors and permits use of the same

leaf in successive experiments. The principal difficulties involved are the accurate metering of the airflow through the absorption units and prevention of excessive temperature buildup in the leaf chambers.

Variations in rate of CO₂ absorption observed under apparently identical external conditions may be attributed to poorly understood internal factors which differ for different leaves. Probably important among these factors is hydration of the protoplasm. Although we observed large variations in net CO₂ absorption, we did not observe the release of CO₂ by leaves in light reported by some of the earlier workers (15). The variability of their data on CO₂ of the air leads one to suspect that some experimental variable was responsible for these reported instances of negative photosynthesis.

An interesting by-product of the air stream method was the data on CO₂ content of the air. Values of 0.594 mg./l., the usually accepted average CO₂ content of the air, were practically never reached under field conditions in western Nebraska. Early morning and late evening values were considerably higher than the midday CO₂ content. The consistently low values obtained in daytime analyses suggest that the lower layers of air above the plants become noticeably depleted of CO₂ during photosynthesis. Two factors tend to reduce this depletion: mixing of depleted air with air of higher CO₂ content and CO₂ evolution by respiring plants and soil organisms. These western dry-land soils are lower in organic matter and generally drier, and night temperatures are much lower than at Ames, Iowa, which may explain why early morning values were not as high as those reported by VERDUIN and LOOMIS (24).

The fact that photosynthesis in the potato was doubled by doubling the CO₂ content of the air, and increased nearly four times by increasing the CO₂ to 0.15% in short time experiments, indicates the importance of the finding that average daytime CO₂ content of the air is 20 to 25% below the accepted normal. Although THOMAS and HILL (23) failed to obtain sustained increases of photosynthesis with added CO₂ in their 6 × 6 ft. greenhouses, the possibility remains that dry matter production by plants under otherwise optimum conditions is limited by the availability of CO₂.

Limitation by CO₂ supply is assumed to explain the low temperature coefficient of photosynthesis in the field, averaging near 1.0, in contrast to coefficients of 2 and more that have been reported in the laboratory with CO₂ concentrations 100 to 200 times normal.

Light saturation of photosynthesis was reached at about 3000 f.c. with normal CO₂ supply, at about 4200 f.c. with twice normal CO₂, and at near 5200 f.c. with five times normal CO₂. At light intensities below saturation, both low CO₂ supply and insufficient light limited the rate of the process. These values suggest that midday light intensity is seldom a seriously limiting factor for photosynthesis in the field. While the lower leaves of trees or thickly planted crops may receive less than optimum light (11, 23), the light intensity under many planted crops varies from 2000 to 4000 f.c.

Wilting was nearly always attended by marked reductions in rate of CO₂ absorption. This reduction may be a result of mechanical interference with

CO₂ entrance or it may be a result of physiological changes interfering with the photosynthetic reactions. After having been nearly equal during the early daylight hours, the midday rate of CO₂ absorption by leaves of dry-land plants was well below that for leaves of irrigated plants. This response seemed to be correlated with availability of soil moisture and severity of atmospheric conditions. Permanent wilting of leaves apparently caused structural or protoplasmic changes from which the leaves recovered fully only over a period of hours or days.

In spite of the fact that varieties differ greatly in total yield of dry matter, vine size, date of maturity, and leaf type, we have not been able to measure differences in their rate of CO₂ absorption per unit leaf area. The magnitude of such differences, if they actually exist, must be small.

Summary

The average variability in rates of CO₂ absorption by paired leaves of potato under field conditions was 28% and the coefficient of variability was 95%. In spite of such variability, evolution of CO₂ from leaves in light was not observed, even on permanently wilted plants.

The CO₂ content of field air averaged about 0.025% during the day with higher values at night, but still generally below 0.03%. Over short periods, photosynthesis was increased directly by increasing CO₂ to 0.15%.

With normal CO₂, photosynthesis showed light saturation in fully exposed leaves at a light intensity of 3000 f.c.; with 2 × normal (0.06%) CO₂ an intensity of 4200 f.c. was required for saturation, and with 5 × normal (0.15%) CO₂, 5200 f.c.

Rates of photosynthesis with normal air averaging 0.025% CO₂, were about 14 mg./dm.² × hr., or 1.4 gm./m.² × hr., equivalent to 0.96 gm. glucose/m.² × hr. With CO₂ at 0.06% the average rate was 32 mg./dm.² × hr., and at 0.15% it was 50 mg.

Even with 5 × normal CO₂, the maximum concentration used, photosynthesis showed a temperature coefficient of approximately unity over the range 18 to 40° C. This lack of temperature response is assumed to be due to the limiting levels of CO₂ present in the field.

Lower mean rates of CO₂ absorption by Triumph leaves were associated with its tendency to wilt more readily than the other varieties tested. We have been unable to measure inherent varietal differences in CO₂ absorption by the air stream method, if such differences actually exist.

Photosynthesis in wilted leaves averaged half that in nonwilted leaves. After watering permanently wilted plants, the rate of recovery of photosynthesis by leaves was directly dependent upon the duration of the period of wilting.

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