APPARATUS AND TECHNIQUES TO MEASURE PHOTOSYNTHESIS OF WHEAT AND OBSERVED DIFFERENCES AMONG CULTIVARS

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PREFACE

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TABLE OF CONTENTS

LIST OF TABLES

Table | Page

FIGURE

CHAPTER I

INTRODUCTION

The research reported here has been prepared in a format for publication in a professional journal. The manuscript appears as it will be submitted except for minor modifications to comply with publication standards of the journal.

To meet world food needs, increased production from available land must be obtained. Also, as costs of production rise, particularly energy costs, ways of producing food more efficiently must be developed. One possible way of increasing production without increasing land use or energy inputs is by increasing the photosynthetic capabilities of the crops we presently grow. Wheat is one of our most important food crops. If the amount of photosynthesis carried out by wheat plants could be increased and this fixed carbon converted to grain we would increase production without increasing other costs. The objectives of this study were to develop a rapid method of measuring photosynthesis in wheat, and to use this method to determine if differences exist in the rate at which winter wheat cultivars photosynthesize. The identification of wheat cultivars with higher levels of total photosynthetic activity could be of substantial benefit to breeding programs concerned with developing high-yielding cultivars.

CHAPTER II

LITERATURE REVIEW

It has been established that increased levels of available carbon dioxide result in higher grain yield in wheat. Fischer and Aguilar (1976) reported yield increases of 23% for spring wheat fertilized with CO_2 in the field. Their results showed that more crop photosynthesis increased grain yield by increasing the number of spikes per area and the number of grains per spike. Krenzer and Moss (1975) also found yield increases in wheat with CO_2 enrichment. Two cultivars grown both in the field and growth chambers responded with increased kernel number per plant and increased kernel size. Kernel number was increased by CO_2 enrichment from the stage of floral initiation to anthesis. Kernel size increased with enrichment after anthesis. They concluded that a screening procedure to classify wheat genotypes according to their photosynthetic capacity would aid the breeder in attempts to increase yield. This suggestion received added support by the findings of Gifford (1977) who observed a 43% increase in grain yield by increasing CO_2 concentration 65% above normal levels. Canopy photosynthetic rates were twice as high for the CO_2 enriched group as the control group. This added photosynthate brought about higher yields by increasing tiller number and grains per spikelet.

These findings suggest that, to obtain increased yield, the search for higher photosynthesizing varieties of wheat should be made.

Differences in rate of photosynthesis within a species have been amply recorded. Curtis, Ogren, and Hageman (1969) reported differences in 36 cultivars of soybeans, Glycine max (L.) Merrill. Criswell and Shibles (1971) observed differences in 20 oat (Avena spp.) genotypes. Crosbie, Mock, and Pearce (1977) measured differences among 64 inbred lines of maize (Zea mays L.).

Comparatively little work has been reported concerning photosynthetic rates of wheat genotypes. A study comparing 21 lines which included both wild progenitors as well as cultivated wheats was completed by Evans and Dunstone (1970). They found that photosynthetic rates ranged from 27.3 to 45.7 mg CO_2 dm^{-2} hr^{-1}. Gale, Edrich, and Lupton (1974) measured photosynthetic rates of 8 commercial wheat cultivars. They found rates that ranged from 12.4 up to 19.2 mg CO_2 dm^{-2} hr^{-1}. Ruckenbauer (1975) compared 5 cultivars of winter wheat ranging from tall to semidwarf types. The photosynthetic rate of the flag leaf at anthesis was found to be as low as 28.0 and as high as 39.0 mg CO_2 dm^{-2} hr^{-1}. The highest rate was found in a semidwarf which also produced highest yield per ear. The carbon dioxide exchange rates (CER) of 18 spring wheat cultivars were compared by Dantuma (1973). He stressed the difficulty of making comparable measurements of photosynthesis on several cultivars. Differences were shown, however, with rates ranging from 32.5 to 41.4 mg CO_2 dm^{-2} hr^{-1}.

Measurements of photosynthesis of agronomic crops was initiated by Musgrave and Moss (1961). Their system, based on an infrared gas analyzer for measuring changes in CO_2 levels, has been adopted by many workers. Hesketh and Moss (1963) describe how the rate of photosynthesis was calculated: a leaf was sealed in a chamber, air of known CO_2 content was passed over the leaf, and the CO_2 content of the starting air minus that of the final air divided by the area of the leaf expressed the rate of CO_2 exchange for that leaf.

To make genotypic comparisons and select for yield improvement, it is necessary that a method be capable of measuring large numbers of plants under specific environments. Wolf and co-workers (1969) developed an air seal on the leaf chamber to enable easy insertion and removal of leaves. The use of this system enabled Nelson et al. (1974) to determine the genetic variability of photosynthetic rate in tall fescue (Festuea arundinacea Schreb.) in the field. They found it necessary to measure 24 leaves of each genotype to detect differences of 2.0 mg CO_2 dm^{-2} hr^{-1}. With four persons and two units they were able to measure 20 plots per hour. Also using the air seal technique, Pearce, Crosbie, and Mock (1976) developed a rapid system for measuring maize and reed canary grass (Phalaris arundinacea L.). The leaves were excised in the field and brought to the lab for preconditioning and measurement. This eliminated the cumbersome problem of transporting the infrared gas analyzer to the field. With this system two workers were able to make 12 to 30 measurements per hour. Another attempt to overcome the problem of collecting large numbers of samples involves the use of radioactively labeled carbon dioxide. Shimski (1969) developed a technique to

measure $^{14}CO_2$ uptake from a 20 second pulse period. Naylor and Teare (1975) improved the technique by adding an air-flow switch driven by an electronic timer. They found that an exposure time of 15 to 20 seconds produced optimum photosynthetic rates in wheat.

A method using infrared gas analysis and short illumination time has been introduced by Sullivan, Clegg, and Bennett (1976). The technique involves attaching a plexiglass chamber to a leaf and use of a syringe to remove an initial air sample. After 15 seconds a second sample is also removed. The two samples are taken to the lab and injected into the analyzer. The difference between the two readings represents the rate of carbon dioxide exchange. Their chamber was designed for measuring photosynthetic rates of sorghum. A similar technique developed by Cary (1977) involves obtaining a gas sample in the field and transferring it to the lab for analysis. The important advantages of such a system are that the infrared analyzer does not need to be taken to the field and the leaves do not need to be excised to be measured.

With these advantages in mind, my objectives were to adapt this type of method for wheat and determine whether differences exist among genotypes for rate of photosynthetic activity. Experiments in the field and growth chambers were conducted during 1977 and 1978 in the development of the apparatus and techniques for its use.

CHAPTER III

METHODS AND MATERIALS

Description of the Apparatus and Its Operation

The leaf chamber as modified for use on wheat is illustrated in figure 1. It is constructed of transparent plexiglass 0.32 cm in thickness. It holds a leaf section 7.45 cm long. The leaf, attached to the plant, is inserted into the chamber and secured at the distal end by a no. 3 rubber stopper. The stopper, slit almost completely, is opened, clamped on the leaf, and inserted into the plexiglass chamber. Another stopper is likewise used to clamp the end of the leaf next to the plant. This, however, has a groove such that the leaf is not tightly pinched and translocation is not hindered. This small space between the leaf and the stopper groove is filled with grease to form an airtight seal.

The rate of photosynthesis is ascertained by comparing the level of CO_2 in two samples drawn from this chamber. The samples are drawn with 5 cc syringes. To facilitate removing two 5 cc samples from the chamber which has a volume of 20.5 cc, a source of air must be available to replace the air which was removed. This is provided by a balloon which holds an additional 40 cc of air. The needles for both the 5 cc syringe and the balloon are inserted through ampul stoppers near each end of the chamber.

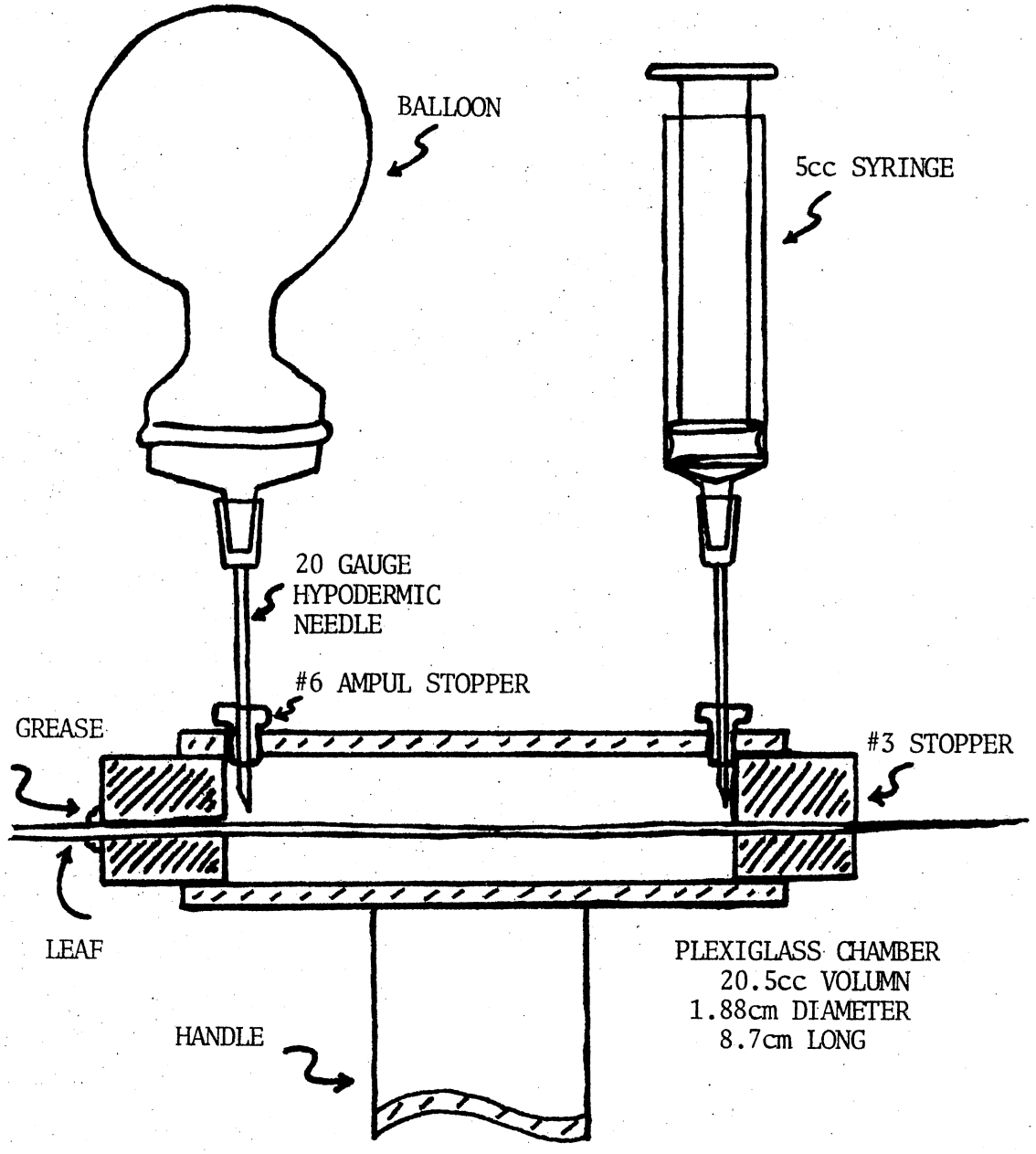

Figure 1. Leaf chamber for collection of air samples in measurements of photosynthesis.

Before the two samples are drawn the chamber is covered to prevent photosynthesis. The chamber and balloon are then filled with outside air by means of a 30 cc syringe. This air must be thoroughly mixed before the first sample can be drawn. This is achieved by inserting a 10 cc syringe and drawing it back and forth ten times. The starting 5 cc sample is then drawn. A rubber stopper is placed on the end of the syringe needle to maintain an airtight sample. The chamber cover is immediately removed and photosynthesis allowed to proceed for 30 seconds. In the meantime a second 5 cc syringe and needle is inserted through the stopper. At the end of the 30 second period the second syringe is drawn. The photosynthetic rate is then determined by the difference in CO_2 between these two samples.

The air samples contained in the two syringes are then transferred to the infrared analyzer in the laboratory. A Beckman Model 865 analyzer and Beckman Model 1005 ten-inch recorder are used. The infrared gas analyzer is connected to a cylinder of dry nitrogen and regulated at 10 lbs per square inch of pressure and a flow rate of 800 ml min^{-1}. Before the CO_2 content of the two samples can be determined, a recorder reading for a known standard must be determined. To do this, a 5 cc sample of 300 ppm CO_2 gas is drawn from a cylinder and injected into the line of nitrogen flowing to the infrared analyzer. The recorder reading of this gas serves as the standard with which to determine the CO_2 level of the other samples. Each sample is then injected into the line and the recorder readings are compared to the reading obtained for the 300 ppm CO_2 standard. The CO_2 level of the 5 cc sample taken after photosynthesis

is then subtracted from the CO_2 level of the sample taken before photosynthesis. This difference represents the amount of carbon dioxide exchanged by that leaf in 30 seconds.

To express the rate of CO_2 exchange on a unit area basis, the area of the leaf must be measured. The leaf is severed at the outside edge of the stopper between the chamber and the plant. The stopper at the distal end of the leaf is removed, with the leaf, from the chamber. A razor blade is used to cut off the leaf at the inside edge of the stopper. The leaf is then reinserted into the groove of the other stopper and also cut off at the inside edge of that stopper. The area of the leaf is measured by means of a LI-Cor Model LI-3000 leaf area meter and Model LI-3050A belt conveyor. Before the area of the leaf is measured, it is taped to a sheet of paper and cut out. This reduces the variation between readings due to bending and curling of the leaf.

Calculation of Rate of CO_2 Exchange

The net quantity of CO_2 removed from a given volume of air by a known area of leaf in the given amount of time is a measure of the rate of photosynthesis. The units are standardized in terms of milligrams of carbon dioxide exchanged per square decimeter of leaf area per hour (mg CO_2 dm^{-2} hr^{-1}).

At 22°C and standard pressure air weighs 1.1959 mg/cm^3 (13). CO_2 weighs 1.8166 mg/cm^3. The weight of one part of CO_2 per one million parts of air (ppm) can be expressed as 1.8166×10^{-6} mg CO_2 per cm^3 of air. The observed difference in CO_2 level is multiplied by the volume of air (20.5 cc in this case) to express the total

weight of CO_2 removed. This value is divided by the area of the leaf and the duration of the illumination period. The standard conversion factor for a change of 1 ppm CO_2 is 0.01090 mg CO_2 dm^{-2} hr^{-1} in this system. Calculation of the CO_2 exchange rate can then be expressed by the formula:

$$\frac{(\Delta ppm)(C)(V)}{(A)(T)} = CER$$

where:

ppm = ppm of CO_2 in sample one minus sample two

C = constant conversion factor (0.01090 mg CO_2 dm^{-2} hr^{-1})

V = volume of air in the leaf chamber in cc

A = area of leaf in chamber expressed in cm^{-2}

T = time of illumination in minutes

CER = carbon dioxide exchange rate expressed as mg CO_2 dm^{-2} hr^{-1}

The rate of CO_2 exchange decreases with lower CO_2 levels. This means that the CO_2 is being exchanged at a faster rate when the first sample is taken than when the second sample is drawn. To adjust for this factor, the calculated rate of CO_2 exchange is designated as the rate for the mean of the two samples. (See Appendix I for an example of the calculations.)

The level of CO_2 in the initial sample comes from the surrounding air. Because of this, variations between starting samples may be as much as 50 ppm. It is desirable to express the rate of photosynthesis at a given CO_2 level. This can be accomplished because the rate of CO_2 exchange for different levels of CO_2 is nearly linear between 200 and 400 ppm. The smaller the difference between the two levels, the more closely the curve approaches linearity. Therefore, to

adjust the rate at the observed level of CO_2 to a standard level, the percentage of CO_2 exchanged at the observed level is multiplied by the standard level. For example, if the observed rate of exchange at an initial level of 370 ppm is 185 ppm, this would represent a change of 50%. To determine the rate at 350 ppm, this is multiplied by 0.50 to find that 175 ppm would have been removed at this lower CO_2 level. This procedure was found to work well in the normal range of atmospheric CO_2 levels.

Plant Material in the Field

Field measurements were made on plants in the Wheat Architecture Nursery at the Agronomy Research Station at Stillwater, Oklahoma, during the 1978 growing season. Four replications, in randomized block design, of 30 cultivars were included in the Nursery which was seeded on October 26, 1978. Plots included four rows 9 m long with 30 cm between rows. The seeding rate was 1000 kernels per plot (67 kg/ha for the variety Turkey).

Because leaf length was determined to be of major importance in determining the amount of photosynthesis per leaf, measurements of the penultimate leaves were made. Twenty leaves from each replication were measured to the nearest 0.01 cm for the cultivars: Osage, TAM W-101, Newton, Payne, and Triumph 64.

CHAPTER IV

RESULTS

Precision of the Analyzer

The precision of the infrared analyzer is listed in the Beckman Manual (1) as 1% of full scale. With the gain adjusted on the analyzer such that full scale represents 500 ppm the possible precision is within 5 ppm. The recorder was adjusted so that 6 inches or 60% of full scale represented 300 ppm. Thus, the theoretical error for the system is 3 ppm. The precision of the analyzer-recorder system was found by analysis of 5 cc samples of the 300 ppm standard gas (Table 1). The average standard deviation of consecutive samples of standard gas is slightly over 1 ppm. Also, the 92 samples estimated the 300 ppm gas as 299.8 ppm. Normal fluctuation in room temperature had no significant effect on readings. It was found that uniformity of readings could be obtained only when the infrared analyzer had been warmed up for the prescribed eight hours.

Precision of the Leaf Chamber

The chamber was designed so that measurements could be made with a relatively short illumination time. This was necessary because of the possible adverse effects from internal heat buildup under high illumination. Furthermore, a large decrease in CO_2

Table 1. Precision of the infrared analyzer and recorder as determined by consecutive 5 cc samples of 300 ppm standard gas.

Date†	Number of samples	Mean ppm CO_2	Standard deviation in ppm CO_2
5/17/78	6	299.3	0.816
5/18/78	4	299.2	0.957
5/19/78	5	299.2	1.788
5/20/78	16	300.0	1.388
5/20/78	6	300.1	0.983
5/21/78	10	300.5	1.354
5/21/78	8	299.6	0.744
5/21/78	5	298.8	1.095
5/22/78	5	299.6	0.547
5/23/78	18	299.3	0.978
5/24/78	9	300.8	1.166
Totals	Σ 92	$\bar{x}$ = 299.8	$\hat{\sigma}$ = 1.095
Temp. 7°C	5	318.4	2.881
Temp. 38°C	6	301.5	1.760

†Temperature 22-26°C for dates 5/17/78 - 5/24/78.

concentration within this time period was advantageous. A smaller experimental error is possible when the change in CO_2 is large compared to the starting concentration. These factors made it essential that the leaf chamber be relatively small. However, a long chamber provided for the measurement of a large leaf area. It was found that a reduction in CO_2 of about 50% in 30 seconds could be obtained by an average sized wheat leaf in a cylindrical transparent chamber as large as 30 cc in volume.

It was found that differences in CO_2 concentration within the chamber resulting from boundary layer effects and chamber shape would increase sampling error. To reduce this effect an attempt was made to circulate the air within the chamber by means of a battery driven fan as Sullivan et al. (1976) had suggested. This could not be accomplished, however, because of the necessarily small chamber. Two other possible ways of reducing this error were to decrease the chamber size or sample a larger proportion of the air in the chamber. Ideally, if all the gas in the chamber were sampled, there would be no error due to differences in CO_2 concentration within the chamber. For this reason an attempt was made to take a 10 cc syringe sample from a 10 cc leaf chamber. The problem encountered here was that air from the auxiliary chamber which had not been reduced in CO_2 content, was mixed with the chamber air before all this air had been removed. In order to reduce all these effects, the optimum size of chamber was found to be 1.88 cm in diameter, 8.70 cm long and hold 20.5 cc with the stoppers and leaf inserted.

To obtain the most precise measurement of rate of CO_2 reduction in the chamber, it is necessary that the best possible estimate be

obtained of the starting CO_2 concentration of that air. It was found that CO_2 mixes with some difficulty and optimum uniformity in the chamber is obtained when mixed 10 times with a 10 cc syringe plus 5 more times with the 5 cc syringe used to take the original sample. Data concerning the uniformity of air within the 20.5 cc chamber and 40 cc balloon after being mixed by this procedure are shown in Table 2. The data indicate that the CO_2 can be uniformly distributed even though large changes in CO_2 level have resulted from a previous measurement of photosynthesis. The standard deviation of 1.182 ppm is not statistically different from the 1.095 standard deviation of readings made on the standard gas. This means that the observed error is due to the analyzer and is not increased by differences between samples of mixed air. Thus, the first sample drawn from the chamber appears to be representative of the CO_2 concentration of all the air in the chamber and balloon.

It was necessary to determine if, during the process of photosynthesis, any of the CO_2 in the reserve balloon could diffuse into the leaf chamber and also be used for photosynthesis. To test this, a sample of the air in the chamber and balloon was taken to determine the original level of CO_2 in the system. Photosynthesis was allowed to proceed for several minutes. The balloon, with its needle, was removed, sealed, and sampled for CO_2 content. This sample was compared in CO_2 content with the original sample. The balloon was replaced and the CO_2 level within the leaf chamber was determined. The results of these tests are shown in Table 3. Large decreases in the CO_2 concentration in the leaf chamber were observed by the illumination periods of several minutes. However, a

Table 2. Uniformity of air in the leaf chamber and balloon after being mixed for initial sample.

Mean CO_2 concentration in ppm†	Standard deviation
304.0	1.000
309.2	0.836
209.0	1.000
369.4	1.516
264.2	1.095
349.3	0.957
193.6	1.949
295.4	0.547
392.2	1.923
275.0	1.000
	average std. dev. = 1.182
	total n = 50

†Each mean is made up of five, 5 cc samples drawn consecutively.

Table 3. Test to determine if CO_2 from the balloon could diffuse into the leaf chamber during the period of photosynthesis.

Initial ppm of CO_2 in the chamber and balloon	Period of photosynthesis in minutes	Final ppm CO_2 in leaf chamber	Change in ppm CO_2 in leaf chamber	Final ppm CO_2 in balloon	Change in ppm CO_2 in balloon
395	13	65	-330	397	+2
397	13	61	-336	399	+2
416	13	57	-359	414	-2
472	13	58	-414	472	0
415	14	58	-357	413	-2
463	18	52	-411	464	+1
417	20	56	-361	414	-3
420	21	53	-367	416	-4
414	30	58	-356	411	-3
460	30	57	-403	459	-1
423	32	60	-363	421	-2
395	35	58	-337	394	-1
353	105	56	-297	355	+2
479	110	54	-425	472	-7
493	330	51	-442	484	-9

significant change in CO_2 in the balloon could not be observed until after at least one hour had elapsed. This meant that in relatively short photosynthetic periods of 30 to 60 seconds no measurable diffusion would take place from the balloon into the leaf chamber.

With this system, the second 5 cc sample is drawn from the leaf chamber after a prescribed period of illumination. If any of the air from the balloon, which has not been reduced in CO_2 content, is mixed with this sample another error is introduced. A test was developed to determine if the second sample was contaminated by CO_2 from the reserve balloon. The chamber and balloon were filled with air and the initial CO_2 level of the air in the chamber was determined. Two samples of this air were taken and their mean was used to improve the estimate of the starting CO_2 level. The balloon and needle were then removed, filled with nitrogen (0% CO_2), and reinserted into the chamber. Another sample was then drawn. If the level of CO_2 in this sample had been lower than the initial level in the chamber, then the last sample would have obtained some of the CO_2 free air from the balloon. The results of these tests are shown in Table 4. The difference between the first two samples and the third sample shows that none of the CO_2 free air was obtained by the third sample. Furthermore, such extreme differences in CO_2 between the chamber and auxiliary supply are not observed in normal photosynthetic measurements. Thus the CO_2 sample taken after photosynthesis will not be contaminated by CO_2 from the reserve balloon.

Table 4. Data to determine if air from the reserve balloon was mixed with the second sample drawn.

Initial ppm CO_2 in leaf chamber (mean of 2 samples)	CO_2 of sample after balloon had been filled with nitrogen	Difference in ppm CO_2 between the 2 samples
226.0	228	+2.0
282.5	281	-1.5
295.5	297	+1.5
317.5	316	-1.5
319.5	319	-0.5
349.0	346	-3.0
350.5	352	+1.5
372.5	372	-0.5
391.5	388	-3.5
493.0	488	-5.0

Precision of the Entire System

To test the precision of the entire system, several measurements were made on individual leaves held under constant conditions. These tests were carried out in a growth chamber held at 22°C and 172 microeinsteins per square meter per second ($\mu E\ m^{-2}\ sec^{-1}$) of photosynthetically active light. The sampling and calculations were carried out as previously described. The data from a typical example of making several measurements on the same leaf are presented in Table 5. It was found that uniform readings were not obtained on a leaf until it had been in the chamber for a period of ten minutes. For this reason, at least this much time was allowed to elapse before measurements were taken. The standard deviation between measurements of the amount of CO_2 removed by this leaf in one minute was found to be 2.99 ppm (Table 5). Expressed in terms of rate per area this represents 0.33 mg $CO_2\ dm^{-2}\ hr^{-1}$. The standard deviation between readings was determined for 25 different leaves from five cultivars. The variation among several readings on the same leaf is shown in Table 6. The pooled standard deviation for the 148 measurements was 3.23 ppm. This is substantially higher than the 1.10 ppm which was found for the analyzer. However, the observed standard deviation expressed as 0.30 mg $CO_2\ dm^{-2}\ hr^{-1}$ is low with respect to the 16.04 mg $CO_2\ dm^{-2}\ hr^{-1}$ average rate of carbon dioxide exchange. This represents a coefficient of variation of only 1.88%. The standard deviation among leaves across the five varieties was 1.76 mg $CO_2\ dm^{-2}\ hr^{-1}$ and was accompanied by a C.V. of 10.97%. This means that the uniformity between measurements of the same leaf

Table 5. Typical examples of data obtained by making several measurements of the same leaf in the growth chamber.†

Test no.	Initial sample ppm	Second sample ppm	Observed difference ppm	Mean CO_2 level§	Portion of CO_2 removed	Predicted CO_2 removed at 350 ppm	Photosynthetic rate$^{\delta}$ mg CO_2 dm^{-2} hr^{-1}
1	377	229	148	303	0.4884	170.9	18.92
2	394	240	154	317	0.4858	170.0	18.82
3	393	237	156	315	0.4952	173.4	19.19
4	395	236	159	315.5	0.5040	176.4	19.53
5	400	240	160	320	0.5000	175.0	19.37
6	400	238	162	319	0.5078	177.7	19.67
7	399	239	160	319	0.5016	175.6	19.43
8	382	228	154	306	0.5049	176.7	19.56
9	401	240	161	320.5	0.5023	175.8	19.46
10	404	239	165	321.5	0.5132	179.6	19.88
11	410	243	167	326.5	0.5115	178.9	19.80
12	401	240	161	320.5	0.4931	172.6	19.10
					Mean	175.2	19.39
					Std. Dev.	2.99	0.33

†Variety: Payne. Replication: 1. Leaf size: 3.3 cm^2. Illumination time: 60 sec. Light: 172 μE m^{-2} sec^{-1}. Temperature: 22°C.
§The starting CO_2 level plus the final CO_2 level divided by 2. The observed difference is expressed for this mean level of CO_2 and then converted to the standard 350 ppm.
δAt a mean CO_2 level of 350 ppm.

Table 6. Precision of the method as determined by variation among several measurements of photosynthesis taken on the same leaf.

Variety	Leaf number†	Readings per leaf	Standard deviation in ppm	Standard deviation $mgCO_2 dm^{-2} hr^{-1}$	Photosynthetic rate $mgCO_2 dm^{-2} hr^{-1}$
Osage	1	11	2.62	0.22	16.20
	2	4	3.78	0.36	12.22
	3	6	1.99	0.20	17.22
	4	4	3.55	0.41	13.85
	5	3	3.21	0.31	15.87
TAM W-101	1	10	4.16	0.43	18.61
	2	4	1.27	0.11	16.66
	3	4	4.91	0.44	15.60
	4	6	3.51	0.34	17.43
	5	3	2.31	0.23	16.36
Payne	1	12	3.00	0.33	19.39
	2	5	2.70	0.26	15.29
	3	4	1.86	0.19	14.48
	4	7	3.82	0.39	16.34
	5	5	1.43	0.14	15.72
Triumph 64	1	11	2.02	0.22	16.17
	2	6	3.98	0.42	12.76
	3	4	2.87	0.36	16.03
	4	6	4.26	0.49	14.36
	5	7	2.45	0.28	15.89
Newton	1	7	4.13	0.33	19.68
	2	4	4.27	0.36	15.64
	3	4	6.32	0.48	15.21
	4	6	2.95	0.25	17.38
	5	5	4.73	0.43	16.63
Totals	$\Sigma = 25$	$\Sigma = 148$	$\hat{\sigma} = 3.23$	$\hat{\sigma} = 0.30$	$\bar{x} = 16.04$
				C.V. = 1.88%	$\sigma = 1.760$
					C.V. = 10.97%

†The plants were grown in the growth chamber under 172 $\mu E\ m^2\ sec^{-1}$ light, fully watered and were in the late tillering stage. The last fully expanded leaf of a tiller was measured and the plants used were grown in five different pots.

is much greater than uniformity between leaves. This method of measuring photosynthesis is sufficiently precise to determine small differences between leaves.

Differences Among Cultivars

The mean rates of photosynthesis of the five winter wheat cultivars were compared. Five leaves from different plants of each variety were measured as previously described. The mean rates of CO_2 exchange are listed in Table 7. The highest rates, 16.93 and 16.91 mg CO_2 dm^{-2} hr^{-1}, were found in "TAM W-101" and "Newton" respectively. These values were statistically (α= .10) higher than the rates of "Osage", 15.07, and "Triumph 64", 15.04 mg CO_2 dm^{-2} hr^{-1}. "Payne" had an intermediate rate of 16.24 mg CO_2 dm^{-2} hr^{-1}.

One of the obvious morphological differences between these varieties is their leaf width. Table 7 shows the mean leaf widths of the five leaves measured at the widest part of the leaf. These plants were measured between the tillering and stem elongation stages, stages 5 and 6 of the Feekes scale (Large 1954). Newton had the widest leaves averaging 5.75 mm and Triumph 64 had the narrowest with an average of 4.27 mm. All the differences among cultivars were significant (α= .01) except the mean differences between TAM W-101 and Osage, 5.02 and 4.90 mm respectively. The data in Table 7 suggests that higher rates of photosynthesis may be associated with wider leaves. The two highest photosynthesizing varieties, TAM W-101 and Newton, also had the widest leaves. The variety showing the lowest rate of photosynthesis, Triumph 64, also had the narrowest leaves. To determine if this relationship exists, the leaf width and

Table 7. Photosynthetic rates of five winter wheat cultivars grown in growth chamber.†

Variety	Leaf width mm	Leaf area cm^2	Rate of photosynthesis mg $CO_2 dm^{-2} hr^{-1}$	Standard deviation among leaves mg $CO_2 dm^{-2} hr^{-1}$
TAM W-101	5.02	3.77	16.93*	1.14
Newton	5.75	4.35	16.91*	1.76
Payne	4.65	3.52	16.24	1.88
Osage	4.90	3.72	15.07	2.00
Triumph 64	4.27	3.18	15.04	1.47

†All values are the means of the five leaves shown on Table 6.
*A one tailed "t" test shows the two cultivars with the highest rates are significantly different from the two cultivars with the lowest rates at the 0.10 level of significance but not at the 0.05 level.

its rate of photosynthesis were compared for each of the leaves examined. Table 8 shows each of those comparisons. A slight positive correlation was found between leaf width and rate of photosynthesis; however, it was only strong enough to explain 7.9% of the variation in rates among those leaves.

From 1972 through 1976 on 28 comparisons from six research stations the variety Osage was the highest yielding cultivar in Oklahoma Agricultural Experiment Station trials (27). It ranked first in four of the five years and averaged 49.6 bushels per acre. Of the nine cultivars tested every year of this period, Triumph 64 ranked eighth with 40.4 bushels per acre. TAM W-101 averaged 45.1 bushels per acre in these tests. The cultivar Payne had been tested along with Osage and TAM W-101 during 1974-1977. Average yields were 48.2, 46.7, and 44.4 for Payne, Osage, and TAM W-101 respectively. Newton had not been compared with the other four cultivars for more than one year.

Another obvious morphological difference among these cultivars is their leaf length. To quantify these differences, ten fully expanded leaves from each cultivar measured for photosynthesis were compared (Table 9). Osage had the longest leaves of these cultivars. Its leaves were 35% longer than the next cultivar. The largest difference between the other four cultivars was only 12%. The order between varieties for width of leaves was the same as had been previously determined. Newton was the widest, followed by TAM W-101, Osage, Payne, and Triumph 64. The leaf area of these leaves was also measured. Osage had the largest area per leaf. Triumph 64 had the smallest area. The reason Osage has the largest area per leaf is

Table 8. Rate of photosynthesis compared to leaf width.

Leaf rank	Cultivar and pot number	Photosynthesis mg CO_2 dm^{-2} hr^{-1}	Leaf width mm†
1	Newton 1	19.68	6.10
2	Payne 1	19.39	4.50
3	TAM W-101 1	18.61	4.76
4	TAM W-101 4	17.43	5.00
5	Newton 4	17.38	5.60
6	Osage 3	17.22	4.68
7	TAM W-101 2	16.66	5.38
8	Newton 5	16.63	5.24
9	TAM W-101 5	16.36	4.72
10	Payne 4	16.34	4.72
11	Osage 1	16.20	5.72
12	Triumph 64 1	16.17	4.46
13	Triumph 64 3	16.03	3.96
14	Triumph 64 5	15.89	4.26
15	Osage 5	15.87	4.86
16	Payne 5	15.72	4.78
17	Newton 2	15.64	5.58
18	TAM W-101 3	15.60	5.38
19	Payne 2	15.29	4.72
20	Newton 3	15.21	6.22
21	Payne 3	14.48	4.54
22	Triumph 64 4	14.36	4.32
23	Osage 4	13.85	4.24
24	Triumph 64 2	12.76	4.36
25	Osage 2	12.22	5.00

$y = mx + b$ $m = 0.04500068$ $b = 3.408256715$ $r = 0.2809$

$r^2 = 0.07890$

†Each width is mean of five measurements on the same leaf.

Table 9. Morphological characteristics of last fully expanded leaves from tillering plants grown in growth chamber.†

Variety	Leaf area cm^2§	Standard deviation	Leaf width mm∂	Standard deviation	Leaf length cmδ	Standard deviation
Osage	14.97	2.27	4.76	0.47	34.21	4.53
Newton	11.87	1.65	5.28	0.45	25.38	2.38
TAM W-101	10.45	1.35	4.91	0.40	22.60	1.65
Payne	9.27	0.94	4.48	0.32	23.69	1.55
Triumph 64	9.26	0.91	4.19	0.36	25.54	1.71

†Each value is a mean of ten leaves from plants in the same stage of growth as described in Table 6.
§The leaf area means are all different (α= .05) except Payne and Triumph 64.
∂The leaf width means are all different (α= .05) except the means of Osage and TAM W-101, also Osage and Payne.
δThe leaf length means are all different (α= .05) except the means of Triumph 64 and Newton, also Payne and TAM W-101.

because of its much longer leaves. Even with the wider leaves of Newton and TAM W-101, their area per leaf is less because their leaves are much shorter than those of Osage. When both width and length are reduced as in Triumph 64, the leaf area is greatly decreased.

These leaf areas were multiplied by the observed rates of photosynthesis for each of the varieties (Table 10). It was found that Osage fixed the most CO_2 per leaf. Triumph 64 fixed the least CO_2 per leaf.

The mean lengths of the penultimate leaves growing in the field are shown on Table 11. Osage was again found to have the longest leaves and Triumph 64 had the shortest leaves in the field.

It seems reasonable to conclude that Osage can fix more CO_2 because of its larger area per leaf which is due to longer leaves.

Observations Made in the Field

The development of the apparatus was accomplished during the 1977 and 1978 spring growing seasons. Experiments in the growth chamber were carried out when plants were not available in the field. Modifications of the apparatus were being made until late in the spring of 1978. For this reason a study of the five cultivars comparable to that carried out in the growth chamber was not obtained. Information was obtained, however, on the potential of the apparatus for making field measurements and the techniques necessarily involved.

The attached chamber did not interfere with the leaf's ability to carry out photosynthesis even though the chamber was kept on the leaf for as long as two hours (Table 12, column 2). This varified the findings in the growth chamber (Table 5) with respect to the leaf

Table 10. Photosynthetic rates calculated by multiplying the observed rate per area times the total area per leaf.

Variety	Leaf area dm^2	Rate of photosynthesis mg CO_2 dm^{-2} hr^{-1}	Total photosynthesis mg CO_2 hr^{-1}*
Osage	1.497	15.07	22.56
Newton	1.187	16.91	20.07
TAM W-101	1.045	16.93	17.69
Payne	0.9276	16.24	15.06
Triumph 64	0.9265	15.04	13.93

*All varieties are significantly different from μ except TAM W-101. The rates of photosynthesis are from the leaves shown in Table 7 and the areas are from leaves growing at the same time shown in Table 9.

Table 11. Length in cm of the penultimate leaf of wheat plants growing in the field.

Replication	Osage	Newton	TAM W-101	Payne	Triumph 64
1	24.77†	25.29	21.26	20.44	18.48
2	27.89	25.84	20.33	18.95	19.75
3	28.89	24.71	19.61	19.24	18.10
4	24.70	23.28	20.23	21.13	18.24
Mean*:	26.56	24.78	20.36	19.94	18.64

*All the means are significantly different at .05 level of significance except the means of Payne and TAM W-101 which were significantly different at the .10 level.
†Mean of 20 leaves.

Table 12. Rate of photosynthesis of one leaf in the field across a period of two hours under a wide range of light intensities.

Sample No. (samples taken between 11:00A.M. and 1:00P.M.)†	Rate of photosynthesis mg CO_2 dm^{-2} hr^{-1}	Samples arranged from lowest to highest light intensity	Light intensity μE $m^{-2}sec^{-1}$	Rate of photosynthesis mg CO_2 dm^{-2} hr^{-1}§
1	14.82	28	140	6.48
2	15.50	29	147	8.16
3	18.78	27	210	10.41
4	17.08	30	220	10.50
5	17.43	26	280	15.43
6	16.42	25	297	15.14
7	20.99	24	310	14.75
8	21.79	1	370	14.82
9	19.63	23	370	16.00
10	20.48	22	395	18.04
11	20.97	5	450	17.43
12	21.88	4	460	17.08
13	21.14	21	480	19.09
14	19.03	2	495	15.50
15	16.74	6	500	16.42
16	21.39	3	520	18.78
17	19.88	7	565	20.99δ
18	19.77	31	630	19.53∞
19	20.88	20	700	20.09
20	20.09	8	765	21.79
21	19.09	11	800	20.97
22	18.04	12	950	21.88
23	16.00	9	1,000	19.63
24	14.75	37	1,000	20.20
25	15.14	38	1,010	20.08
26	15.43	17	1,200	19.88

Table 12. (Continued)

27	10.41	32	1,550	20.17
28	6.48	36	1,600	18.72
29	8.16	19	1,750	20.88
30	10.50	33	1,900	19.22
31	19.53	16	2,000	21.39
32	20.17	10	2,000	20.48
33	19.22	13	2,150	21.14
34	15.65	15	2,175	16.74
35	15.47	14	2,250	15.47
36	18.72	35	2,250	15.47
37	20.20	34	2,300	15.65
38	20.08	18	2,350	19.77

†Variety: TAM W-101 (Flag leaf). Date: May 12, 1978. Conditions: Alternating cloudy and clear.
∞The chamber used to measure this leaf was an earlier model of the chamber in Figure 1, and its inherent error was greater because of varying CO_2 contamination from the auxiliary air supply. For this reason, the variation among readings under saturated light is greater than would be expected with the final model.
§Column 5 shows the general pattern of increased photosynthetic activity with increasing light intensity.
δLight saturation for this leaf occurred at about 550 $\mu E\ m^{-2}\ sec^{-1}$.

chamber not upsetting the homeostatic condition of the leaf.

It was found that one person making one measurement per leaf could set up the chamber, attach a leaf, take the two samples, tape the leaf for future measurement, and record the syringe numbers in an average time of eight minutes.

The optimum period of illumination of the leaf was found to be 30 seconds. Under high sunlight and rapid transpiration a slight amount of condensation formed inside the leaf chamber. Under moderate sunlight it is felt that this did not lower the internal illumination below that which was required for light saturation. However, under maximum light this may have been a problem as indicated by the last five readings in column 5 of Table 12. This problem should be investigated further before measurements in the field under maximum light intensity are accepted.

It was found that if the leaf were excised before the rate of photosynthesis was measured, severe reductions were observed in the amount of CO_2 fixed. This was especially evident for plants under water stress.

Measurements were difficult to make on extremely windy days. It was also very hard to make large numbers of measurements on plants before the tillering stage because of their short leaves.

The most severe limitations to comparing genotypes was caused by reduced photosynthetic rates of older leaves and changing environmental conditions. Changing light levels during the day (Table 12) and changing moisture stress between days made large numbers of measurements under uniform conditions difficult to obtain. Differences between plants of the same variety were accentuated

greatly under partial water stress and in early senescence. Extreme differences were observed in the rate of photosynthesis between well watered plants and the same plants a few days later under water stress.

That the rate of photosynthesis was highest in the early morning and declined as the morning progressed is indicated by the data in Tables 13 and 14. Tables 15 and 16 show how the rate of photosynthesis decreased with drought conditions. On April 20th, no effects of water stress were evident. However, by April 23rd, the lack of water severely limited the rate of photosynthesis. The average amount of carbon dioxide fixed by two varieties on each day dropped from 20.8 mg CO_2 dm^{-2} hr^{-1} on April 20th to 2.61 mg CO_2 dm^{-2} hr^{-1} on April 23rd. On April 26th (Table 17) one leaf from 18 varieties was measured and great variation among leaves was found. The mean rate was 5.26 and the standard deviation was 6.25 mg CO_2 dm^{-2} hr^{-1}. The great range in rates suggested that some varieties may have still been photosynthesizing while others had completely stopped. To test this, ten leaves from two varieties found to differ on April 26th were measured on April 27th. Table 18 shows the results. TAM W-101 and Payne were found to have rates of 5.17 and 5.12 mg CO_2 dm^{-2} hr^{-1} respectively. These two varieties did not differ in average rate of photosynthesis but did exhibit great variation among leaves. This indicates that these two varieties were under the same amount of water stress. It seems probably that this was true for all the varieties in the study.

These field tests showed that differences in average rates of photosynthesis between varieties could be proven only with great

Table 13. Rates of photosynthesis of TAM W-101 and Plainsman V in the field under good growing conditions.

Variety	Leaf no.	Change in CO_2 per 30 sec. at 350 ppm	Rate of photosynthesis mg CO_2 dm^{-2} hr^{-1} δ	Time
TAM W-101	1	234.6	21.67	9:40 A.M.†
	2	205.8	14.44	10:25
	3	158.4	10.79	11:00
	4	218.6	16.71	11:35
			$\bar{x}$ = 15.90	
			σ = 4.55	
Plainsman V	1	284	29.20	10:00 A.M.
	2	233	23.21	10:40
	3	117	12.71	11:25
	4	197	20.51	12:00 Noon
			$\bar{x}$ = 21.41	
			σ = 6.84	

†Date: April 15, 1978. Temperature: air 23°C, soil 18°C. Wind: 25-40 km ha^{-1}. Moisture: light rain the previous night. Sunlight: Clear (2100 μE m^{-2} sec^{-1}).
δNote the variation in rates across time.

Table 14. Rates of photosynthesis of TAM W-101 and Payne showing variation among leaves and across time.

Variety	Leaf no.	Change in CO_2 per 30 sec. at 350 ppm	Rate of photosynthesis mg CO_2 dm^{-2} hr^{-1}	Time
TAM W-101	1	307.5	22.22	8:30 A.M.†
	2	209.5	16.56	10:12
	3	219.8	19.56	10:25
	4	194.8	15.19	10:35
	5	157.8	14.66	10:49
	6	175.1	14.99	11:03
	7	183.0	15.82	11:18
			$\bar{x}$ = 17.00	
			σ = 2.84	
Payne	1	213.5	16.10	8:55
	2	197.7	17.99	10:18
	3	217.7	19.44	10:30
	4	159.6	14.85	10:43
	5	193.5	16.57	11:18
	6	168.5	15.09	11:10
	7	193.8	15.60	11:25
			$\bar{x}$ = 16.52	
			σ = 1.66 Average C.V. = 13%	
			$\bar{\sigma}$ = 2.25δ	

†Date: April 16, 1978. Temperature: Air 21°C, soil 18°C. Wind: 10 km hr^{-1}. Sunlight: hazy but minimum of 600 μE m^{-2} sec^{-1}. Stage of growth: floral primordia are being formed and the last leaf is just visible (stage 8 of Feekes Scale).

δWith the average standard deviation of 2.25 mg CO_2 dm^{-2} hr^{-1}, if 6 samples had been taken from each variety, a difference between means of 2 mg CO_2 dm^{-2} hr^{-1} could have been proven. A difference of 1 mg CO_2 dm^{-2} hr^{-1} would have required 24 samples from each. The observed difference between means of 0.48 mg CO_2 dm^{-2} hr^{-1} would have required 104 samples of each to be statistically different at the .05 level of significance.

Table 15. Rates of photosynthesis before conditions of water stress prevailed.

Variety	Leaf no.	Change in CO_2 per 30 sec. at 350 ppm	Rate of photosynthesis mg CO_2 dm^{-2} hr^{-1}	Time
TAM W-101	1	312.4	25.74	9:27 A.M.†
	2	224.3	19.10	9:56
	3	286.3	28.65	10:40
	4	305.1	25.98	11:05
	5	233.5	20.00	11:22
	6	210.6	16.20	11:40
			$\bar{x}$ = 22.61	
			σ = 4.86	
Osage	1	254.7	25.14	9:15
	2	208.5	19.93	9:43
	3	213.1	23.27	10:15
	4	186.5	18.10	10:30
	5	110.2	11.94	11:14
	6	170.2	15.25	11:30
			$\bar{x}$ = 18.94	t = 1.30
			σ = 4.89	Average C.V. = 24%
			$\bar{\sigma}$ = 4.88	

Difference between means in mg CO_2 dm^{-2} hr^{-1}	Number of samples necessary from each variety$^{\delta}$
3.67 (observed)	9
2	30
1	119

†Date: April 20, 1978. Temperature: Air 13.5°C, soil 13°C. Wind: 5-10 km hr^{-1}. Light: clear 2,000 μE m^{-2} sec^{-1}.

$^{\delta}$Number of samples necessary to show that the means of two varieties are different at α= .05 with the observed standard deviation of 4.88 mg CO_2 dm^{-2} hr^{-1}.

Table 16. Rates of photosynthesis of TAM W-101 and Triumph 64 after onset of water stress but before visible symptoms were observed.

Variety	Leaf no.	Change in CO_2 per 30 sec. at 350 ppm	Rate of photosynthesis mg CO_2 dm^{-2} hr^{-1}	Time
TAM W-101	1	32.11	2.50	9:15 A.M.†
	2	27.65	1.89	10:15
	3	- 7.11	-1.19δ	11:15
Triumph 64	1	79.52	8.03	9:45
	2	28.10	2.49	10:45
	3	21.31	1.95	11:45
			$\bar{\bar{x}}$ = 2.61	
			$\hat{\sigma}$ = 2.99	

†Date: April 23, 1978. Temperature: Air 22.5°C, Soil 13°C. Wind: Calm. Sunlight: Clear 2,400 μE m^{-2} sec^{-1}. Plant Growth Stage: Flag leaves appearing on Triumph 64 but not TAM W-101. Moisture status: Last major rain was April 10.
δDenotes net respiration rather than net photosynthesis.

Table 17. Rate of photosynthesis of one leaf from 18 cultivars under water stress conditions.

Variety	Change in CO_2 per 30 sec. at 350 ppm	Rate of photosynthesis mg CO_2 dm^{-2} hr^{-1}	Time
TAM W-101	0	0	10:40 A.M.†
Triumph 64	149.3	15.24	
Payne	114.3	10.21	
Osage	87.1	7.97	
Burgas 2	- 28.9	- 1.79	
Newton	187.6	13.60	
Sadovo 1	- 0.019	- 0.0012	
Plainsman V	105.9	8.77	
Scout 66	38.7	2.99	
Blueboy	69.9	4.44	
Vona	183.0	12.37	
Bordenave Puan 5	26.0	1.56	
Turkey	10.8	0.85	
Bezostaia 1	11.8	0.68	
F 23-71	228.7	17.59	
TX7162-6	- 13.7	- 1.12	
OK 722721	- 4.6	- 0.35	
OK 711248-176	11.1	1.00	2:35 P.M.
		$\bar{x}$ = 5.26	
		σ = 6.25	C.V. = 119%

Difference between means in mg CO_2 dm^{-2} hr^{-1}	Number of samples necessary from each varietyδ
3	17
2	38
1	150

†Date: April 26, 1978. Temperature: Air 25°C, soil 16°C. Wind: 5-10 km hr^{-1}. Sunlight: Clear 2000 μE m^{-2} sec^{-1}. Moisture status: Dry. Plant growth stage: Heads emerging on some varieties.

δSamples necessary from each variety to show difference between two means at α = .05 with the observed standard deviation of 6.25 mg CO_2 dm^{-2} hr^{-1}.

Table 18. Rate of photosynthesis of two cultivars found to differ in rate the previous day under water stress.

Variety	Leaf no.	Change in CO_2 per 30 sec. at 350 ppm	Rate of photosynthesis mg CO_2 dm^{-2} hr^{-1}	Time
TAM W-101	1	8.0	0.55	9:00†
	2	98.9	7.22	9:35
	3	38.9	2.93	
	4	81.2	5.69	
	5	14.0	1.05	
	6	123.2	8.77	
	7	126.8	9.00	
	8	2.9	0.20	
	9	128.4	10.25	
	10	103.0	7.25	
	11	52.0	3.99	12:40
			$\bar{x}$ = 5.17	
			σ = 3.63	C.V. = 70%
Payne	1	30.3	2.54	9:45
	2	166.2	12.52	
	3	126.4	10.84	
	4	50.4	4.16	
	5	36.1	4.45	
	6	29.1	2.60	
	7	133.0	13.94	
	8	16.1	1.33	
	9	2.7	0.21	
	10	10.9	0.89	12:50
			$\bar{x}$ = 5.12	
			σ = 5.35	C.V. = 96%
			$\bar{\sigma}$ = 5.15	

Difference between means in mg CO_2 dm^{-2} hr^{-1}	Number of samples necessary from each variety δ
3	10
2	21
1	83
0.03 (observed)	91,562

†Date: April 27, 1978. Temperature: Air 23°C, soil 15°C. Wind: 7-15 km hr^{-1}. Sunlight: Clear 2,000 μE m^{-2} sec^{-1}.
δSamples necessary from each variety to show difference between two means at α = .05 with the observed standard deviation of 5.15 mg CO_2 dm^{-2} hr^{-1}.

difficulty because of changing environmental conditions. General daily observations on the rate of photosynthesis were easy to make. However, obtaining enough samples to prove statistical differences between genotypes was hindered most by leaf to leaf variation within genotypes.

CHAPTER V

DISCUSSION

Clegg and Sullivan (4) introduced the method of measuring photosynthesis by using syringes to collect CO_2 samples in the field. They developed a chamber to be used on sorghum leaves. To adapt this system for use on smaller wheat leaves, the size of the chamber had to be greatly reduced. To facilitate the removal of two air samples from this smaller leaf chamber, an auxiliary air supply was attached. The data presented here has shown that the air can be mixed and an initial sample obtained which is representative of the air within the chamber. It has also been shown that while photosynthesis is proceeding, no diffusion of CO_2 takes place from the auxiliary air supply into the leaf chamber. Finally it was shown that no air from the reserve supply is obtained by the second sample drawn from the chamber. These factors along with the precision of the infrared analyzer allow measurement of the rate of photosynthesis with relatively small error. The observed standard deviation between many measurements of the same leaf was found to be 0.30 mg CO_2 $dm^{-2}hr^{-1}$ as compared to a standard deviation of 1.76 mg CO_2 dm^{-2} hr^{-1} between different leaves of plants growing under growth chamber conditions. This shows that the system is relatively precise in its ability to measure the rate of photosynthesis per leaf area.

The primary advantage of this system is its simplicity and ease of operation. It eliminates the necessity of moving the infrared analyzer to the field or the use of $^{14}CO_2$ to make measurements under natural conditions. Because of these advantages, it is suggested that this method has great potential in measuring photosynthetic plant responses to changing environments.

With the adaptation of the apparatus and development of the necessary techniques, study of the relationship between genotypic photosynthesis and yield in wheat has been initiated. From published comparisons it is obvious that Osage has a yield advantage under many growing conditions. Our comparison of rates of photosynthesis in the growth chamber showed that this variety did not have a higher rate of photosynthesis per leaf area. It was found that it did have longer leaves and because of this a greater leaf area. The fact that Osage also has longer leaves in the field was shown to verify the growth chamber findings. Triumph 64 was found to have the smallest leaf area of plants grown in the growth chamber and the shortest leaves of the same cultivars in the field. In the five year comparisons, Triumph 64 had the lowest yield of the varieties compared for photosynthesis. In the growth chamber study Osage fixed the most CO_2 per leaf because it had the largest leaf area due to its longer leaves. Triumph 64 fixed the least CO_2 per leaf because it had the smallest leaf area.

A wheat ideotype as described by Donald (1968) is characterized by a short, strong stem, small erect leaves, and a single culm. These concepts were developed to apply to plants under high populations in the climate of Northern Europe and would apply to plants

under somewhat favorable conditions in terms of water relations and duration of photosynthetic area. The advantage of smaller, more erect leaves was thought to be derived from their ability to allow light to reach lower leaves and leaves of other plants especially during the grain filling period. With respect to the carbon fixed late in the plants' life cycle, Austin, et al. (1977) found that 48 per cent of the final grain dry weight was contributed by photosynthesis after anthesis. This suggests that increases in yield under such conditions may be obtained by increasing photosynthetic area duration and this should be emphasized in breeding programs. Likewise, Rawson and Evans (1971) showed that stems could contribute as little as 2.7 per cent of the final grain weight.

Morphological characteristics related to high wheat yields under dry-land conditions have also suggested small, narrow, semi-erect leaves (33).

Austin and co-workers (1976) studied two winter wheat genotypes with contrasting leaf postures of erect and lax leaves. They found that over the grain filling period, the net carbon dioxide fixation during the daytime was nearly always greater for the erect leaf genotype than the lax leafed one. As predicted, in general, a greater proportion of the fixation took place in the lower leaves of the erect genotype than those of the lax leafed type. A slightly higher leaf area index and slower senescence of its lower leaves accounted for the erect leafed genotype's advantage in canopy photosynthesis. However, they found that over the grain filling period, more dry matter was lost from the stems of the lax leafed genotype than those of the erect type. They suggested that the shortfall of assimilate

for grain filling was met, at least in part, by translocation of materials from the stems. Furthermore, their depletion in the lax leafed type made up for the lower contribution from current assimilation in this genotype. The genotypes were studied two years. Normal rainfall was present the first year and drought conditions (for England) prevailed the second year. Yields were not significantly different either year. A small observed advantage accompanied the erect type in the normal year, but the observed yield advantage accompanied the lax leafed genotype in the year when drought stress occurred.

Formal models to express leaf area relationships were developed by Monteith (1965) and DeWitt (1965). Each of the models predict that with leaf area indices higher than three to four, photosynthesis will be greater in canopies with erect than with lax leaves. However, at lower leaf area indices the situation will be reversed. Thus, in early stages of growth, canopy photosynthesis can be expected to be higher in the lax than the erect leaf types.

Austin et al. (1976) state that in most winter wheat crops the leaf area index is greater than three only for a few weeks before anthesis and during the early stages of grain growth. Thus, they say only a small portion of the assimilate produced when leaf area indices are greater than three will be used directly for grain growth.

Biscoe et al. (1975) studying barley showed that the rate of net photosynthesis of the whole canopy was at its maximum three weeks before anthesis and declined to harvest time.

These studies suggest that the photosynthetic advantage would be with the lax leafed types up to about three weeks before anthesis.

It follows from this that if conditions were poor for photosynthetic activity after this time, an erect leafed type would not be able to exploit its proposed advantage during the grain filling period. If it were also true that a lax leafed type could utilize its stored reserves for grain filling and the erect type could not, then the net result would be higher grain yield for the lax than the erect leafed type.

Gallagher et al. (1975) found that in barley up to 70 per cent of the grain weight could be derived from the stems.

Hot, dry conditions, not conducive to high photosynthetic activity are common in the Southern Great Plains during the grain filling period. Environmental conditions favorable to the development of high leaf area indices and thus advantageous to the erect leafed genotypes are not the norm.

The cultivar Osage with long, large leaves is consistantly higher yielding in Oklahoma than Triumph 64 with short, small leaves. It is the conclusion of the author that this occurs because Osage has larger leaves during the middle stages of plant growth when growing conditions in Oklahoma are favorable for photosynthetic activity. Furthermore, the author suggests that the excess CO_2 fixed during this period can later be mobilized for grain filling when conditions for high photosynthetic activity are not present.

Failure to correlate unit rates of photosynthesis of crop varieties with growth rates is the rule rather than the exception (23). Potter and Jones (1977) stress the importance of leaf area partitioning as a component of growth. They found that relative growth rates were closely correlated with leaf area partitioning in

seven of nine species studied. Furthermore, the net assimilation rate times leaf area partitioning was shown to be equal to the relative leaf area expansion rate.

The conclusion drawn from results of my study is that area per leaf is more important in determining total leaf photosynthesis than is rate of photosynthesis per area. The data indicate that a higher area per leaf can be obtained by increasing leaf length rather than leaf width.

In the context of the findings of the above researchers the suggestion is made that wheat yields may be increased in the Southern Great Plains by breeding for higher area per leaf and emphasizing storage capacity before anthesis.

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APPENDIX

CALCULATION OF RATE OF CARBON DIOXIDE EXCHANGE BY THE TWO SYRINGE METHOD

Example of calculations to determine rate of CO_2 exchange from two samples of air:

Given: sample #1 = 400 ppm

sample #2 = 225 ppm

constant conversion factor = 0.01090 mg CO_2 dm^{-2} hr^{-1}

volume of chamber = 20.5 cc

area of leaf = 7.25 cm^{-2}

time of illumination = 0.5 min.

Formula: $\frac{(\text{ ppm})(C)(V)}{(A)(T)} = \text{CER}$

Calculation: $\frac{(400 \text{ ppm} - 225 \text{ ppm})(0.01090 \text{ mg} CO_2 dm^{-2} hr^{-1})(20.5 \text{ cc})}{(7.25 \text{ cm}^{-2})(0.5 \text{ min})}$

= 10.88 mg CO_2 dm^{-2} hr^{-1} for the CO_2 level of 312.5 ppm.

Procedure to convert this to the standard CO_2 level of 350 ppm:

Mean = $\frac{\text{Sample \#1 + Sample \#2}}{2}$

= 312.5 ppm mean

Difference = Sample #1 - Sample #2

= 175 ppm difference

Portion Removed = $\frac{\text{difference}}{\text{mean}}$

$\frac{175 \text{ ppm}}{312.5 \text{ ppm}} = 0.56$

Parts removed at 350 ppm = portion removed x 350 ppm

0.56 x 350 ppm = 196 ppm

CER at 350 ppm = 196 ppm replaces 175 ppm in the formula

= 11.79 mg CO_2 dm^{-2} hr^{-1}.

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