Field studies on photosynthesis in soybeans

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JEFFERS, Jr., Daniel Louis, 1938-
FIELD STUDIES ON PHOTOSYNTHESIS IN SOYBEANS.

Iowa State University, Ph. D., 1968
Agronomy

University Microfilms, Inc., Ann Arbor, Michigan
FIELD STUDIES ON PHOTOSYNTHESIS IN SOYBEANS

by

Daniel Louis Jeffers, Jr.

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Major Subject: Crop Production
and Physiology

Approved:

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Iowa State University
Ames, Iowa
1968
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INTRODUCTION

One major objective of crop research is to establish which plant characteristics are responsible for improvements in yield. With such knowledge in hand a plant breeder can objectively breed and select for morphological or physiological characters that will increase his chance of developing superior genotypes.

One fundamental physiological character is the fixation of carbon dioxide in photosynthesis. Hesketh and Moss (27) and Hesketh (26) have established that species differences in rates of photosynthesis exist; the magnitude of the differences seem to explain a large proportion of the differences in growth among species. It is logical to hypothesize that varietal differences in yield may be attributable to differences in photosynthesis.

Although there has been a large amount of research on rates of photosynthesis in individual plants and leaves of plants under artificial environment, there has been not nearly the same amount on plants under field conditions. The principal reason is that field conditions require either complex control of environmental factors or equally complex measurement of the affecting environmental factors. Consequently, field research has had to await refinement of techniques and improvement of instruments.

The objectives of this study were (1) to establish a portable apparatus for measuring photosynthesis under field
conditions, (2) to determine the effects of solar radiation, leaf area and air temperature on photosynthesis of "narrow-row" soybeans, and (3) to conduct a test of differences in rates of photosynthesis among 3 varieties of soybeans.
LITERATURE REVIEW

Photosynthesis Measuring Systems

Measuring CO₂ assimilation of crops in the field requires a portable system. The system requires elaborate control of the environmental factors or it requires extensive measurement of the varying, uncontrolled environment.

Monteith and Szeicz (48) and Lemon (40) used an aerodynamic method, which is a completely open system, for measuring CO₂ assimilation in field crops. The rate can be calculated from wind speed and CO₂ concentration profiles above a field crop. The method has the main disadvantage of requiring a large crop area and proper wind speed profiles, but it avoids an artificial environment.

Monteith and Szeicz (48) obtained CO₂ assimilation rates in sugar beets by the aerodynamic method that agreed with dry matter accumulation within experimental error, which was 18% for CO₂ assimilation and 17% (coefficients of variability) for dry matter. Wright and Lemon (85) found 60 g CO₂ fixed/m² land surface in corn in one clear day by use of the aerodynamic method. This rate agreed well with known rates of dry matter accumulation. However, instantaneous rates obtained by the aerodynamic method give results too variable to study the effect of other factors on photosynthesis. The method is useful as an accuracy check on other methods of measuring crop photosynthesis.
Musgrave and Moss (61) built a small, refrigerated, plastic-film-covered chamber (closed system) for enclosing small plots of corn. Carbon dioxide exchange was measured by metering CO₂ to replace that used in photosynthesis or by measuring the increase in CO₂ concentration due to respiration. This type of system, while small, is not very portable because the cooling system is heavy, and it is difficult to seal leaks once the system has been moved.

Baker and Musgrave (6) used a system for small plants where atmospheric air was drawn from a mixing tank and pumped through a plant enclosure (open system). The CO₂ assimilation was calculated from the CO₂ concentration difference in the inlet and outlet air streams and from the rate of air flow. This system has the advantage of being easily moved, and small air leaks do not significantly affect the results.

Radiant Energy and Photosynthesis

It is well established that plant leaves convert radiant energy to chemical energy most efficiently at low radiation. For example, Gaastra (23) found in sugar beet, turnip, cucumber, spinach and tomato leaves a linear increase in net photosynthesis (P) with increasing radiation at low radiation, followed by a less rapid increase and, then little change at high radiation. His interpretation was that at low radiation the photochemical process limits photosynthesis. A transition phase occurs as CO₂ becomes increasingly limiting, until under high radiation
CO₂ is the sole limiting factor. Photosynthesis could be increased by increasing the CO₂ concentration above the normal atmospheric concentration of 0.03%.

Not all species show radiation saturation of photosynthesis. Hesketh and Moss (27) found no saturation in corn, sunflower and sugar cane leaves, but they did find saturation in 10 other species. Soybean leaves respond most efficiently at low radiation, but photosynthesis is nearly saturated at about half maximum solar radiation (36).

In a crop canopy most leaves are not oriented normal to the sun, so they do not receive maximum possible radiation. This is an efficient arrangement because leaves use radiant energy most efficiently at low levels. More radiation falls on lower leaves and their photosynthesis is increased more than photosynthesis of upper leaves is reduced. Also, some leaves, because of their position and angle, receive solar radiation on both surfaces. This, also, is efficient exposure (51).

In crop communities radiant energy saturation has been shown not to occur or to occur at higher levels than for single leaves. Alexander and McCloud (1) found the photosynthesis of bermudagrass swards radiation saturated at greater than 5,000 ft-c whereas single leaves were saturated at 3,000 ft-c. Similarly, Murata (56) observed saturation of rice leaves at 40-50 Klux (about half maximum solar radiation), but the crop community was saturated at higher radiation (or not at all)—the level depending on stage of plant development. Pearce et al.
(66) found crop and leaf differences in the pattern of orchard grass response to radiation; leaves reached 50% of maximum photosynthesis \( P_{\text{max}} \) at 500 ft-c whereas stands reached 50% \( P_{\text{max}} \) at 1300 ft-c. Eighty percent of \( P_{\text{max}} \) was obtained at 2000 and 3700 ft-c for leaves and stands, respectively. Baker (3) with cotton, and Moss et al. (54) with corn have found that crop \( P_{\text{max}} \) requires maximum solar radiation. Wilfong et al. (81) reported no radiation saturation of photosynthesis in alfalfa and ladino clover canopies at 10,000 ft-c. In soybeans Murata and Iyama (57) and Kumura (36) noted that net photosynthesis, as well as the radiation saturation level, increased as the foliage density increased.

In most cases the effect of radiant energy on \( P \) has not been determined independently of other factors. The most apparent covariants to radiation are temperature and water deficit, which are highly correlated. It is probable that many of the findings of response of photosynthesis to radiation are affected by variable leaf temperature or variable water status.

Interaction of Radiant Energy and Leaf Area

Monsi and Saeki (45) investigated the distribution of solar radiation in plant communities and found it to be exponential. It followed the relationship \( \frac{I}{I_o} = e^{-kL} \), where \( I_o \) is the incident radiation, \( I \) is the radiation penetrating a quantity of crop leaf area index, \( L \) (leaf area/ground area), and \( k \) is a constant characteristic of the plant community.
Values of $k$ were low for grasses (0.3 - 0.5) and high for broad leaf plants (0.7 - 1.0).

Saeki (67) made calculations of plant community dry matter production based on varying relationships between the magnitude of incident radiation and values of $k$ and $L$. His theoretical production curves show that under high radiation the optimum $L$ ($L_{opt}$) (the leaf area index where crop dry matter production is at the maximum rate) and dry matter production are highest at low $k$ and lowest at high $k$. Conversely, under low radiation $L_{opt}$ and dry matter production are highest at high $k$ and lowest at low $k$. This theory is based on a declining rate of increase of $P$ with increasing radiation. His calculations show that the $L_{opt}$ and crop community photosynthesis should increase as radiation increases. That is, as radiation increases a larger area of leaves is exposed above the compensation point.

Experimental evidence that $L_{opt}$ increases with increasing radiation comes from Black (11), who measured dry matter production in subterranean clover, and from Nichiporovich and Malofeev (62), who measured photosynthesis in kale. However, Ludwig et al. (41) showed little or no effect of radiation up to 3300 ft-c on $L_{opt}$ in artificial cotton communities (potted plants in a growth chamber). Kumura's (36) limited data showed little trend toward increasing $L_{opt}$ with increasing radiation in soybeans.
Carbon Dioxide Concentration

Gaastra (23) found CO₂ limiting to photosynthesis in high radiation up to about 1000 ppm CO₂ in sugar beet, turnip, cucumber, spinach and tomato. Hesketh (26) observed increased photosynthesis in sunflower, maize, tobacco and castor bean as the CO₂ concentration was increased from zero to 1000 ppm. Photosynthesis was related to stomatal diffusion of CO₂ into leaves in some cases, but, in general, variation among species was believed due to differences in mesophyll diffusion or dark reaction kinetics. Bierhuizen and Slatyer (9) with cotton leaves and Baker (3) with a cotton crop have observed enhancement of photosynthesis by increased CO₂ concentration above atmospheric concentration. Moss et al. (54) found a similar response in a corn crop.

Gaastra (23) has evaluated the movement of CO₂ into sites of fixation within leaves. The major resistances are the air, stomata, and mesophyll cells. Diffusion of CO₂ in air is a slow process compared to turbulent transfer. Thus, CO₂ assimilation could be reduced by inadequate air flow because the effective CO₂ concentration about the leaf was reduced. Moss (49) has shown that the rate of photosynthesis of a sugar cane leaf in 200 ppm CO₂ atmosphere with turbulence was equivalent to the rate in 300 ppm with zero turbulence. Warren-Wilson and Wadsworth (79) examined the effect of air flow on leaf photosynthesis and showed that the optimum rate varied among species
but was mostly 30-100 cm/sec. They concluded that harmful effects of wind occurred only at "gale" or "hurricane" speeds.

Sakamoto (69) monitored the diurnal CO₂ concentration at 0.3 m over a soybean field at Ames, Iowa. The range during the daylight hours was about 280 to 350 ppm. At night the concentration rose to 500 ppm. The normal range above a crop is probably a response to crop photosynthesis and respiration, and during sunlight hours variation due to other factors is small and of no consequence to crop photosynthesis.

Soil and plant respiration raises atmospheric CO₂ concentration. Monteith (47) measured 3 mg/dm²·hr soil CO₂ evolution under beans and Musgrave and Moss (61) found 8 mg/dm²·hr evolved under corn from wet soil. In either case soil respiration would not compensate photosynthesis under maximum solar radiation.

Dark respiration rates have been commonly used for plant CO₂ evolution estimates. Recent evidence shows that CO₂ evolution in the light is different from dark respiration (52, 87). Monteith (47) also concluded that estimates of plant respiration were inadequate to fully account for CO₂ fluxes in a bean field. Zelitch (87) suggested that CO₂ evolution in the light (photorespiration) is considerably larger in magnitude than dark respiration.

Temperature

The effect of heat on net photosynthesis varies among species. Murata et al. (60) found that the temperature optimum
(T_{\text{opt}}) for photosynthesis corresponded closely to adaptation areas for 19 species grown in Japan. Warm climate species (bermudagrass, bahiagrass, and rhodesgrass) have temperature optima of 30-40° C. A cool climate species, common vetch, has a 10° C temperature optimum and the most widely adapted of the 19 species, barnyard grass (Echinochola sp.), has a wide temperature optimum of 20-40° C. Stoy (75) observed in winter wheat, which has wide adaptability, a small decrease of about 10% leaf net photosynthesis with change of temperature from 25 to 15° C and a slight decrease of about 5% from 30 to 35° C.

High leaf temperatures depressed net photosynthesis in sorghum, cotton, sunflower, and Thespesia populnea (L.), but with increasing optimum temperature among the species net photosynthesis increased (15). However, at 50° C net photosynthesis of cotton was about 50% of maximum, and that of sunflower was zero, even though sunflower had the highest P_{\text{max}}. In soybean leaves Fukui et al. (20) found an air temperature optimum of 15-30° C for photosynthesis, but the rate dropped to zero at 40° C.

Moss et al. (54) found that net photosynthesis in a corn community increased up to the highest temperature obtainable-44° C. The effect of temperature on net photosynthesis in a cotton community depended on the solar radiation and the time of day (3). Net photosynthesis declined as temperature increased from 20 to 40° C in the afternoon and at low radiation, but net photosynthesis increased in the morning at high radiation.
as temperature increased. A plant community may be expected to have a higher $T_{\text{opt}}$ or a greater range of $T_{\text{opt}}$ for net photosynthesis than a single leaf because the heat load is distributed over more vegetation.

Gaastra (23) showed that leaf temperature in a closed measuring system is often greater than air temperature under high radiation. The leaf temperature could be brought near to that of the air by moving air rapidly over the leaf and by cooling the walls of the enclosing leaf chamber. These findings bring into question the results of those who assume leaf temperature to be the same as the measured air temperature. Weigand and Namken (80) reported water stressed cotton plants had upper leaves 11° C greater than air temperature at 1.6 ły/min solar radiation.

Zelitch (87), Moss (52), and Forrester et al. (18) have established that respiration in the light (photorespiration) is different from dark respiration. Photorespiration is the evolution of $CO_2$ from glycolate synthesized in photosynthesis. The process depends greatly on $O_2$ concentration and temperature; dark respiration is less affected by $O_2$ and temperature. Thus, $T_{\text{opt}}$ for apparent photosynthesis is, perhaps, more related to photorespiration than to true photosynthesis, which increases with increasing temperature in the physiological range. So, the variation in $T_{\text{opt}}$ for net photosynthesis among species may be due to variation in photorespiration. El-Sharkawy and Hesketh (16) concluded that variation in photorespiration, which was
associated with variation in leaf anatomy, is a possible cause of variation of net photosynthesis among species. *Amaranthus, Zea, Sorghum, Cynodon*, which evidently do not have photorespiration, have a larger internal cell surface to cell volume than *Helianthus, Gossypium, Avena, Thespesia, Glycine* and *Beta*, which show photorespiration.

**Leaf Age and Nutrient Status**

Saeki (68) suggested, on the basis of studies with *Celosia cristata*, that total photosynthesis of a plant community would be much like that of a younger upper leaf because lower leaves receive little radiation, are older and, thus, less active, photosynthetically. Brown et al. (12) measured lower rates of net photosynthesis in lower, older leaves than in younger, upper leaves in white clover and alfalfa. Kumura (36) observed a similar relationship in soybean leaves.

Moss and Peaslee (53) found that older, lower maize leaves were only slightly less active photosynthetically when potassium status was high (>4350 μg/g fresh weight), but much less active when the potassium status was low (<2150 μg/g fresh weight). Deficiency of phosphorous, nitrogen, and magnesium was said to have a similar effect.

Ojima et al. (64) found that phosphorous and potassium hardly affected leaf photosynthesis in non-nodulating soybeans but low nitrogen caused a large reduction. They also observed the highest leaf net photosynthesis (about 30 mg CO₂/dm²·hr)
occurred at maximum expansion, was maintained for a week, and declined thereafter.

In a dense crop of soybeans, where new leaf growth is apical, the upper leaves are probably the most efficient producers, and because of their position, also receive the most radiant energy. Consequently, the lower increments of leaf area probably contribute less, proportionately, to canopy dry matter production than the surface increments.

Variation among Genotypes within Species

Milner and Hiesey (44) detected large differences in net photosynthesis in response to light and temperature of six climatic races of *Mimulus cardinalis* Dougl. Björkman and Holmgren (10) found that ecotypes of *Solidago virgaurea* L. had different rates of leaf photosynthesis. Those from shaded habitats had lower rates than those from exposed habitats and could not be entirely adjusted upward by growing them in strong light.

Work with more closely related genotypes has not shown much promise for obtaining higher yields by selecting for higher net photosynthesis. Muramoto et al. (55) found large differences in net photosynthesis among cotton leaves, but not among varieties of cotton. They reported that differences in rate of dry matter production were associated with differences in rates of leaf area development.

Stoy (75) reported differences in net photosynthesis among
three varieties of wheat differed by about 3% whereas differences in dry matter production and seed yield varied by 15 and 20%. The dry matter production advantage was mainly due to persistence of the green leaf area and the seed yield advantage was also related to better translocation of carbohydrate to the seed.

Kleese (33) and Miflin and Hageman (43) have found differences in rates of photophosphorylation among barley and corn genotypes respectively.

Thus, one may expect varietal differences in net photosynthesis to exist but perhaps to account for only a small part of yield differences. Further work is needed before definite conclusions can be drawn.
METHODS AND MATERIALS

Management of the Crop

Soybeans (Glycine max L., Merr.) were planted in 25 cm north-south rows at about 7 seeds per 30 cm of row length. The plots consisted of nine rows (30 m in length) of which 2 rows on each side were border. The plots were thinned at the second trifoliolate stage to about 1 plant every 15 cm of row. This gave a density of about 26 plants per m$^2$.

Planting was the third week of May, 1966 at the Beach Avenue experimental site at Ames, Iowa. The soil is a clay loam. It was known to be highly productive for soybeans and no fertilizer was applied following the previous corn crop. The growing season began with a full supply of soil moisture, but little rainfall occurred after July 1; so, irrigation was necessary. The site was flood irrigated with about 18-25 cm of water in the second week of July, the first week of August and the third week of August.

Because soybeans grow unusually tall under solid-drilled conditions, wire mesh (10 x 15 cm) was laid horizontally over the plots at a height of 1 m and suspended between steel posts for the plants to grow through. This prevented lodging without disturbing the normal canopy shape.

Weeds were controlled by herbicide (Treflan) and by hand weeding. Insects were controlled with Malathion.
Treatments

Rates of photosynthesis in 1.16 m$^2$ areas of the field plots were measured on 3 varieties, Harosoy 63, Amsoy and Harosoy na na, which is a Harosoy x T-204 backcross (6x) and has small, lanceolate leaflets. The other varieties have ovate leaflets. Measurements were taken on 25 of the 67 days from July 5 to September 9. Time and equipment did not permit use of all varieties on all days. Harosoy 63 was not sampled after July 20 in order to allow time for more measurements on the two remaining varieties.

A range of L (0.36 to 8.01) was obtained by natural growth and by removing various quantities of lower leaves in the 1.16 m$^2$ areas the day before photosynthesis measurements were taken. Leaflets were removed from the ground upward to a height necessary to leave the desired leaf area index. Little damage was done to the border row plants on the 'sun' side because leaflet removal was practiced mainly from the east and north ends.

The field plots were arranged to facilitate the placement of chambers so that among variety and within variety comparisons of photosynthesis could be made on any one day. The plot arrangement was 2 plots of Harosoy na na, 2 plots of Harosoy 63, and 2 plots of Amsoy. The instrument trailer was placed, permanently, in the middle of the site so that all plots were within easy reach of power lines and air sampling lines. To minimize the amount of crop used as border, sample areas proceeded from
north to south with time.

The Chamber System

The photosynthesis measuring system is a semi-closed system (Fig. 1). Air is blown into a chamber at the top of one side, circulated and allowed to pass out through a duct attached at the base. Photosynthesis rates were calculated from difference in CO₂ concentration of the inlet and outlet air streams and from the rate of air flow through the system. The inlet blower was a 21-cm, 5-bladed fan having a maximum speed of 3300 rpm. The fan speed was regulated with a variac to achieve the desired air flow through the system. The inlet duct was a 25-cm-diameter, neoprene-coated, canvas duct with a wire core. It was 3 m in length. A filter was placed over the inlet duct to keep out dust. The outlet duct was 10-cm. white, vinyl, spiral-wire ducting; it was 2 m long. The spiral shape and size of the ducting seemed to mix the air and equalize the CO₂ concentration within the duct.

The chambers were constructed of 2 x 8 lumber (base), an electrical conduit upper frame and a removable unit of clear, polyvinyl chloride, cast film covering. The outlet duct was attached to the base. A 5-bladed, air-circulating fan and the inlet duct mounting were affixed to the conduit frame.

To prevent wind damage and dirt accumulation, the film cover was removed when not in use. It had 94% light transmission when clean and about 90% in the field because of dust
accumulation. The bottom was sealed into loops through which aluminum rods were placed and fastened at the base corners.

Air leakage was prevented by sealing the film cover to the base with masking tape. The base, in turn, was sealed to the soil by packing soil around the bottom. Various ways of sealing possible air leaks were tried including using masking tape on all connections and sealing the base with wet soil. The most extreme measures gave no measurable change in outlet air flow over simply sealing the base with soil at field moisture and taping the cover to the base. The permeability of polyvinyl chloride to CO₂ is high compared to other atmospheric gases, but at the maximum inside to outside differentials of CO₂ (about 40 ppm) the leakage of CO₂ was less than 1% of photosynthesis, which was considered a negligible error.

Control and Measurements

Soil CO₂ flux

Soil CO₂ flux was expected to be a factor of importance. In a preliminary test, the field chambers were placed over bare soil, which was shielded with aluminum foil to simulate leaf cover. CO₂ flux was not detectable in dry soil and varied from 0 to 2 mg CO₂/dm²·hr in wet soil with debris removed from the soil surface. However, the presence of decaying organic material such as corn stubble and dead leaves caused rates of up to 15 mg CO₂/dm²·hr soil CO₂ flux. In the CO₂ assimilation experiments care was taken to remove all dead leaves, stems and
stubble from the soil surface. Soil CO₂ flux was measured twice more during the season with similar results. Thus, it was concluded that soil CO₂ flux was negligible when all decaying organic material was removed from the soil surface.

**Interior air circulation**

As discussed in the literature review, circulation of air inside the chamber was believed important. A test was made of the effect of circulating-fan speed on photosynthesis. The results are presented in Fig. 2 as deviation of photosynthesis (after adjusting for linear effect of solar radiation) versus the fan speed in rpm. Each point is the average of about 6 determinations and solar radiation varied from 0.9 to 1.2 ly/min. It was decided that running the fan full speed was sufficient to maintain maximum photosynthesis. This speed created air movement of 50 to 300 m/min at various points near the leaf canopy surface, as determined with an Alnor Velometer.

**Air flow**

Air flow through the system was measured with an Alnor Velometer. Since the total air flow through the system could not be accommodated by the velometer, probes, which sampled a portion of the area of outlet flow, were attached to a 10 cm diameter by 15 cm aluminum pipe affixed to the outlet duct. (The pipe served also as a mount for a mercury thermometer and an air sampling line.) The Alnor Velometer was calibrated with a highly accurate Taylor windmill anemometer. It would measure the equivalent of from 60 to 300 m/min air flow through the 10
cm pipe.

**Temperature**

Temperatures were taken with aluminum foil shielded mercury thermometers in the outlet ducts. Preliminary trials showed that air temperature increased little in the chamber, but preheating in the inlet duct caused up to 4°C rise under high solar radiation. This rise was kept down to 1-2°C by keeping the inlet duct shaded between the field plots. Under a low solar heat load the chamber temperature was the same as the outside air temperature. Under high solar radiation an air turnover rate of about once per minute was found to give a favorable balance between sufficient heat removal and carbon dioxide differentials that could be easily detected (about 40 ppm).

**Solar radiation**

Continuous measurement of incident solar radiation was taken with an Eppley Pyrehieliometer mounted on the trailer roof and recorded with a strip chart recorder. The readings were multiplied by 0.9 to correct for light reflection and absorption by the plastic chamber cover.

**CO₂ differentials**

Carbon dioxide concentrations were measured with a Beckman infrared gas analyzer. Air samples were selected by timer activated solenoid valves (a sketch of the system is shown in Fig. 3). Each air stream was sampled and analyzed for three minutes. A diaphragm pump drew the air through tygon tubing from the
source, through solenoid valves, and pumped it through a CaSO₄ drying column, filter, flowmeter and the analyzer. Carbon dioxide concentrations were recorded on a strip chart recorder. The analyzer was calibrated with standard CO₂ and N₂ gas mixtures obtained from Matheson, Inc.

Rates of CO₂ assimilation were calculated on the basis of 1.16 m² ground area (about 30 plants).

Assimilation was calculated as mg CO₂/dm² soil surface area • hr = \( \frac{CO₂ \text{ (ppm) } \times 10^{-6} \times \text{air flow} \times 44,010 \text{ mg CO}_2/\text{mole} \times RT}{116.1 \text{ dm}^2} \)

where \( CO₂ \) is the carbon dioxide concentration difference in ppm by volume between chamber inlet and outlet air streams, air flow is in liters/hr, \( R \) is the gas constant of 0.08205 1/mole °K at 1 atmosphere, and \( T \) is absolute air temperature. Carbon dioxide differentials could be measured to only 2 significant digits. The barometric pressure varied only in the third or fourth significant digit among the days when assimilation measurements were taken, so one atmosphere was taken as the air pressure for all calculations.

Leaf area

After having measured CO₂ assimilation for a period of time sufficient to get a full range of sunlight conditions, leaf area measurements (one side) were taken on the plants used for CO₂ assimilation measurements. When leaves were removed in the field, they were placed in plastic bags and refrigerated until measured (usually within 2 hours). When whole plants were
removed, they were refrigerated with the stem bases in water and the foliage covered with plastic bags until measured.

The leaf area was measured with a photoelectric planimeter, which had been calibrated with soybean leaf punches. On the planimeter one microampere current reduction equalled $25.12 \pm 0.77 \text{ cm}^2$ leaf area.
Fig. 1. Diagram of the plant chamber for measuring CO$_2$ assimilation
Fig. 2. Photosynthesis versus air circulating fan speed in an Amsoy soybean community at about 0.9 to 1.2 ly/min solar radiation, 30° C and 6 L
Relative Photosynthesis - Percent

0  20  40  60  80  100

500
1000
1500
2000
2500
3000
3500

Circulating Pan Speed - RPM
Fig. 3. Diagram of the gas sampling and CO₂ measuring system. Point 1 is chamber 1 inlet, 2 is chamber 1 outlet, 3 is chamber 2 inlet and 4 is chamber 2 outlet. Switching frequency was 3 minutes.
RESULTS

The number and regularity of photosynthesis observations depended primarily upon the weather and to a smaller degree upon the reliability of the measuring system. Table 1 is an outline of the experiment. The date, day number, variety, leaf area index (L) and number of simultaneous observations (n) of net CO₂ assimilation (P), solar radiation and temperature are listed. Most measurements were taken in the afternoon. The data were fitted to linear, quadratic, and cross product terms in a multiple regression analysis of P on the other variables. Not all combinations of cross products were used because this would lead to an unwieldy model and not all combinations are biologically important. Thus, the results were analyzed with some subjectivity. Furthermore, under natural, uncontrolled conditions situations which would make the parameters orthogonal seldom exist. For example, diurnal variation in solar radiation was correlated with temperature. Thus, high radiation and low temperature only occurred when air mass changes in temperature occurred.

The results from the first fitting are given in Table 2. The parameters are as follows: X₁ is CO₂ assimilation in mg CO₂/dm²·hr, X₂ is days from July 4, X₃ is a dummy variable with value 1 or 0 for the Amsoy variety, X₄ is the same for Harosoy na na, X₅ is leaf area index, X₆ is solar radiation in ly/min, X₇ is temperature in °C, X₈ is the average CO₂ concentration
between the inlet and outlet air streams in ppm by volume, \( X_9 \) is the velocity of air flow in the outlet duct in m/min, and \( X_{10} \) is the hour of the day (9 a.m. CST equals 0). The remaining variables are quadratic and cross product terms. The first analysis contained 1232 observations of \( \text{CO}_2 \) assimilation.

A test was made to determine whether varieties had a common regression of photosynthesis on the other variables (Table 3). The data for each variety were fitted to the model. The reduction in the residual sums of squares by combining separate regressions was compared with the common regression. Although the reduction in residual sums of squares was significant, the increase in \( R^2 \) was only 2.3%. This was not considered large enough to preclude using the common regression in calculating the effect of variables on \( P \). Because the observations were unbalanced in time and number among varieties, it seemed desirable to avoid separate analyses, if possible.

Inspection of the correlation matrix (Table 4) revealed that the hour of the day (\( X_{10} \)) was highly correlated (-0.7) with solar radiation. Therefore, \( X_{10}, X_{15} \) and \( X_{20} \) were not used because hour of the day could have only a minor effect compared to that of solar radiation. The square root of solar radiation (\( X_{12} \)) was tried in lieu of linear and quadratic terms with no better fit, so it also was not used.

The multiple \( R^2 \) of 0.67 was less than satisfactory to draw general conclusions. Inspection of the results of simple regressions of photosynthesis on linear and quadratic terms showed
that solar radiation accounted for 42% of the variation in photosynthesis. Observation of plots of photosynthesis versus solar radiation for single treatments on each day showed that on 4 days the estimation of photosynthesis in response to solar radiation was very poor (for examples of good and poor estimates see Fig. 4). Evidently, some other unmeasured factor, perhaps water stress, had a major influence on photosynthesis on these days. With such a high proportion of the variation being due to radiation, it would be necessary to estimate photosynthesis in response to solar radiation with high precision to accurately assess the effects of other factors. Consequently, the data for the 4 days of highly variable response (Aug. 3, 9, 11, Sept. 1) were discarded.

The remaining data were fitted to a second model. The least significant term was rejected and the equation recalculated. Rejection of variables was on the basis of t tests at the 0.01 probability level; that is, the probability of rejecting a true reduction in the lack of fit is 0.01. The \( X_8, X_{17}, X_{18}, \) and \( X_{19} \) terms were rejected in this manner. The new multiple \( R^2 \) was 0.76. The resulting equation is given in Table 5.

The second model was tried with and without varieties (variables 3 and 4). An F test for no variety contribution is shown in Table 6. Varieties contributed a significant reduction in the residual sums of squares. The average magnitude of variety difference is the difference in the coefficients.
That is, CO₂ assimilation in Amsoy was 2.8 mg/dm²·hr higher than Harosoy na na which was 5.2 mg/dm²·hr higher than Harosoy 63 (see Table 5).

Day (X₂) and air flow (X₉) factors were negatively correlated because the air flow rate was increased from about 250 to about 300 m/min after the first several days. This gave a more favorable balance between temperature and CO₂ differentials. Thus, the observed day effect of -7 mg CO₂/dm²·hr from July 5 to September 9 is a minimum estimate. Air flow variation caused variation in photosynthesis of about 2 mg CO₂/dm²·hr.

The effects of leaf area index, solar radiation and temperature on canopy photosynthesis are shown in Fig. 5, 6, and 7. Day 40 (August 13), the Amsoy variety, 30°C and leaf area index 5 are taken as standards. The fitted curves were not extrapolated beyond the data.

The leaf area index effect on photosynthesis at 1.1 ly/min is plotted uncorrected for any other factors in Fig. 5. A positive relationship between photosynthesis and leaf area index is evident in the data.

The predicted response of P to radiation and leaf area index is plotted in Fig. 6. The leaf area index by radiation interaction (X₁₀) is an important factor. Under low radiation P_max is attained at 4-5 L. Under high radiation P increases to the highest L attainable. Saturation of P by solar radiation occurs only at low leaf area indices. At zero radiation the model predicts positive photosynthesis. This is probably due
to the inadequacy of a quadratic model to fit the data precisely.

Figure 7 shows the effect of solar radiation and heat on photosynthesis in a three dimensional response surface plot. As was expected, no data for high radiation-low temperature and low radiation-high temperature were obtainable, because such conditions occur very infrequently in July and August. The optimum air temperature for CO₂ assimilation was about 25-30°C. On any one day the solar radiation and temperature varied together, with the result that an apparent radiation saturation of photosynthesis occurred when the temperature exceeded the optimum. As the solar altitude declined in the late hours, photosynthesis decreased not only in response to decreased radiation, but often in response to suboptimal temperature. There was no detectable interaction of temperature with solar radiation, or temperature with leaf area index on photosynthesis.
Table 1. Experiment outline of date, day, variety, leaf area index (L) and the number of observations (n) of P, solar radiation and temperature

<table>
<thead>
<tr>
<th>Date</th>
<th>Day</th>
<th>L</th>
<th>n</th>
<th>Date</th>
<th>Day</th>
<th>L</th>
<th>n</th>
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Table 2. Multiple regression of photosynthesis on all other measured variables, plus some quadratics and cross products

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<th>Source</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean square</th>
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<td>9,561</td>
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<tr>
<td>Residual</td>
<td>1212</td>
<td>86,492</td>
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<tr>
<td>Total</td>
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<table>
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<tr>
<th>Variable</th>
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<th>t value</th>
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<tr>
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<td>3 Amsoy</td>
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<tr>
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<tr>
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<td>7 Temp</td>
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<sup>a</sup>Intercept

\[ t_{0.01, \text{df} = 2.58} \]
Table 3. Analysis of variance for within varieties deviations from regression compared to among varieties deviations from a common regression

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<th>Mean square</th>
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<td>24,396.77</td>
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<tr>
<td>Harosoy 63</td>
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<td>Total residual</td>
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<tr>
<td>Deviations due to varieties (by difference)</td>
<td>31</td>
<td>4,920.02</td>
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\[ F \text{ ratio} = \frac{158.71}{69.07} = 2.30 \text{ significant at the 0.01 level} \]
Table 4. Correlation matrix ($X \times 10^2$) from all 1232 observations of each variable

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<th>4</th>
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<th>6</th>
<th>7</th>
<th>8</th>
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<td></td>
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<td>67</td>
<td>13</td>
<td>50</td>
<td>99</td>
<td>63</td>
<td>73</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>20 (7) x (10)</td>
<td>-10</td>
<td>-61</td>
<td>-63</td>
<td>-1</td>
<td>3</td>
<td>-47</td>
<td>-56</td>
<td>-12</td>
<td>-46</td>
<td>100</td>
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</table>
Table 5. Multiple regression of photosynthesis on some other factors

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Regression</td>
<td>11</td>
<td>137,692</td>
<td>12,517</td>
</tr>
<tr>
<td>Residual</td>
<td>1005</td>
<td>43,680</td>
<td>43.463</td>
</tr>
<tr>
<td>Total</td>
<td>1016</td>
<td>181,372</td>
<td></td>
</tr>
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</table>

Multiple $R^2 = 0.76$  
Multiple $R = 0.87$

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>t value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 P</td>
<td>-77.31$^a$</td>
<td>-4.00</td>
</tr>
<tr>
<td>2 Days</td>
<td>-0.1095</td>
<td>-5.50</td>
</tr>
<tr>
<td>3 Amsoy</td>
<td>8.051</td>
<td>9.26</td>
</tr>
<tr>
<td>4 H na na</td>
<td>5.234</td>
<td>6.08</td>
</tr>
<tr>
<td>5 L</td>
<td>1.868</td>
<td>3.21</td>
</tr>
<tr>
<td>6 Solar radiation</td>
<td>39.18</td>
<td>11.89</td>
</tr>
<tr>
<td>7 Temp</td>
<td>4.463</td>
<td>3.45</td>
</tr>
<tr>
<td>9 Air flow</td>
<td>0.04634</td>
<td>4.95</td>
</tr>
<tr>
<td>11 (5)$^2$</td>
<td>-0.1753</td>
<td>-2.90</td>
</tr>
<tr>
<td>13 (6)$^2$</td>
<td>-29.63</td>
<td>-9.34</td>
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<td>14 (7)$^2$</td>
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<td>-3.72</td>
</tr>
<tr>
<td>16 (5) x (6)</td>
<td>3.660</td>
<td>9.55</td>
</tr>
</tbody>
</table>

$t_{.01, \infty} \text{ df} = 2.58$

$^a$Intercept
Table 6. Analysis of variance for varieties after fitting all other variables

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
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<th>Mean square</th>
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</thead>
<tbody>
<tr>
<td>With varieties, regression</td>
<td>15</td>
<td>138,309.68</td>
<td>922.06</td>
</tr>
<tr>
<td>Residual</td>
<td>1001</td>
<td>43,062.32</td>
<td>43.019</td>
</tr>
<tr>
<td>Total</td>
<td>1016</td>
<td>181,371.99</td>
<td></td>
</tr>
</tbody>
</table>

Without varieties, regression

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Regression</td>
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<td>134,714.00</td>
<td>10,363</td>
</tr>
<tr>
<td>Difference, regression</td>
<td>2</td>
<td>3,595.68</td>
<td>1,797.84</td>
</tr>
</tbody>
</table>

\[
F \text{ ratio} = \frac{1797.84}{43.019} = 38.6 \text{ significant at 0.01 level}
\]
Fig. 4. Photosynthesis versus solar radiation in Amsoy soybeans on August 3 (below) and August 18 (above)
Fig. 5. Photosynthesis at 1.1 ly/min versus leaf area index in soybean communities. (The data points are uncorrected for variety, date or temperature)
Fig. 6. The leaf area index - solar radiation interaction on photosynthesis in Amsoy soybean communities (adjusted to August 13 and 30° C)
13 AUG.
30°C
R² = .76

LY/MIN.

LEAF AREA INDEX

PHOTOSYNTHESIS - mg CO₂/dm².hr.

SOLAR RADIATION - LY/MIN.

LAI

0.5
0.2
0.4
0.8
1.2

0 - 60

0 - 1.2
Fig. 7. Photosynthesis versus solar radiation (fitted curves) and temperature in Amsoy soybean communities adjusted to August 13 and leaf area index 5
13 AUG.
$R^2 = 0.76$
$\text{LAI} = 5$

PHOTOSYNTHESIS - mg CO$_2$/dm$^2$.hr

AIR TEMPERATURE - °C

SOLAR RADIATION - lW/min

20 25 30 35 40

20 40 60
DISCUSSION

Net Assimilation System

In this discussion, the first objective is to summarize some limitations imposed upon the estimation of crop photosynthesis. In these experiments, limitations imposed by ambient CO₂ variation, leaf water deficit and air circulation are considered the major factors of interest in relating the field chamber environment to the real field environment.

Variation in the ambient CO₂ concentration, appeared to be the primary contributor to variation in photosynthesis estimates. Apparently, photosynthesis and respiration of surrounding crops, and combustion of automobile and heating fuels, changed the ambient CO₂ concentration. From the surrounding area, the wind brought to the chamber area parcels of air which varied widely in CO₂ concentration. Air from 3 meters above the crop seemed to have no less variation than air at ground level. Perhaps air at a greater height is more uniform in CO₂ concentration. Or perhaps, premixing air sources in a large tank would provide uniformity of sample intake.

In the preliminary trials air circulation within the chamber markedly affected canopy photosynthesis (Fig. 2). It was assumed that turbulent transfer of CO₂ from air to leaf stomata produced this effect (23). However, the distribution of solar radiation may be changed significantly by wind-produced leaf movement. This leaf movement causes a fluctuation in the
radiation environment of leaves and, probably, in physiological response. The intermittent periods of low radiation may allow time for regeneration of the CO₂ acceptor, for replenishment of CO₂ in the leaf mesophyll, and for translocation of assimilates. It is not known whether or not light flecking is important in canopy photosynthesis.

It was indicated in the methods and materials section that soil water was maintained at a high level by irrigating. So, it was assumed that plant water potential varied only in response to the vapor pressure deficit of the air. In preliminary trials at moderate or high solar radiation, the relative humidity of the chamber outlet air was about 25% higher than inlet air. At the existing temperature, this was a vapor pressure deficit of about 60 millibars in inlet air and 18 millibars in outlet air. In cotton an increase from 10 to 45 millibars of vapor pressure deficit in chamber air resulted in 30% decrease of crop photosynthesis (3). So, in the soybean chambers the average vapor pressure deficit of about 40 millibars was at a level which could have reduced crop photosynthesis. In an atmosphere of varying water vapor deficit, stomatal resistance, which is controlled by leaf turgor, regulates CO₂ assimilation. Leaf turgor, which relates closely to stomatal resistance is used to estimate water deficit effects on photosynthesis rather than measuring stomatal resistance.

Some relative turgor measurements were taken on upper leaves of plants outside the chambers. Leaf relative turgor was
correlated with solar radiation and temperature. So, in the statistical analysis relative turgor could not be entered as an independent parameter. Relative turgor was commonly about 95% in early morning, decreased to a low point of 87% at midday, and rose to around 92% at sundown. The relative turgor measurements of several upper leaves, sampled from within chambers, averaged 2% higher than those from outside the chambers (92.5% inside and 90.7% outside). Laing (39) found net assimilation in soybean canopies was constant when top leaves were above 90% relative turgor; the rate of assimilation dropped sharply to 50% of maximum at about 85% relative turgor. Thus, in this study the relative turgor of chamber leaves may have been below the critical level (90%) occasionally. However, in the statistical model the air temperature parameter also accounted for leaf water deficit, because relative turgor and chamber air temperature were correlated.

Effect of Crop Age

In view of the results of Sakamoto and Shaw (70) the decline in net photosynthesis with age of crop (days) was expected (Table 5). These investigators found a decline in $P_{\text{max}}$ after mid-August; this decrease was attributed to leaf age or seed respiration. This decline agrees with the findings of Kumura and Naniwa (37), Kumura (36), and Ojima et al. (64). Both increasing seed respiration and decreasing leaf efficiency lower crop net photosynthesis. Kumura and Naniwa (37) found
that seed plus pod respiration reached a maximum midway during the seed formation period and equalled total leaf respiration. Other workers have established that leaf photosynthesis decreases both with age of leaf and mineral content (64).

The reduction of photosynthesis from July 5 to September 9 was 7 mg CO$_2$/dm$^2$.hr, which represented 12% of $P_{\text{max}}$. By contrast, over a similar time period Sakamoto and Shaw (70) found a reduction of about 70% from $P_{\text{max}}$ in 76 cm row soybeans. The difference between their results and these from 25 cm row soybeans (Table 5) may be due to leaf area index and row spacing.

The topography of 76 cm rows allows a greater proportion of solar radiation to be intercepted by lower, older, less efficient leaves than in 25 cm rows (32). So, one advantage of narrow-row soybeans is that the youngest, most active leaves are the principal receivers of solar radiation, which may cause canopy photosynthesis to decrease less than in wide-row soybeans as lower leaves senesce.

**Effect of Varieties**

The detection under field conditions of differences among crop varieties in photosynthesis has important implications in crop breeding and improvement. Photosynthesis is a fundamental process and field conditions remove much uncertainty in relating varietal differences in photosynthesis to the real situation. The following interpretation of the results is concerned with independent varietal differences in photosynthesis (cause) and
with photosynthesis in varieties as related to other parameters (result).

In Table 5 the coefficients of the variety parameters for Amsoy and Harosoy are a large proportion of the approximate \( P_{\text{max}} \) of 60 mg CO\(_2\)/dm\(^2\).hr; so, variety differences are large. Because varieties were entered in the model before other factors correlated with variety such as L, these coefficients reflect the influence upon photosynthesis of all other factors (except days). Leaf area index was the most evident covariant; Amsoy produced the highest L. In previous determinations Amsoy was found highest in yield, dry matter production, and single leaf photosynthesis. So, Amsoy is a superior variety probably because of superior CO\(_2\) assimilation.

Because of dissimilar varietal maturity and total leaf area production, the variety coefficient differences in Table 5 are due partly to leaf amount, leaf age and crop respiration (this was discussed in the previous section). This confounding effect becomes more evident by comparing the magnitude of the variety coefficients in Table 5 with the contribution to reduction in lack of fit given in Table 6. This latter amount is only 2% of the total variation. Varietal photosynthesis differences alone (Table 6) are small, but unadjusted differences are large (Table 5), partly due to leaf area production. Similar results have been found by Stoy (75) and Muramoto et al. (55) in other crops. So, varietal photosynthesis differences, which were readily detectable, seem to be a measure of rather than a cause of
differences in productive capability among varieties.

It is reasonable that the interaction of variety by days, leaf area index, solar radiation, or temperature would contribute somewhat to differences in varietal photosynthesis rates. In this study interactions of varieties with other variables, while significant, were small. Consequently, little information could be gained by breaking out simple interactions involving varieties, and this was not done. Future investigations of such relationships could be fruitful. For instance, among races of *Mimulus*, Milner and Hiesey (44) found similar values of temperature optima for photosynthesis, but wide ranging photosynthesis responses to temperature extremes. This suggests that varietal selection resulting from responses to environmental extremes would be productive.

Response of Photosynthesis to Solar Radiation

The level and direction of CO₂ assimilation in response to solar radiation are discussed in this section. Comparisons are made between photosynthesis of leaves versus canopies, of wide versus narrow row spacings and of canopies where radiation varies due to solar altitude and cloudiness.

The $P_{\text{max}}$ of about 60 mg CO₂/dm² ground area·hr (Fig. 6) is similar to rates for 76 cm rows reported by Sakamoto and Shaw (70). Murata and Iyama (57) found rates of 35 mg CO₂/dm² ground area·hr at 4.1 L and 70 klux (about 70% full sunlight). This compares closely with the 38 mg CO₂/dm²·hr at 4 L and 1.0 ly/min shown in Fig. 6. In contrast, single leaves show lower $P_{\text{max}}$ per unit area. Rates have been reported of 25 mg CO₂/dm² leaf
area·hr for young soybean leaves and 15 for old leaves (36), and mean values of 20 (37) and 27 mg CO₂/dm² leaf area·hr (16). For comparison, corn leaves have general rates of 60 mg CO₂/dm² leaf area·hr (16). So, the maximum assimilation rates for soybean canopies are much larger than rates reported for leaves. However, rates for leaves and canopies of soybeans are potentially higher if the reported rates for corn leaves are a level which could be attained in soybeans through breeding.

Canopies have higher rates than single leaves. The basis for the advantage of canopies over single leaves was cited in the literature review. Oblique orientation of canopy leaves and wind movement of leaves allows solar radiation to be distributed over more than 1 L, an improvement because leaves are more efficient CO₂ assimilators at low radiation than at high radiation. For example, in Fig. 6 at 1 L the rate is about 22 mg CO₂/dm²·hr which is lower than cited rates above for single leaves. Apparently, some radiation is not intercepted, thus in the normal canopy light is distributed over more than 1 L.

Canopy photosynthesis is not radiation saturated (Fig. 6) except at low L where solar radiation interception is incomplete. Other results have shown radiation saturation of soybean canopy photosynthesis at greater than 1 L and under somewhat different conditions of solar radiation and canopy topography (36, 57, 70). Row spacing and manner of solar radiation variation (by changing solar altitude or by changing cloudiness) may vary the response of crop photosynthesis to radiation. The radiation,
in this experiment, varied most often due to changes in solar altitude. When the sun is high, or when crop rows are separated (such as the 76 cm rows of Sakamoto and Shaw (70), lower leaves are in a position to receive supraoptimal radiation. In a dense canopy (such as the 25 cm rows in this experiment) lower leaves are shaded regardless of solar altitude. This difference between 25 cm and 76 cm rows is a possible explanation of no apparent radiation saturation in this experiment (Fig. 6) and apparent saturation shown in the results of Sakamoto and Shaw (70).

Wide rows have lower extinction coefficients (radiation more widely distributed) than narrow rows (32). The "furrow" between wide rows allows more radiation to reach lower leaves than reaches lower leaves in narrow rows. The extinction coefficient varies diurnally and affects canopy photosynthesis in corn (6). So, differences in the radiation environment among soybean canopies probably account for differences in the radiation saturation level. In a dense canopy (25 cm rows) increasing radiation increases the photosynthesis of shaded lower leaves, whereas in wide rows increasing radiation only saturates exposed lower leaves. Thus, the saturation radiation level is lower in wide row canopies than in narrow row canopies. Equal rates of photosynthesis and lower saturation level indicates that wide rows are more efficient than narrow rows. Previous work (32) has shown that wide rows produce more dry matter per unit intercepted radiation than narrow rows. However, wide
rows intercept less total radiation and produce less dry matter and seed than narrow rows.

When interception approaches 100%, rates of dry matter production are equal but senescence of lower leaves quickly becomes a limiting factor, especially in wide row canopies. It seems likely that development of varieties with higher photosynthesis rates and higher dry matter production rates will reverse the trend to narrow rows because total interception will be less important and radiation distribution more important.

Interaction of Leaf Area and Solar Radiation

It was assumed that removal of lower leaves would not affect photosynthesis of remaining tissues. Ludwig et al. (41) examined the photosynthesis of upper leaves in cotton before and after lower leaf removal. The photosynthetic rate of upper leaves was not affected. So, it was presumed that the same treatment had no effect on soybeans. However, as L approaches zero (Figs. 5, 6) it appears that photosynthesis is positive. This may be due to lack of fit of the model, and to photosynthesis of stems and petioles whose light environment was enhanced by defoliation. This point was not investigated further.

The maximum quantity of leaf area occurred at midseason and then declined. So, the rates of photosynthesis at 5-8 L were not independent of seasonal effect. The cause and effect relationship is obscure, but high photosynthesis is associated
with large L at midseason. The importance to crop production is that attainment of large L is indicative of superior photosynthesis. However, the converse is not necessarily true. What is desired is sufficient L to attain and maintain the maximum rate of dry matter production. Previous data (32) show that soybeans may produce up to 12 L, although abscission of lower leaves prevents more than 8 L from accumulating on the plants. The optimum total leaf area production is unknown, but probably would vary with length of season.

From the curves in Fig. 6 it is evident that \( L_{\text{opt}} \) increases as the radiation level increases, which upholds the suggestion of Saeki (67). However, Saeki assumed the same potential photosynthesis for all leaves of a canopy; so, his predictions of canopy photosynthesis would be in error to the extent that leaf photosynthesis varies due to age or mineral deficiency. Also, the predictions would be affected by species morphology. For example, in soybeans lower leaves are older and less photosynthetically active than upper leaves, but, in grasses tillers commonly arise in the shade. Thus shaded leaves may be more active than upper leaves in grasses. How these factors affect canopy photosynthesis could be calculated from single leaf photosynthesis responses to solar radiation, and from leaf area distribution data. Whether the values in Fig. 6 are reasonable could be verified by this method.

Of particular interest is the continuous increase in photosynthesis up to 8 L (Fig. 6). Obviously, at high solar radiation
(and high solar altitude) the lowest leaves in the canopy have net CO₂ assimilation. At less than full sunlight (and lower solar altitude) direct radiation traverses a greater path length to the lower-most leaves than at full sunlight. For instance, with a canopy of 4 L and solar altitude of 30° direct radiation must traverse a path to reach lowest leaves equivalent to a canopy of 8 L and solar altitude 90° (that is, sine 30° = 4/8). This is approximately correct if leaf inclination to the sun is random. DeWit (82) has covered the calculation of solar radiation distribution in detail. At 75° solar inclination, about 9% of the solar radiation is transmitted through a planophile canopy (having horizontal leaves) of 5 L. Soybean leaves are plagiophile (highest frequency at oblique leaf orientation), and so would transmit a higher percentage, a large absolute amount in full sunlight. Consideration of solar altitude, then, explains how photosynthesis may increase up to an L of 8 whereas previous determinations of Lopt for dry matter production (72, 73) and total daily solar radiation distribution (32) suggest an Lopt of 3-4. This presents the question of why Lopt, as determined by dry matter production, does not reach a level of 8. One explanation is that the additional carbon fixed by the additional leaf area is compensated by night respiration. Also, the rates at high radiation may occur very rarely due to water deficit, and thus, contribute little to the dry matter production.

Saeki also assumed the same rate of respiration for all
leaves; so his theoretical production curves show a narrow optimum leaf area index. Black's data (11) for subterranean clover fit this pattern well, probably because emerging leaves arise from stems in the shade. Thus lower, shaded, rapidly-growing leaves may detract from total production at high L. The same argument holds for rice or other grains where emerging tillers may draw reserves from the main culm.

However, soybeans show no decline in rate of dry matter production at supraoptimal L (73). Photosynthesis also shows no decline (Fig. 6) at supraoptimal L when radiation is low. So, it is concluded that canopy respiration does not increase with an increase in leaf area and, so, does not detract from net photosynthesis. Then, individual leaf respiration must decrease as leaf area increases. This may be due to decreasing substrate for CO₂ evolution or to a non-association of respiration to leaf area. Some other findings (87) show that respiration in the light depends on immediately prior synthesized photosynthate. If true, this suggests that respiration is proportional to photosynthesis. The relationship of respiration to leaf area would be significant only up to values of L necessary for total solar radiation interception, because interception is correlated with photosynthesis, and photosynthesis, with respiration.
Temperature

The temperature parameter may be accounting for water deficit as well as the direct effect of heat on the photosynthetic or respiratory apparatus. As discussed previously, turgor measurements were taken but the results were inconclusive. Increasing water deficit, caused by high transpiration and low water supply would reduce photosynthesis by causing stomatal closure. Turgid excised leaves of sorghum, cotton, sunflower and *Thespesia populnea*, L. have been found with fully open stomata at very high temperatures (48°-60° C) in a humid atmosphere. Nevertheless, photosynthesis in cotton, sunflower and *Thespesia* was lower at 40° C than 30° C which indicates an independent temperature effect (15). Soybean leaves in the chambers at 40° C appeared turgid so stomata were probably open. If so, the temperature response was independent of moisture stress. In any case, these results were under humid conditions and indicative of the best response which could be expected for field soybeans. Assessment of water and temperature effects, independently, requires controlled temperature, water supply, humidity and measurement of leaf temperature and leaf water potential. As discussed previously, leaf relative turgor greater than 90% is probably optimum. In this experiment the atmosphere was constantly renewed and a combination of high vapor pressure deficit and soil-root resistance could have, occasionally, affected photosynthesis through lowering leaf water potential.
The optimum temperature was 25-30°C (Fig. 7). At less than 25°C the temperature response is likely independent of water deficit. At 40°C photosynthesis was about half $P_{\text{max}}$ in contrast to results of Fukui et al. (20), who found that single leaf photosynthesis fell to zero at 40°C. The difference is probably due to the fact that leaves in a canopy are oriented at various angles to the sun and leaf temperature may vary about air temperature. Consequently, some leaf temperatures might be near optimum even at 40°C air temperature. Genotypes with upright leaves would be expected to show less reduction in photosynthesis (or heat saturation) than genotypes with horizontal leaves because the high temperature effect comes at midday when the sun is at a high altitude.

Other studies (16) indicate that differences in response of photosynthesis of species to heat are due to a heat response of respiration. The ability to maintain $P_{\text{max}}$ at high temperature (>35°C) with fully open stomata indicates an efficient mechanism for CO$_2$ fixation in chloroplasts. Studies by El-Sharkawy and Hesketh (15) and Milner and Hiesey (44) suggest that advancement in crop production can come by selecting genotypes with high temperature optima. They found a positive correlation between $P_{\text{max}}$ and $T_{\text{opt}}$.

The lack of a significant interaction of temperature and leaf area on photosynthesis indicates no change in heat load distribution as leaf area index changes. Ludwig et al. (41) found an interaction in cotton; photosynthesis was reduced by
high temperature (40° vs 20° C) more at high leaf area index than low leaf area index. The difference was attributable to variation in dark respiration. This caused a broad optimum L of 3.0 or greater at 20° C and a narrow optimum L of 3.5 at 40° C. Perhaps, a long period of hot weather in the field might result in an apparent narrow Lopt in soybeans too. One manifestation of high temperature found by Ludwig et al. (41) was that the maximum L attainable was limited by high temperature due to abscission of lower leaves.

The nature of the radiation by temperature interaction (Fig. 7) suggests that the frequently observed light saturation effect is due to associated increase in temperature with increasing radiation. Sakamoto and Shaw (70) reported that light saturation of soybean canopies occurs regularly. Such was the case in these studies when midday temperature exceeded 30° C. Fig. 4 in which photosynthesis is not corrected for temperature effects shows a tendency for photosynthesis to be saturated at less than maximum solar radiation (about 1.5 ly/min). At low radiation, i.e. low solar altitude, temperature falls below optimum. With equal radiation but lower temperature photosynthesis was usually higher near midday than late afternoon. Of course, this difference may have been due to factors associated with time of day, such as, accumulation of photosynthate. Nevertheless soybean canopies demonstrate maximum photosynthesis in full sunlight and moderate temperature when water is adequate.
SUMMARY

Soybean (Glycine max L., Merr.) varieties Amsoy, Harosoy 63 and Harosoy na na were grown in the field in 25 cm rows at a density of 26 plants/m². Soil fertility was adequate and supplemental irrigation was provided.

Apparent photosynthesis (P) (CO₂ assimilation) was estimated in 1.2 m² crop areas within transparent plastic chambers. Photosynthesis rates were calculated from measurements of CO₂ concentration, air temperature, and air flow rates.

The leaf area index (L) of the sample areas varied naturally, and it was also varied by removing lower leaves in discrete layers. A range of L from 0.36 to 8.01 was achieved.

Estimates of P and associated parameter were taken on 25 of the 67 days from July 5 to September 9, 1966. The data were fitted to a multiple regression model by regressing P on varieties, days, leaf area index, solar radiation, air temperature, air flow rate, and some quadratics and cross products.

Increasing maturity (days) accounted for a reduction of 7 mg CO₂/dm²·hr from the first to last day when measurements were taken. Evidence indicates this reduction was due to decreasing leaf efficiency (brought on by age) and possibly by increasing pod respiration.

Variety differences averaged 8 mg CO₂/dm²·hr from highest to lowest. In addition to differences in potential leaf photosynthesis, leaf area production may have caused these differences.
between varieties. Interactions involving varieties were small and they were disregarded. It is concluded that variety differences in yield potential can be detected by measuring P, but leaf area production rates and leaf area duration are also important parameters determining yield. It is suggested that response of P to extremes in temperature would be a useful index in selecting superior varieties because of the relationship of temperature response to the efficiency of the CO₂ fixation mechanism.

The optimum temperature for photosynthesis was 25-30°C and there were no significant interactions involving temperature. Increasing solar radiation caused an increase in air temperature; so, P responded simultaneously to radiation and air temperature. As air temperature exceeded the optimum, there was no further increase in P when solar radiation increased. This caused P to be radiation saturated due to excess heat.

At constant air temperature, P was not radiation saturated up to 1.2 ly/min solar radiation. The response of P to increasing radiation was much greater in a canopy of 8 L than in one of 1 L, probably because of loss of radiation to the soil in the 1 L canopy.

The L required for maximum photosynthesis was about 4 at 0.2 ly/min and would have been greater than 8 at 1.2 ly/min. Also, soybean canopies did not describe an L<sub>opt</sub>, i.e. P did not decrease at L exceeding that needed for maximum photosynthesis.
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ACKNOWLEDGEMENTS

I wish to acknowledge those who aided me in the research and its presentation herein. Appreciation goes to Dr. Richard Shibles who directed my studies and research and who has been most helpful in many other ways. I would like to thank Dr. Robert Shaw, Dr. C. R. Weber, and Dr. Irvin Anderson who aided, advised and supplied material or equipment in this work.

Many thanks go to my wife, Barbara, who contributed her labor in the research and who helped prepare this dissertation. Finally, I wish to acknowledge the inspiration of my children who may likewise be inspired to continue their education when reading this thesis.