PHOTOSYNTHETIC RATES IN PLANTS AS RELATED TO STAGE OF DEVELOPMENT, POSITION IN CANOPY, AND WATER STRESS

BY

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B. S., KANSAS STATE UNIVERSITY, 1971

A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1974

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INTRODUCTION

The $^{14}CO_2$ technique of measuring photosynthesis appeared to be the method best suited to our study because of its low cost and portability. However, the two field techniques described in the literature were not satisfactory for our study. The best features of the two techniques plus additional ideas were incorporated to produce the $^{14}CO_2$ technique described in Chapter I.

Photosynthesis is a major determinant in crop yield, but much of our knowledge is based on laboratory experiments under narrowly defined and often unnatural conditions. Most photosynthetic measurements in the field are made using transparent chamber-infrared gas analyzer systems. This type of system is expensive, difficult to move, and has a sampling time of ten to fifteen minutes. $^{14}CO_2$ techniques do not have these disadvantages and we were able to develop and test a simple model for predicting total plant photosynthesis in a sorghum canopy (Chapter II).

Photosynthetic rates in soybeans are influenced by many factors, including variety, preconditioning to light levels, and temperature. Researchers have reported that reduction of available soil moisture reduced shoot growth, and photosynthetic rates in tissue slices. We measured photosynthetic rates in water-stressed and nonstressed soybeans to observe interactions among water-stress, physiological age, and photosynthesis. Canopy and yield data were also correlated with water stress and photosynthesis (Chapter III).

CHAPTER I

AN IMPROVED RAPID FIELD METHOD FOR MEASURING PHOTOSYNTHESIS WITH $^{14}CO_2$

D. G. Naylor and I. D. Teare

AN IMPROVED RAPID FIELD METHOD FOR MEASURING PHOTOSYNTHESIS WITH $^{14}CO_2$[1/]

D. G. Naylor and I. D. Teare[2/]

ABSTRACT

A portable field technique that one man can operate to measure photosynthesis using $^{14}CO_2$ was developed. The system's solenoid on-off air flow switch driven by an electronic timer eliminates human error in judging exposure times. The miniature photosynthesis chamber by design ensures adequate ventilation of the air flow through the chamber. To prepare it for scintillation counting the $^{14}CO_2$ exposed leaf sample is digested in an organic solubilizer. The method has been successfully used to determine photosynthetic rates of different varieties and/or treatments on the same variety. Measured photosynthetic rates were comparable with those measured by infrared gas analyzers.

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INTRODUCTION

Although the basic technique of measuring photosynthetic rates by $^{14}CO_2$ has been worked out, the present techniques have received relatively little attention. Admittedly, errors arising from isotope discrimination and dilution of $^{14}CO_2$ and $^{12}CO_2$ mixtures by respiratory $^{12}CO_2$ limit $^{14}CO_2$ techniques to semi-quantitative and comparative determination of photosynthetic rates rather than absolute rates (Sesťák et al., 1971). However, in many experiments, semi-quantitative and/or comparative photosynthetic rates are sufficient. The portability, relatively low cost, and ease and quickness of sampling in $^{14}CO_2$ techniques are definite advantages in many experiments.

After evaluation of two field $^{14}CO_2$ techniques (Incoll and Wright, 1969; Shimshi, 1969) a new technique was developed which incorporated new ideas plus the best features of the two foregoing techniques.

Experience indicated that the technique developed by Shimshi had problems in both leaf exposure and leaf digestion. We had problems with leaks developing in the tyre valve seal and in reproducability of exposure times. The digestive technique was tedious and $^{14}CO_2$ leakage from the scintillation bottle was suspected during autoclaving as photosynthetic rates were abnormally low.

The technique proposed by Incoll and Wright is good for tobacco with most of their stomata on the lower leaf surface. However, most crop plants have a good portion of their stomata on the upper side of the leaf and some even have a majority of their stomata on top of the leaf. Thus, the idea of exposing only the bottom side of the leaf to

$^{14}CO_2$ is questionable for most plants. Also, the problem of timing errors (as with Shimshi) is suspected.

The technique proposed in this paper is designed for one man operation (not two as in the above techniques); both sides of leaf (top and bottom) are exposed to $^{14}CO_2$ (slight modification can limit exposure to one side if desired); timing errors are reduced by controlling the on-off flow of the $^{14}CO_2$-$^{12}CO_2$ gas mixture with an electronic timer and solenoid; and flow rates are variable and optimum rates can be determined experimentally for individual plant species in relation to their differences in leaf surface and photosynthetic rates.

Description of Technique

The technique involves 3 basic operations: exposing leaves to $^{14}CO_2$, obtaining and assaying a sample from the exposed area, and evaluating the assay.

Exposure

The apparatus (Fig. 1) used to expose a leaf segment to $^{14}CO_2$ can be divided into (Fig. 2):

A. $^{14}CO_2$ gas supply: The radioactive gas is purchased in a small compressed-gas bottle[3/] which has a pressure regulator, with an outlet needle valve. An additional needle valve may be placed in the flow line to give finer adjustment.

[3/] Matheson Gas Products, East Rutherford, New Jersey.

B. Flowmeter (0-200 ml/min): Used to measure gas flow rates.

C. Solenoid and electronic timer: A small solenoid[4/], used to control the on-off supply of $^{14}CO_2$ to the chamber, is normally closed; it is opened by an electronic timer; the timer is driven, as the solenoid, by a small lead-acid battery[5/]. The timer circuit is shown in Fig. 3.

D. Photosynthesis chamber (Fig. 4, 5): Constructed with two pieces of 1 cm clear plexiglass (A). The moleskin gaskets (B) have a thin layer of RTV silicon rubber. An 0.6 cm butt hinge (C) connects the two pieces of plexiglass. Two conduit holders (D) operate the scissor-action that opens and closes the chamber. A small spring (E) keeps the chamber normally in a closed position.

Six-tenth cm O.D. tygon tubing (F) is used for air lines. RTV (G) is used to seal the tygon tubing to the holes in the plexiglass leading to the chamber. The solenoid (H) is fastened to the plexiglass by two springs (I) with a hook (J) at each end.

E. Absorbing column: The lime-soda absorbing column, made from 3.2 cm I.D. plexiglass tubing, is 23.5 cm long.

[4/] Peter Paul Electronics Co., Inc., 251 Whiting Street, New Britain, Conn. Series 50, Model 52.

[5/] Globe-Union Inc., 5757, North Green Bay Avenue, Milwaukee, Wisc.

Obtaining and Assaying Sample

Obtaining sample: The exposed area of the leaf is marked by putting a zinc-oxide-glycerol mixture on the upper gasket before placing the chamber over the leaf. Using a suitable leaf disc punch (Shimshi, 1969; Incoll and Wright, 1969) a segment is punched out of the center of the exposed area.

Assaying sample: The leaf disc is placed in a scintillation vial containing 1 ml of 0.6 N solution of a surface-active organic base in toluene[6/] and allowed to digest overnight. The solution is bleached with 1 ml of a saturated solution of bensoyl peroxide in toluene. The vial is filled to 20 ml with scintillation fluid. The solution is then counted at ambient temperature with a scintillation counter.

Evaluation

Parameters used in calculating photosynthetic rates are: exposure time, sample area, counting efficiency, $^{14}CO_2$ concentration in gas, CO_2 concentration in gas, and sample counting rate.

$$P = K \times (C-B) \times T^{-1} \times A^{-1} \times E^{-1} \times \frac{44(^{12}C) + 46(^{14}C)}{46(^{14}C)}$$

where,

P = photosynthesis (mg $dm^{-2}hr^{-1}$)

[6/] Amersham/Searle Corporation, 2636, S. Clearbrook Drive, Arlington Heights, Ill.

K = .321 x 10^{-9} (conversion factor from cpm to mg $^{14}CO_2$)

C = sample counting rate (cpm)

B = background counting rate (cpm)

T = time (hr)

A = area (dm^2)

E = counting efficiency (decimal)

12_C = $^{12}CO_2$ in gas (ppm)

14_C = $^{14}CO_2$ in gas (ppm)

RESULTS AND DISCUSSION

Enclosing a portion of a leaf in a chamber changes its environment. Therefore, to minimize changes, exposure time should be as short as possible, though not so short as to permit disproportionate errors in "dead time" and variations in timing. The use of an electronic timer reduces timing errors and facilitates experimental determination of the optimum exposure time. The solenoid requires only about 0.01 seconds to open or close, thus minimizing dead time.

Exposure times of 15, 20, 30, and 45 seconds were used to measure the significance of exposure time on wheat, sorghum, and soybeans (Table 1). Sestak et al. (1971) has stated that 15 seconds is about the minimum exposure time allowable if significant "dead time" errors are to be avoided. We found that exposure times of 15 to 20 sec apparently produced optimum rates, as opposed to lengthier exposure (Table 1), except for sorghum. The highest photosynthesis rate in sorghum (45 seconds) however, was not significantly higher than the 20-sec exposure.

In wheat and soybeans, the 45-sec exposure produced the lowest photosynthesis rates.

Flow rates of gas through the photosynthetic chamber are more important than exposure times. Adequate flow rates must be maintained to ensure that CO_2 depression causes no decrease in photosynthesis and that no large boundary layer resists CO_2's diffusion into the leaf.

A photosynthetic rate of 50 mg $dm^{-2}hr^{-1}$ will result in absorption of about 16% of the available CO_2 (ambient (CO_2) - 350 ppm) or an average CO_2 concentration about 25 ppm below ambient at a flow of 150 ml/min.

Photosynthesis increased with increased flow rate through the chamber, then leveled off (Fig. 6). The curve's shape probably resulted from boundary-layer resistances to CO_2 transfer. Because adequate ventilation is important, we designed the chamber to spread the air flow across the chamber width. The optimum flow rate needs to be determined for each crop when measuring photosynthesis because the leaf surface may tend to resist CO_2's transfer from the atmosphere to the photosynthetic cells of the leaf. Soybean, with a hairy leaf, has a higher optimum flow rate for photosynthesis than do wheat, sorghum, and corn (Fig. 4). For correct comparable measures, the same flow rate should be used each time within genotypes.

This technique proved to be a reliable, easy to use, one-man technique. Sampling time is short, the system portable and rugged. If consistent exposure times and flow rates are used, the technique can be a valuable tool for comparing photosynthetic measurements between different treatments in an experiment.

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3. Shimshi, D. 1969. A rapid field method for measuring photosynthesis with labeled carbon dioxide. J. of Expl. Bot. 20:381-401.

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Table 1. Variation of photosynthetic rate with exposure time at a flow rate of 150 ml/min.

Time (sec)	15	20	30	45
Soybean	33.1	28.8	28.1	26.9
Sorghum	47.1	43.0	39.8	46.9
Wheat	16.5	17.3	18.1	14.8

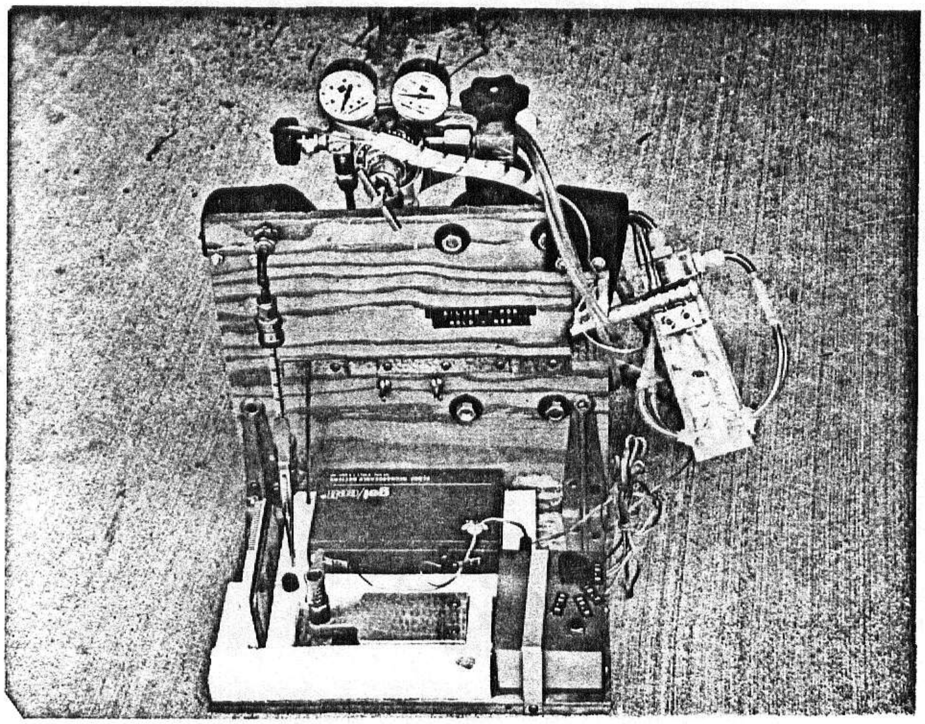

Fig. 1. Front view of assembled apparatus.

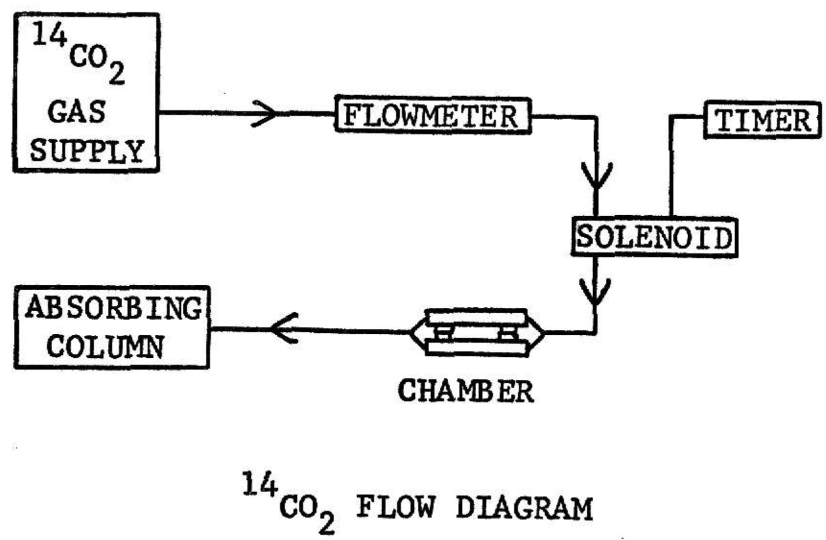

Fig. 2. Components of exposure-apparatus

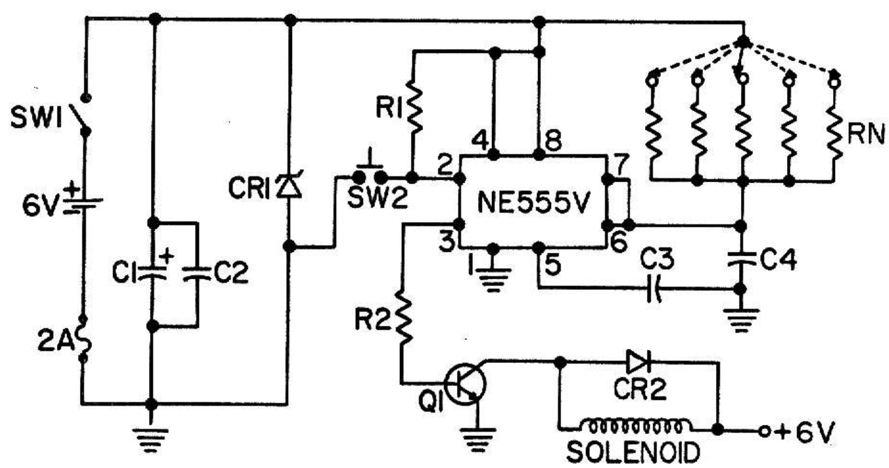

Fig. 3. Electrical circuit for automatic timer: SW1 - Off-on switch to battery; SW2 - push button switch to start timing sequences; 2A - 2 amp fuse; C1 - .1μF; C2 - 1000μF; C3 - .01μF; C4 - 15μF; CR1 - 18v zener (1N4001); Q1 - TIP31 transistor (heat sink); R1 - 10μK; R2 - 33Ω; RN - resistor value (depends on desired time) 15s (910KΩ), 20s (1.24MΩ), 30s (1.82MΩ), 45s (2.7MΩ), 60s (3.86MΩ) (approx. resistor values).

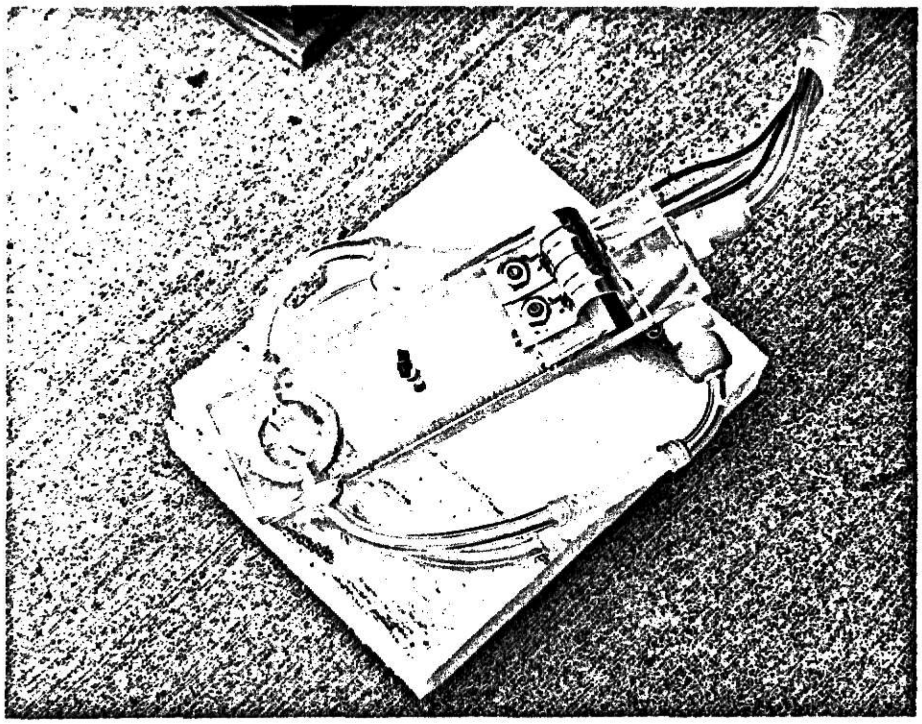

Fig. 4. Close-up view of photosynthesis chamber.

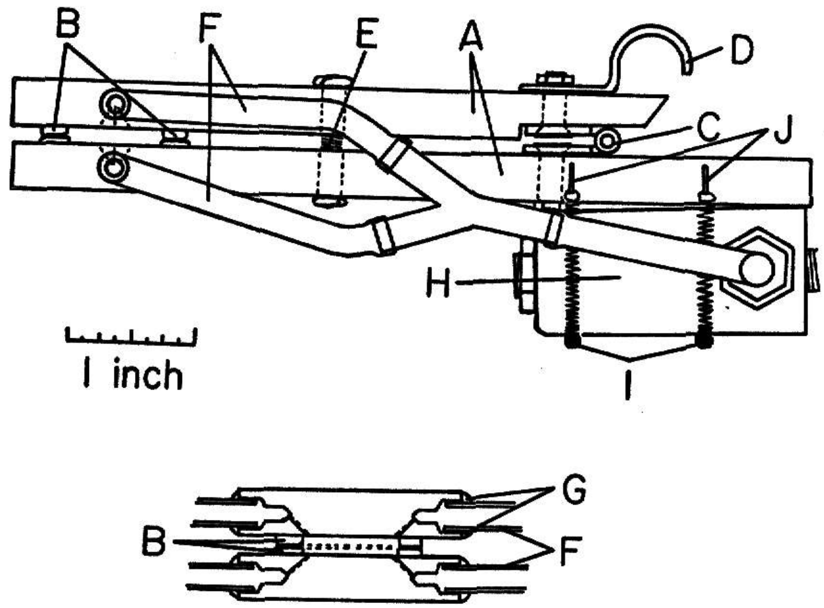

Fig. 5. Photosynthesis chamber.

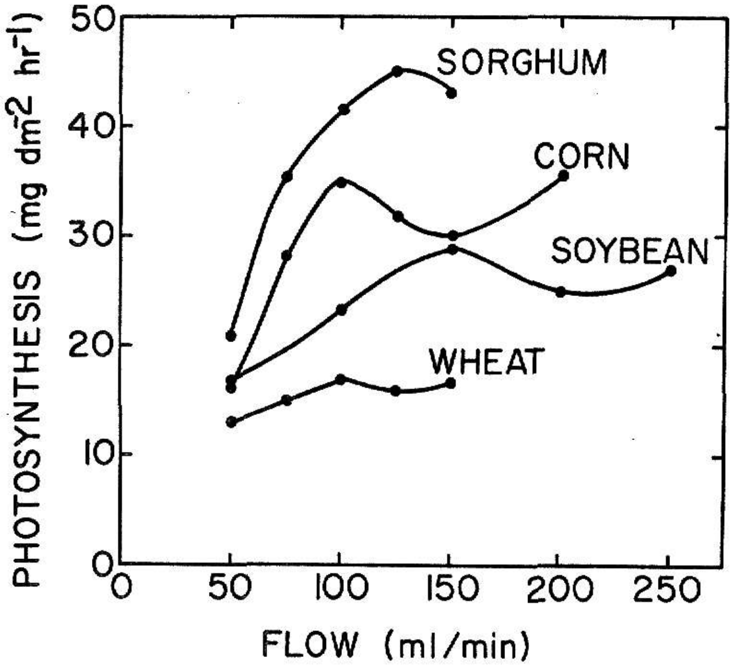

Fig. 6. Flow rate vs. photosynthesis at 20 sec exposure time.

CHAPTER II

PHOTOSYNTHESIS IN FIELD GROWN SORGHUM

D. G. Naylor, I. D. Teare, and E. T. Kanemasu

PHOTOSYNTHESIS IN FIELD GROWN SORGHUM[1/]

D. G. Naylor, I. D. Teare, and E. T. Kanemasu[2/]

ABSTRACT

Photosynthesis was measured periodically during the growing season in a sorghum canopy. Photosynthesis in the upper sunlit canopy appeared to reach a maximum at half bloom. Degree of leaf exposure to illumination and the vertical distribution of photosynthesis were determined three times in one day during half bloom (stage 6). A simple model to estimate total photosynthesis in a canopy is presented; it is based on amounts of sun and shaded leaves in the canopy and photosynthetic rates in sun and shaded portions of the canopy.

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INTRODUCTION

Photosynthesis is the final determining factor of crop yield, yet most of our knowledge of photosynthesis is based on laboratory experiments under narrowly defined, and often unnatural, conditions. Photosynthesis in the field has generally been measured either by an aerodynamic method with photosynthetic rates calculated from wind velocity and CO_2 gradients (1, 2, 4), or by monitoring the exchange of CO_2 by plants or leaves enclosed in transparent chambers (5, 8). Both techniques require elaborate instrumentation.

Materials used in radioactive carbon dioxide ($^{14}CO_2$) methods are relatively inexpensive, portable and can be used relatively easily and quickly. (6, 7, 10).

We measured photosynthesis at various times during the growing season (to see if photosynthesis varied significantly with changes in physiological age or physical location in the canopy) and photosynthetic activity of sun and shade leaves in the sorghum canopy (to obtain a basis for a simple method to estimate total photosynthesis in a canopy).

MATERIALS AND METHODS

Sorghum (*Sorghum bicolor* (L.) Moench cv. Pioneer #846) was planted June 1, 1971, and June 1, 1973, in a 1-ha field, 11 plants/meter, in NS rows (91 cm apart) in an alluvial silt-loam soil on the Evapotranspiration Research Field (14 km south of Manhattan, Kansas).

Photosynthetic rates were measured using techniques by Shimshi (7) in 1971, with one modification: we used commercially-prepared bottled air[3/] containing 277 ppm CO_2 (with 6% of the CO_2 being $C^{14}O_2$) instead of laboratory-prepared air. In 1973 we used the Naylor and Teare (6) method. The latter technique is simpler to operate, more precise and shows higher photosynthetic rates than the Shimshi technique does.

We sampled leaves half way between the tip and base, and half way between midrib and leaf edge. Sun leaves were sampled in an area normal to the sun. "Shaded leaves" were usually shaded by upper leaves in the canopy. The shaded leaves were sampled normal to the ground.

Visual estimates of percentages of individual leaves in full sunlight and in shade were made when the plants were at a physiological growth stage 6.3 (Aug. 4, 1971) at approximately complete anthesis (12). Estimates were made on three plants selected as representative of the field.

Relative light intensities at selected heights in the canopy were measured on a clear, sunny day at 12:30 and 15:00 July 30 with a Spectroradiometer[4/].

RESULTS AND DISCUSSION

Seasonal variation:

Photosynthetic rates were measured on the upper, collared, sunlit

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[3/] Matheson Gas Products

[4/] Instrumentation Specialties Company, Inc.

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leaves in the sorghum canopy nine times during the growing season -- stages 4-9. Photosynthesis was lower during early growth, peaked at stage 6 (half bloom) and then decreased less abruptly than it rose (Figure 1).

Watson (11) suggests that photosynthetic products building up faster than they can be removed sometimes limits photosynthesis. However, maximum photosynthesis occurs after the canopy is fully developed, so the reduced rates during early season suggest: (1) a small sink for photosynthesis products before head filling, (2) a not yet fully developed transportation system that limits the rate products are moved from the leaf, or (3) immature leaves limiting photosynthesis[5/].

Profile variation:

Photosynthetic rates are about 6 times greater in sun leaves than in shaded leaves (Figure 2A), which reaffirms observations on other crops (3, 9) that the upper canopy contributes heavily to photosynthate produced by a plant. Observing photosynthetic rates in the upper canopy over time should indicate photosynthetic activities of the whole plant.

Light intensity in the canopy's shaded areas (measured at 480 and 740 nm) was only about 5% of full sun intensity, so photosynthetic rates are low in the shaded leaves (Figure 2A). Photosynthetic rates in both sunlit and shaded portions of the canopy were fairly constant (Figure 2A), therefore photosynthetic rates in the canopy could be designated as

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[5/]Photosynthesis in soybean leaves increases as leaf expands to fully expanded.

either in sun or shaded leaves[6/].

Modeling:

Using photosynthetic contributions to the plant as sun or shade produced, one can calculate the relative portions contributed when leaf area in the sun and leaf area in the shade are known (Table 1).

Figure 2B shows percentages in the sun of each leaf (upper surface) in a sorghum canopy at three different times during a single day. Leaf area for individual leaves (stage 6) is shown in Figure 3.

Multiplying percentage of leaf in sun by leaf area gives leaf area in the sun; the remaining percentage is the shaded area. The product of the total sun-leaf area and sun leaf-photosynthetic rate is the contribution of the sunlit portion of the canopy to the total photosynthate produced by the plant. A similar calculation gives the contribution from the shaded portion of the canopy.

Data in Table 2 were taken at stage 6. The shaded portion of the canopy then contributed about 30% of the total photosynthate. Incorporating plant population density (12 plants/meter^2 ground surface) gave a photosynthetic measurement (Table 1)on a ground area basis of 95.6

[6/]Additional observations on rates of photosynthesis were determined August 12 and 13, 1971, using an open-chamber system and infrared, gas analysis techniques described by Sij et al. (8). Average net photosynthesis of all leaves in the canopy was 17.8 $mgCO_2dm^{-2}hr^{-1}$. The net photosynthesis of the upper 4 leaves was 34.3 $mgCO_2dm^{-2}hr^{-1}$; remaining leaves 11.56 $mgCO_2dm^{-2}hr^{-1}$. Removing the upper 8 leaves to expose to direct sunlight made average net photosynthesis 19.1 $mgCO_2dm^{-2}hr^{-1}$. The lower leaves were not so high as those of the upper sunlit leaves, our data indicate that low light intensity is a primary factor in reducing photosynthesis of lower leaves and that lower leaves are capable of much greater photosynthesis.

$mgCO_2dm^{-2}hr^{-1}$, which is consistent with data (90.0 $mgCO_2dm^{-2}hr^{-1}$) obtained on the same plots using a plexiglass, open-chamber system (8).

This simple model for estimating total photosynthesis in a sorghum canopy is quick, easy, and inexpensive but gives meaningful results, especially for comparing photosynthesis among treatments or experiments.

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Table 1. Sample Calculations:

Leaf area (dm^2) x % leaf in sun = Leaf area in sun (dm^2)

Leaf area (dm^2) - leaf area in sun (dm^2) = Leaf area in shade (dm^2)

Leaf area in sun (dm^2) x Average sun photosynthetic rate (mg CO_2 $dm^{-2}hr^{-1}$) = Photosynthesis of sun portion of leaf (mg CO_2 hr^{-1})

Leaf area in shade (dm^2) x Average shade photosynthetic rate (mg CO_2 $dm^{-2}hr^{-1}$) = Photosynthesis of shade portion of leaf (mg CO_2 hr^{-1})

Photosynthesis of sun portion (mg CO_2 hr^{-1}) + Photosynthesis of shade portion of leaf (mg CO_2 hr^{-1}) = Total photosynthate of leaf (mg CO_2 hr^{-1})

Σ Total photosynthate of leaf (mg CO_2 hr^{-1}) = Total photosynthate for plant (mg CO_2 hr^{-1})

Total photosynthate for plant (mg CO_2 hr^{-1}) x Number plants per dm^2 = Photosynthesis per dm^2 ground area (mg CO_2 dm^{-2} hr^{-1})

Table 2. Estimated contributions to total plant photosynthate by each leaf at 13:00 CDT, July 31.

Leaf number	Leaf area (dm^2)	% leaf in sun	Leaf area in sun (dm^2)	Photosynthesis* of sun portion $mg_{CO_2}\ hr^{-1}$	Photosynthesis** of shaded portion $mg_{CO_2}\ hr^{-1}$	Total photosynthesis for leaf $mg_{CO_2}\ hr^{-1}$
16 (Top)	1.02	43	.44	25.9	5.3	31.2
15	2.86	63	1.80	106.0	9.6	115.6
14	2.80	32	.90	53.0	17.3	70.3
13	3.56	43	1.53	90.1	18.5	108.6
12	4.30	27	1.16	68.3	28.6	96.9
11	4.64	33	1.53	90.1	28.3	118.4
10	4.40	13	.57	33.6	34.9	68.5
9	3.70	20	.74	43.6	26.9	70.5
8	2.96	15	.44	25.9	23.0	48.9
7	2.19	17	.37	21.6	16.6	38.2
6	1.36	0	0	0	12.4	12.4
5	1.36	0	0	0	12.4	12.4
4	.60	0	0	0	5.5	5.5
Total for plant	34.17		9.24	558.1	239.3	797.4

*Average sun photosynthetic rate = 58.9 ± 8.9 $mgCO_2dm^{-2}hr^{-1}$ (average 10 measurements on sunlit leaves

**Average shade photosynthetic rate = 9.1 ± 1.5 $mgCO_2dm^{-2}hr^{-1}$ (average 13 measurements of shaded leaves

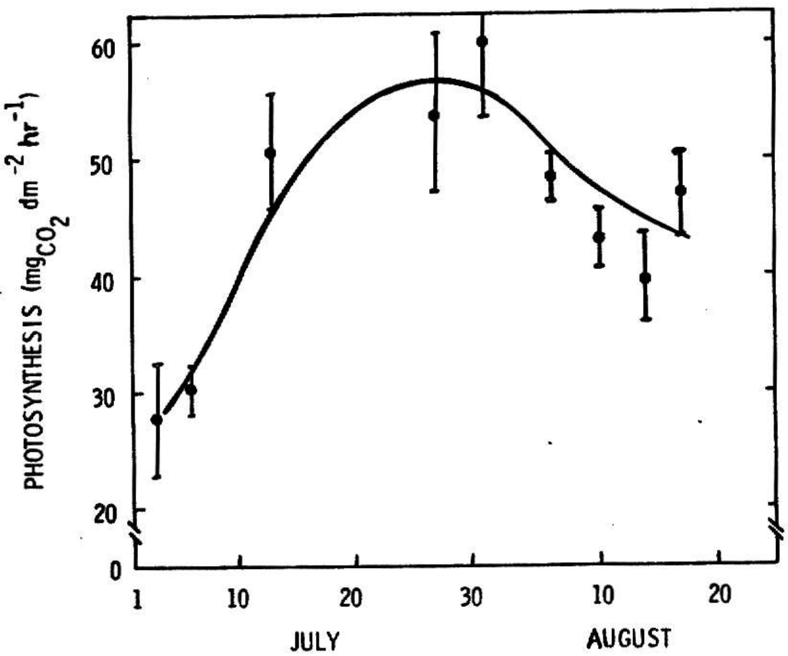

Figure 1. Photosynthetic measurements from upper sunlit leaves of sorghum at indicated times during the growing season.

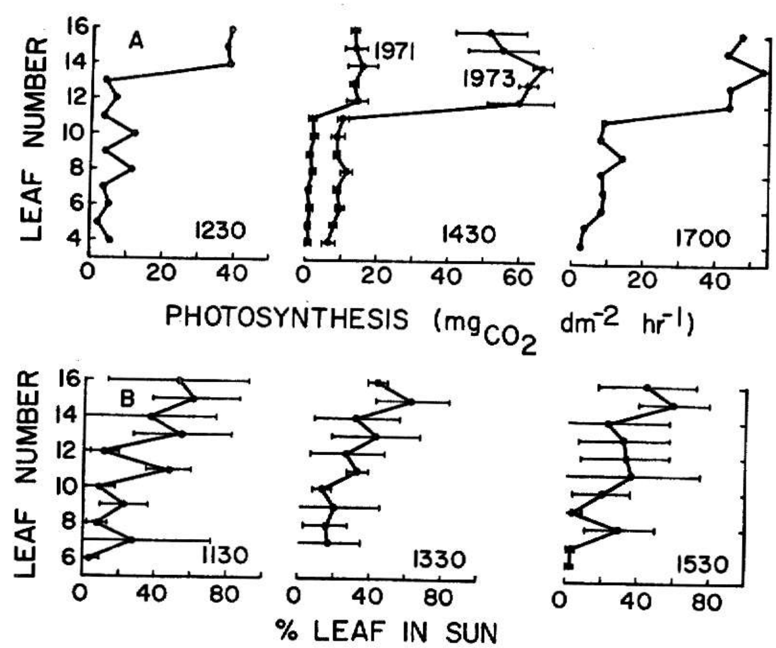

Figure 2. Photosynthesis measurements (A) and percentages of leaf in sun (B) at three times July 31.

CHAPTER III

VARIATIONS IN PHOTOSYNTHESIS OF SOYBEAN UNDER NONSTRESSED AND STRESSED CONDITIONS

D. G. Naylor and I. D. Teare

VARIATIONS IN PHOTOSYNTHESIS OF SOYBEAN UNDER NONSTRESSED AND STRESSED CONDITIONS[1/]

D. G. Naylor and I. D. Teare[2/]

ABSTRACT

Photosynthesis was measured in soybean during the growing season in open field under nonstressed conditions and in drainage lysimeters with available moisture levels depleted 40%, 60%, 80% and nearly 100% Photosynthesis in nonstressed soybeans increased during early growth, peaked at rapid-pod-growth stage (stage 6). A dip in photosynthesis occurred between stage 6 and 7 which we believe to be related to physiological age. Water stress in soybeans lowered photosynthesis, reduced shoot growth, reduced yield, and hastened maturity.

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INTRODUCTION

Various researchers have estimated net photosynthesis rate in soybean leaves to range from 8 to 65 mg CO_2 assimilated $dm^{-2}hr^{-1}$ (Bowes et al., 1972). Causes for the wide variation are associated with varietal differences (Dornhoff and Shibles, 1970, Hanway and Weber, 1971), preconditioning of plants to light levels during early growth, which influences subsequent net photosynthesis (Bowes, et al., 1972) as does temperature (Jeffers and Shibles, 1969), and lack of adequate soil moisture, which decreases shoot growth while increasing root growth (Read and Bartlett, 1972). We previously found photosynthetic rates related to physiological age of sorghum (Naylor et al. in process). That suggested measuring photosynthetic rates in water-stressed and nonstressed soybeans to look for interactions among water-stress, physiological age, and photosynthetic rates. Canopy and yield data also were correlated with water stress and photosynthesis.

METHODS AND MATERIALS

Soybeans (Glycine max L. cv. Calland) were grown 14 km south of Manhattan, Kansas, on an alluvial, silt loam soil.

Drought-stressed soybeans were grown under a rainout shelter in conjunction with twelve lysimeters (Teare et al., 1973) to control moisture levels. Additional soybeans were grown around the shelter to act as control plots and provide fetch. Field grown soybeans received sufficient rainfall so no moisture stress (measured as by Ψ_{leaf}) was observed in 1973. Average row density was 28 plants/meter in rows 91 cm apart.

Available water in the lysimeters was depleted to 40%, 60%, 80% and nearly 100%, with three replications each.

Soil moisture was measured using gravimetric measurements (0-30 cm) and a neutron moisture probe (30-152 cm). The lysimeters were irrigated as needed to maintain desired moisture levels, or in the nearly 100% depleted group, to keep the plants alive.

Photosynthesis was measured using the $^{14}CO_2$ technique developed by Naylor and Teare (1974). The measurements were taken periodically on upper fully expanded leaves in relation to physiological age, as described and indexed by Hanway and Thompson (1971). Additional measurements also were taken in relation to degree of leaf expansion on expanding leaves.

Stomatal resistance (Kanemasu et al. 1969) was measured on both adaxial and abaxial surfaces of soybean leaves, in the same canopy locations where photosynthetic measurements were taken.

Canopy data were taken by measuring height and width of plants on each lysimeter. An "average" plant on each lysimeter was selected and the number of leaves (trifoliates) counted. Leaflet length and width measurements were then made on four leaves (12 leaflets) in the top one third, and bottom two-thirds (i.e. 24 leaflets per plant) of the canopy. Based on previous measurements with individual soybean leaves, leaflet area was determined from length and width by

$$\text{Leaflet area} = .73 \text{ (length x width)}$$

Total leaf area for the plant was calculated from average leaflet area and number of leaves in each of two sections.

All plants on each lysimeter were harvested for yield. Each lysimeter was divided into two parts, and seed weight for each part was measured.

RESULTS AND DISCUSSION

Physiological Age: Photosynthesis of fully expanded leaves in the upper sunlit canopy of soybeans is shown as a function of physiological age in Figure 1. Photosynthetic rates increased until rapid-pod-growth stage (stage 6) then slowly decreased as the pod filled.

Between stages 6.2 and 6.5 photosynthesis seemed to dip in the lysimeter-grown soybeans (Fig. 2). Because of differences in physiological maturity when we sampled, the dip was more evident in lysimeters with water depleted 40, 60, or 80%. Stomata resistance did increase then but the closure did not correlate with leaf water potential or soil water content, indicating a physiological response rather than a drought response. We, therefore, hypothesize that reduced photosynthesis at stage 6.2-6.5 was related to physiological age of pods at the base of the leaf petiole. The pod was formed but seed had not yet developed as a sink of any great size, i.e. the overall sink had been reduced, so surplus photosynthate from the corresponding leaf resulted. Photosynthesis being reduced by insufficient sink size, and CO_2 building up in leaves could explain stomatal closure when soil and leaf water potentials were low (absolute value). This phenomenon would be localized because pods on different parts of the plant differed by developmental stages. Therefore, the dip we observed for individual leaves might not be evident if photosynthesis were measured on a canopy basis (i.e., in large photosynthetic chambers).

Profile Variations: We measured photosynthetic rates in different areas of the canopy July 6 (stage 4) and July 31 (stage 6) (see Table 1). At stage 4, plants were just beginning to bloom and the canopy was not closed (91 cm row spacing). At stage 6 plants were in rapid pod growth and the canopy was closed to form a continuous surface. During stage 6 photosynthetic rates of all leaves increased, irrespective of location in the canopy profile.

Measuring photosynthesis of leaves of nonstressed soybeans at different degree of expansion (about 25% and 50% expanded) showed rates of 6 mg $dm^{-2}hr^{-1}$ for leaves about 25% expanded and 14 mg $dm^{-2}hr^{-1}$ for leaves about 50% expanded. Rate for fully expanded leaves was 23 mg $dm^{-2}hr^{-1}$, so photosynthesis rates increased as leaves expanded. Once the leaf was fully expanded, photosynthesis seemed to stabilize or decrease (Fig. 1). As in sorghum (Teare et al., in process) we found shaded lower leaves of soybeans capable of much higher photosynthetic rates when exposed to full sunlight (Table 1), indicating that reduced light affects photosynthetic capability more than age of leaves does.

In the drainage lysimeter study, where soybeans were grown under various levels of water stress, photosynthesis rates under 40, 60, and 80% water depletion did not vary widely (Table 2) but dropped in the near 100% depletion lysimeters.

Shoot growth dropped slightly more in the 80% and 100% depleted lysimeters than in the 40 and 60% depleted lysimeters (Table 3). We think photosynthate was shunted to the root system of 80% depleted plants for increased root growth (not measured). If so, that would account for the decreased shoot growth (Read and Bartlett, 1972).

Reduction in available water reduced the average surface area per leaflet (Table 3). Reduction in number of leaves on a plant as water stress increased magnified the reduction in leaf area per plant caused by smaller leaves. However, neither leaf size nor number of leaves differed significantly between 80% and 100% depleted lysimeters.

Yield decreased as water stress increased (Table 3). Lower yields in the 40%, 60%, and 80% depleted lysimeters were attributed to reduced leaf area because photosynthetic rates of all were about the same. Yield reduction between 80% depleted and 100% depleted lysimeters were attributed to reduced photosynthesis because leaf areas were the same.

Water stress noticeably increased physiological aging in the 100% depleted lysimeters. After 80 days, control plants were about a week nearer maturity than other plants.

Severe water stress had the following effects: decreased leaflet size, fewer leaves, lowered photosynthesis, earlier maturity, and lower yield.

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Table 1. Photosynthesis (mg CO_2 $dm^{-2}hr^{-1}$) in open-field soybean at indicated canopy locations.

Canopy	Stage 4	July 31 Stage 6
Top, Sun	22.7	33.8
Middle, Sun	23.0	35.1
Middle, Shade	3.9	10.0
Bottom, Shade	1.9	3.7
Bottom, Sun	14.8	----*/

*/Canopy was closed, therefore no bottom, sun leaves

Table 2. Photosynthesis (Ph) (mg $CO_2 dm^{-2} hr^{-1}$) and physiological age (PA) of lysimeter grown-soybeans.

Moisture depletion, %		July 17	July 27	August 3	August 10	August 17
40	Ph	16.3±6.0	31.7±6.0	23.2±6.3	28.4±6.4	27.5±3.4
	PA	4.7	5.7	6.3	6.8	7.3
60	Ph	19.6±3.3	30.9±3.0	23.7±3.0	29.3±6.2	29.8±6.8
	PA	4.8	5.8	6.4	6.8	7.2
80	Ph	12.0±4.2	32.6±6.6	23.3±6.6	32.3±6.9	31.3±3.2
	PA	4.4	6.1	6.3	6.9	7.4
Control (near 100)	Ph	9.1±8.0	23.2±3.8	25.8±4.1	16.0±3.0	8.5±3.3
	PA	4.2	6.3	6.8	7.0	7.7

Table 3. Canopy and yield data for lysimeter-grown soybeans; canopy data (August 6, 1973)

Treatment	Physiol. age (stage)	Height (cm)	Width (cm)	Leaf area per leaflet (cm^2)	Leaf area per plant cm^2	Yield (gm/lysimeter)
40% Depleted	6.6	109 ± 04	85 ± 8	54.9 ± 6.0	3273 ± 950	63.7 ± 2.0
60%	6.7	105 ± 15	90 ± 9	45.1 ± 6.7	2589 ± 179	56.1 ± 3.2
80%	6.7	91 ± 04	86 ± 6	33.7 ± 3.1	1452 ± 230	38.8 ± 2.1
C 100%	6.8	91 ± 05	78 ± 8	34.3 ± 5.3	1339 ± 208	19.9 ± 1.7

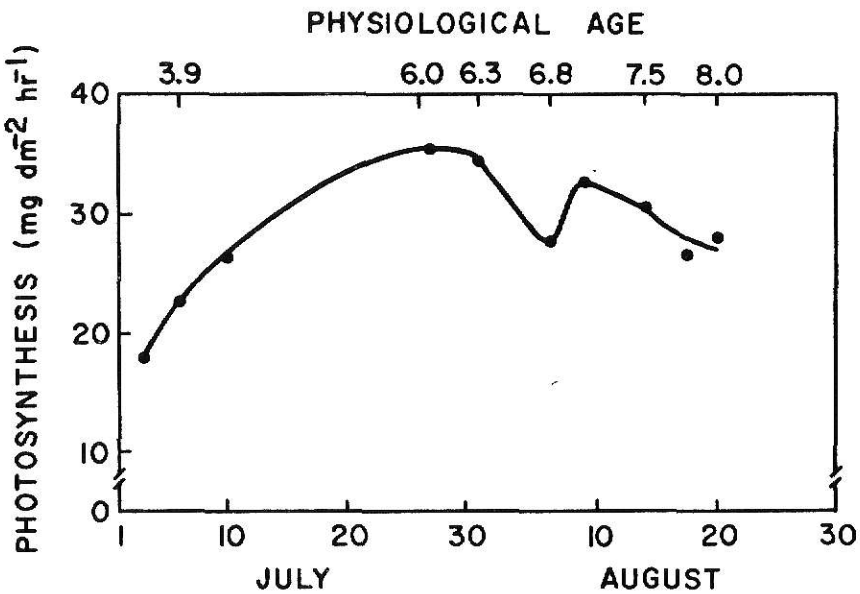

Figure 1. Photosynthesis in open field soybeans.

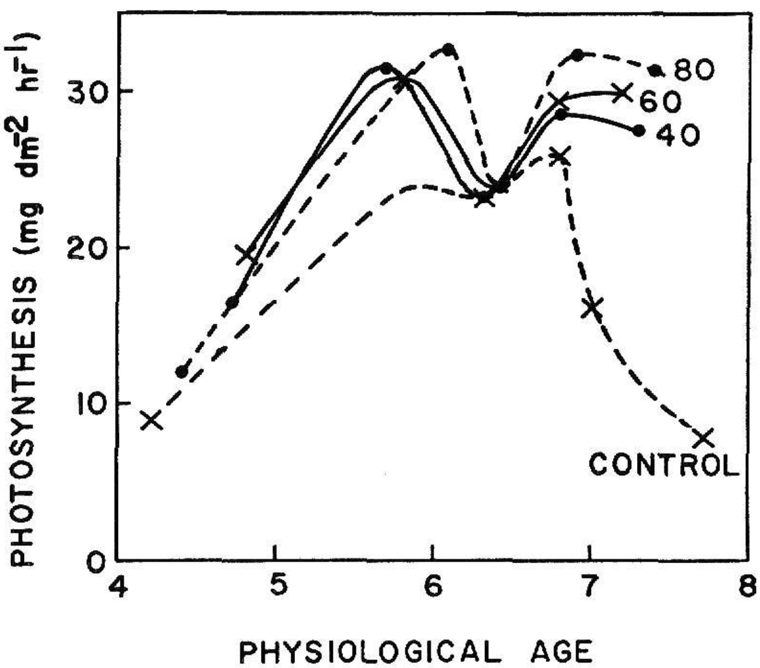

Figure 2. Photosynthesis related to physiological age in lysimeter-grown soybean.

APPENDICES

Raw Data from Research

APPENDIX A

VARIATION OF PHOTOSYNTHETIC RATE (mg $CO_2 dm^{-2} hr^{-1}$) WITH FLOW RATE AT AN EXPOSURE TIME OF 19.7 SEC. IN WHEAT, SOYBEAN, SORGHUM, AND CORN

TABLE I. WHEAT

SAMPLE	FLOW RATE (ml/min) 45	80	100	125	150
1	13.5	15.7	15.5	17.7	15.7
2	8.6	16.5	14.9	13.8	17.8
3	14.6	15.8	15.9	18.2	15.0
4	13.0	12.1	13.7	14.0	18.3
5	14.1	16.5	18.6	14.6	20.9
6	13.6	17.7	16.7	13.2	14.6
7	13.8	12.6	20.6	15.1	16.2
8	14.1	12.2	16.7	16.9	15.1
9	13.4	13.5	19.8	17.5	14.3
10	13.0	16.2	15.8	16.9	19.5
$\bar{x}$	13.0	14.9	16.8	15.8	16.7
s	1.7	2.1	2.2	1.8	2.2

TABLE II. SOYBEAN

SAMPLE	FLOW RATE (ml/min) 50	100	150	200	250
1	13.9	26.8	24.4	21.0	20.3
2	13.8	22.7	30.9	24.3	31.3
3	15.5	23.2	33.6	24.0	30.0
4	20.4	23.1	26.9	26.4	22.7
5	18.0	22.5	29.2	24.6	26.2
6	19.2	22.2	23.2	29.1	31.5
$\bar{x}$	16.8	23.4	28.0	24.9	27.0
s	2.8	1.7	4.0	2.7	4.7

TABLE III. SORGHUM

SAMPLE	FLOW RATE (ml/min) 45	75	100	125	155
1	22.4	31.9	42.1	44.2	43.4
2	28.5	35.8	35.3	47.8	43.2
3	28.9	34.2	45.8	51.2	43.1
4	14.5	31.6	25.1	45.5	40.7
5	17.2	33.7	51.4	43.1	42.1
6	13.3	44.0	49.2	38.4	45.2
$\bar{x}$	20.8	35.2	41.5	45.0	43.0
s	6.9	4.6	9.8	4.3	1.5

$\bar{x}$ = Mean
s = Standard Deviation

VARIATION OF PHOTOSYNTHETIC RATE (mg $CO_2dm^{-2}hr^{-1}$) WITH FLOW RATE AT AN EXPOSURE TIME OF 19.7 SEC. IN WHEAT, SOYBEAN, SORGHUM, AND CORN (cont'd)

TABLE IV. CORN

SAMPLE	FLOW RATE (ml/min) 50	75	100	125	150	200
1	16.5	31.2	37.7	30.2	40.4	35.6
2	12.8	33.5	36.4	35.5	31.3	34.0
3	13.4	28.0	39.3	33.7	24.5	27.4
4	19.8	23.9	34.2	29.5	23.3	32.2
5	18.8	31.9	31.4	35.0	27.2	43.0
6	15.5	20.4	30.3	26.0	34.1	41.6
$\bar{x}$	16.1	28.2	34.9	31.7	30.1	35.6
s	2.8	5.1	3.6	3.1	6.5	5.9

APPENDIX B

VARIATION OF PHOTOSYNTHETIC RATE (mg CO_2 $dm^{-2}hr^{-1}$) WITH EXPOSURE TIME AT A FLOW RATE OF 150 ML/MIN IN WHEAT, SOYBEAN, AND SORGHUM.

TABLE I. WHEAT

	EXPOSURE TIME (sec)			
SAMPLE	14.5	19.7	29.9	43.8
1	17.2	17.1	19.4	13.3
2	17.8	21.4	20.6	19.9
3	17.3	18.6	16.3	12.9
4	18.1	17.2	18.8	12.9
5	14.2	17.0	18.5	14.6
6	17.0	16.8	17.6	10.8
7	15.6	18.0	17.8	16.6
8	16.0	16.2	18.2	14.6
9	15.4	11.4*	17.3	15.5
10	16.5	13.3	16.6	16.9
$\bar{x}$	16.5	16.7	18.1	14.8
s	1.2	2.7	1.3	2.6

TABLE II. SOYBEAN

	EXPOSURE TIME (sec)			
SAMPLE	14.5	19.7	29.9	43.8
1	34.2	24.3	22.4	24.6
2	27.7	28.9	26.0	30.2
3	27.7	25.9	30.0	24.3
4	34.5	26.2	27.8	31.9
5	29.7	36.8	27.3	24.7
6	44.8	30.7	35.0	25.5
$\bar{x}$	33.1	28.8	28.1	26.9
s	6.5	4.5	4.2	3.3

TABLE III. SORGHUM

	EXPOSURE TIME (sec)			
SAMPLE	14.5	19.7	29.9	43.8
1	47.2	43.4	34.4	51.7
2	47.3	43.2	39.6	42.6
3	40.8	43.1	40.9	42.4
4	47.8	40.7	39.7	37.1
5	48.4	42.1	45.6	49.8
6	51.0	45.2	38.8	57.9
$\bar{x}$	47.1	43.0	39.8	47.8
s	3.4	1.5	3.6	8.1

APPENDIX C

PHOTOSYNTHETIC MEASUREMENTS (mg CO_2 $dm^{-2}hr^{-1}$) FROM UPPER SUNLIT LEAVES OF SORGHUM DURING THE GROWING SEASON.

SAMPLE	JULY 3	JULY 6	JULY 13	JULY 27	JULY 31	AUGUST 6	AUGUST 10	AUGUST 14	AUGUST 17
1	26.7	27.8	54.3	55.8	53.7	46.3	43.4	33.3	50.1
2	30.0	31.6	52.7	59.7	63.7	50.6	43.2	36.2	40.6
3	36.8	31.7	55.5	45.5	38.7	48.8	43.1	42.1	48.5
4	21.7		50.6		55.7	48.7	40.7	44.3	48.7
5	23.9		42.7		68.2	47.7	42.1	38.6	
6			48.5		64.3		45.2	43.0	
7					64.1				
8					62.1				
9					66.3				
10					52.4				
$\bar{x}$	27.8	30.4	50.7	53.7	58.9	48.4	43.0	39.6	47.0
s	5.9	2.2	4.7	7.3	8.9	1.6	1.5	4.3	4.3

APPENDIX D

PERCENTAGE OF LEAF IN SUN AS ESTIMATED ON JULY 31 IN A SORGHUM CANOPY.

TABLE 1. 11:30 A.M.

	SAMPLE #				
LEAF #	1	2	3	$\bar{x}$	s
16(top)	90%	60%	10%	53%	40%
15	90	40	60	63	25
14	10	80	20	37	38
13	80	25	60	55	28
12	0	20	10	10	10
11	60	35	50	48	13
10	0	20	5	8	10
9	40	15	15	23	14
8	0	10	10	7	6
7	0	5	80	28	45
6	0	10	0	3	6

TABLE II. 1:30 P.M.

	SAMPLE #				
LEAF #	1	2	3	$\bar{x}$	s
16	40	50	40	43	6
15	80	70	40	63	21
14	40	50	5	32	24
13	70	40	20	43	25
12	20	10	50	27	21
11	30	30	40	33	6
10	10	20	10	13	6
9	50	5	5	20	26
8	10	5	30	15	13
7	0	0	50	17	29
6	0	0	0	0	0

TABLE III. 3:30 P.M.

	SAMPLE #				
LEAF #	1	2	3	$\bar{x}$	s
16	40	20	75	45	28
15	60	80	40	60	20
14	35	40	5	23	25
13	25	60	10	32	26
12	30	10	60	33	25
11	25	80	5	37	39
10	40	10	10	20	17
9	0	10	0	3	6
8	30	50	10	30	20
7	0	5	0	2	3
6	0	5	0	2	3

APPENDIX E

LEAF AREA OF INDIVIDUAL LEAVES ON A SORGHUM PLANT.

TABLE I.

	PLANT #		
LEAF #	1	2	$\bar{x}$
16(top)	78.1	125.2	102
15	231.0	340.2	286
14	237.3	324.4	280
13	321.6	391.8	356
12	411.5	447.4	430
11	470.1	456.8	464
10	490.3	391.6	440
9	393.7	348.4	370
8	334.9	257.5	296
7	249.5	188.0	219
6	122.1	149.9	136
5	151.5	120.6	136
4	119.2	0.0(dead)	60

APPENDIX F

DIURNAL PHOTOSYNTHETIC MEASUREMENTS (mg CO_2 $dm^{-2}hr^{-1}$) AS RELATED TO INDIVIDUAL SORGHUM LEAVES ON JULY 31 (1971 & 1973).[1/]

TABLE I. 12:30 P.M., JULY 31, 1971[2/]

LEAF #	PLANT # 1	2	$\bar{x}$	s
16	4.5**	9.2*	9.2*	-
15	1.8**	8.9*	8.9*	-
14	.3**	9.2*	9.2*	-
13	.5**	11.8*	.5**	-
12	1.0**	11.2*	1.0**	-
11	.5**	10.8*	.5**	-
10	1.8**	1.8**	1.8**	0.0
9	.1**	-	.1**	-
8	1.4**	2.2**	1.8**	.5
7	.6**	.5**	.6**	.1
6	.9**	.8**	.8**	.1
5	.3**	.4**	.3**	.0
4	.9**		.9**	-

TABLE II. 14:30 P.M., JULY 31, 1971

LEAF #	PLANT # 1	2	$\bar{x}$	s
16	5.8**	13.1*	13.1*	-
15	11.2*	15.8*	13.5*	3.3
14	12.2*	18.6*	15.4*	4.6
13	12.3*	13.9*	13.1*	1.1
12	11.9*	16.5*	14.2*	3.3
11	1.6**	1.5**	1.6**	.0
10	2.4**	2.7**	2.6**	.2
9	.5**	1.5**	1.0**	.7
8	1.8**	2.3**	2.1**	.4
7	.6**	.4**	.5**	.1
6	1.0**	1.6**	1.3**	.4
5	.7**	1.5**	1.1**	.6
4	.6**	1.5**	1.1**	.6

TABLE III. 17:00 P.M., JULY 31, 1971[2/]

LEAF #	PLANT # 1	2	$\bar{x}$	s
16	13.5*	8.9*	11.2*	3.2
15	7.9*	12.5*	10.2*	3.2
14	15.0*	10.2*	12.6*	3.4
13	10.9*	9.9*	10.4*	.7
12	1.3**	10.4*	10.4*	-

APPENDIX F (cont'd)

DIURNAL PHOTOSYNTHETIC MEASUREMENTS (mg CO_2 $dm^{-2}hr^{-1}$) AS RELATED TO INDIVIDUAL SORGHUM LEAVES ON JULY 31 (1971 & 1973).1/ (

TABLE III. 17:00 P.M., JULY 31, 1971 2/ (cont'd)

	PLANT #			
LEAF #	1	2	x̄	s
11	13.9*	12.8*	13.3*	.8
10	1.6**	.9**	1.2**	.5
9	1.4**	3.0**	2.2**	1.1
8	1.6**	.9**	1.2**	.5
7	8.1*	1.4**	1.4**	-
6	1.6**	1.1**	1.3**	.4
5	-	.5**	.5**	-
4	-	.4**	.4**	-

TABLE IV. 14:30 P.M., JULY 31, 1973

LEAF # 3/	1	2	3	4	x̄	s
16	63.7*	38.7*	53.7*	55.7*	53.0*	10.4
15						
14	68.2*	64.3*	64.1*	62.1*	64.7*	2.6
13						
12	66.3*	52.4*	10.4**	12.1**	59.3*	9.8
11					11.3**	1.2
10	8.1**		9.1**	8.2**		
9						
8	9.2**	8.3**		8.0**		
7						
6	9.3**	11.5**		8.0**		
5						
4	9.7**	6.5**				

1/ *DATA MEASURED ON LEAVES IN SUN, **DATA MEASURED ON LEAVES IN SHADE

2/ The average photosynthetic rates (mg CO_2 $dm^{-2}hr^{-1}$) of sun leaves and shade leaves for both 1971 and 1973 were calculated.

	1971	1973	1973/1971 Ratio
Sun	13.9	58.9	4.2
Shade	1.6	9.1	5.7

Table 1 and Table III of Appendix F were mutiplied by the appropriate (sun or shade) ratio to produce parts of Figure 2 in Chapter 2.

3/ DATA MEASURED ON PLANTS 3 and 4 USED AS DATA FOR ODD-NUMBERED LEAVES

APPENDIX G

PHOTOSYNTHETIC MEASUREMENTS (mg CO_2 $dm^{-2}hr^{-1}$) FROM THE UPPER SUNLIT LEAVES OF SOYBEANS DURING THE GROWING SEASON.

DATE	SAMPLE # 1	2	3	4	5	6	$\bar{x}$	s
JULY 3	20.9	20.0	11.0	17.3	19.0	19.0	17.0	3.6
JULY 6	19.7	26.3	21.8	22.9			22.7	2.8
JULY 10	27.3	28.3	25.6	22.2	24.5	29.6	26.3	2.7
JULY 27	35.7	36.8	35.6	33.7			35.5	1.3
JULY 31	31.9	36.2	35.3	31.8			33.8	2.3
AUG. 6	29.5	34.1	29.6	30.1	20.0	23.0	27.7	5.2
AUG. 9	35.5	35.2	24.8	32.2	35.6	33.0	32.7	4.1
AUG. 10	24.3	28.9	25.9	26.2	36.8	30.7	28.8	4.5
AUG. 14	28.2	25.8	27.2	35.7	26.9	39.4	30.5	5.6
AUG. 17	27.3	30.9	20.6	27.5			26.6	4.3
AUG. 20	24.4	30.9	33.6	26.9	29.2	23.2	28.0	4.0

APPENDIX H

PHOTOSYNTHETIC MEASUREMENTS (mg $CO_2 dm^{-2}hr^{-1}$) AT DIFFERENT LOCATIONS IN A SOYBEAN CANOPY AT STAGE 4 and STAGE 6.

TABLE I. STAGE 4 (JULY 6)

LOCATION	SAMPLE # 1	2	3	4	$\bar{x}$	s
25% EXPANDED	5.4	6.6			6.0	
50% EXPANDED	12.1	15.9			14.0	
TOP SUN	19.7	26.3	21.8	22.9	22.7	2.8
MIDDLE SUN	18.0	25.9	25.9	22.1	23.0	3.8
MIDDLE SHADE	4.7,4.1	4.4,3.2	3.3	3.9	3.9	0.6
BOTTOM SUN	12.1	11.4	15.2	20.3	14.8	4.1
BOTTOM SHADE	1.6,2.0	1.9	1.5	2.6	1.9	0.4

TABLE II. STAGE 6 (JULY 31)

LOCATION	SAMPLE # 1	2	3	4	$\bar{x}$	s
TOP SUN	31.9	36.2	35.3	31.8	33.8	2.3
MIDDLE SUN	37.6	35.4	30.2	37.1	35.1	3.4
MIDDLE SHADE	5.2	8.3	11.8	14.8	10.0	4.2
BOTTOM SHADE	3.9	3.4	1.5	6.1	3.7	1.9

APPENDIX I

VARIATION OF PHOTOSYNTHETIC RATE (mg CO_2 $dm^{-2}hr^{-1}$) IN LYSIMETER-GROWN SOYBEANS DURING THE GROWING SEASON.

TREATMENT	LYSIMETER	JULY 17	JULY 27	AUG. 3	AUG. 10	AUG. 17
40% DEPLETION	1	17.3	39.5	15.4	27.3	31.0
		9.2	23.5	19.7		
	2	13.3	28.1	26.1	22.6	27.3
		16.8	33.2	29.7		
	3	26.9	28.8	30.3	35.3	24.3
		14.3	37.1	18.2		
	$\bar{x}$	16.3	31.7	23.2	28.4	27.5
	s	6.0	6.0	6.3	6.4	3.4
60% DEPLETION	4	20.7	33.1	26.1	35.6	22.3
		23.4	31.9	24.5		
	5	16.6	31.2	25.7	23.3	35.7
		23.3	30.1	25.5		
	6	16.5	24.8	21.7	28.9	31.4
		16.8	34.0	18.5		
	$\bar{x}$	19.6	30.9	23.7	29.3	29.8
	s	3.3	3.3	3.0	6.2	6.8
80% DEPLETION	7	13.1	33.8	23.3	24.4	28.2
		9.0	30.6	19.6		
	8	17.7	42.1	26.0	35.3	34.6
		15.9	33.1	31.4		
	9	9.5	27.4	27.2	37.3	31.0
		7.0	28.4	12.5		
	$\bar{x}$	12.0	32.6	23.3	32.3	31.3
	s	4.2	5.3	6.6	6.9	3.2
CONTROL	10	13.0	22.7	26.1	19.2	6.6
		22.5	23.4	29.0		
	11	7.8	25.8	28.7	13.2	6.6
		8.9	22.7	28.0		
	12	1.3	16.6	24.8	15.5	12.3
		1.0	27.9	18.1		
	$\bar{x}$	9.1	23.2	25.8	16.0	8.5
	s	8.0	3.8	4.1	3.0	3.3

APPENDIX J

CANOPY DATA ON LYSIMETER-GROWN SOYBEANS FOR AUGUST 6, 1973

TREATMENT	LYSIMETER	HEIGHT (cm)	WIDTH (cm)	LEAFLET AREA (cm^2)1/ TOP 1/3	BOT. 2/3	# LEAVES TOP	BOT.	PLANT LEAF AREA (cm^2)
40% DEPLETION	1	105	90	57.2	62.0	7	17	4363
	2	112	89	49.9	47.9	6	12	2623
	3	110	75	69.9	47.7	6	11	2832
	$\bar{x}$	109	85	54.9		19.7		3273
	s	4	8	6.0		3.8		950
60% DEPLETION	4	110	80	53.1	50.2	7	10	2621
	5	120	95	38.6	48.9	6	14	2749
	6	90	95	41.9	36.1	7	14	2396
	$\bar{x}$	107	90	45.1		19.3		2589
	s	15	9	6.7		2.1		179
80% DEPLETION	7	95	90	41.1	34.2	5	9	1540
	8	90	88	38.3	31.8	5	11	1624
	9	88	79	32.8	28.6	6	7	1191
	$\bar{x}$	91	86	33.7		14.3		1452
	s	4	6	3.1		1.5		230
CONTROL	10	95	85	26.7	46.4	5	8	1514
	11	93	78	34.3	36.6	5	8	1393
	12	85	70	28.8	28.2	5	8	1109
	$\bar{x}$	91	78	34.3		13.0		1339
	s	5	8	5.3		0		208

1/ $\bar{x}$ (Leaflet Area) = Plant Leaf Area ÷ (3 x # leaves)

APPENDIX K

SOYBEAN YIELD DATA FOR LYSIMETERS, 1973

TREATMENT	LYSIMETER	# PLANTS N½	# PLANTS S½	YIELD (gm) N½	YIELD (gm) S½	TREATMENT YIELD $\bar{x}$ (gm)	s
40% DEPLETION	1	7	7	63.5	64.7		
	2	7	7	65.9	61.7	63.7	2.0
	3	7	7	65.5	61.0		
60% DEPLETION	4	7	7	56.9	58.3		
	5	8	7	59.5	51.9	56.1	3.2
	6	6	7	57.7	52.5		
80% DEPLETION	7	7	8	34.6	39.5		
	8	7	6	40.3	40.0	38.8	2.1
	9	7	7	38.7	39.9		
CONTROL	10	6	7	22.1	20.0		
	11	7	7	21.2	18.4	19.9	1.7
	12	7	6	19.9	17.5		

ACKNOWLEDGMENTS

I wish to express my graditude to Dr. Iwan D. Teare for his help, advice, encouragement, and many acts of kindness during the past three years.

I also wish to thank Mrs. Pam Barnes who helped with the typing of my thesis and provided much encouragement.

To all other personnel associated with the Evapotranspiration Laboratory, I express my thanks for their advice and help.

Finally, to my wife Trudy, thank you for your patience and encouragement.

PHOTOSYNTHETIC RATES IN PLANTS AS RELATED TO STAGE OF DEVELOPMENT, POSITION IN CANOPY, AND WATER STRESS

by

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B. S., KANSAS STATE UNIVERSITY, 1971

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1974

An improved portable field technique for measuring photosynthesis using $^{14}CO_2$ was developed that one man could operate. The system's solenoid off-on air flow switch, driven by an electronic timer, eliminates human error in judging exposure times. The miniature chamber by design ensures adequate ventilation of the air flow through the chamber. To prepare the $^{14}CO_2$ exposed leaf sample for scintillation counting, it is digested in an organic solubilizer. The method was subsequently used in research in sorghum and soybeans.

Photosynthetic measurements were made periodically in a sorghum canopy during the 1973 growing season. Photosynthesis in the upper sunlit canopy appeared to reach a maximum at stage 6 (half bloom). Degree of leaf exposure to direct sun illumination and the vertical distribution of photosynthesis were measured three times on a single day during stage 6. A simple model for estimating total photosynthesis in the canopy is presented, based on the amounts of sun and shade leaf area in the canopy, and the photosynthetic rates of the sun and shade portions. The model predicted a value within 5% of the photosynthetic rate measured using an open-chamber infrared gas analyzer system.

Photosynthesis was measured in soybeans during the 1973 growing season in the open field under nonstressed conditions and in drainage lysimeters with available moisture levels depleted 40%, 60%, 80%, and nearly 100%. Photosynthetic rates in the nonstressed soybeans increased during early growth and peaked at rapid-pod-growth (stage 6). A dip in photosynthesis occurred between stages 6 and 7 which we believe to be related to physiological age. Water stress in soybeans lowered photosynthesis, reduced shoot growth, reduced yield, and hastened maturity.

CHAPTER III

VARIATIONS IN PHOTOSYNTHESIS OF SOYBEAN UNDER NONSTRESSED AND STRESSED CONDITIONS

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