ESTIMATING CARBON BALANCE OF FIELD-GROWN SOYBEANS

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ii

TABLE OF CONTENTS

	PAGE
ACKNOWI	LEDGMENTSii
LIST OF	F TABLESv
LIST OF	F FIGURESvii
ABSTRAC	стхі
CHAPTER	R
I. J	INTRODUCTION1
II. I	LITERATURE REVIEW
	Carbon Dioxide Exchange Rate
III. M	METHODS AND MATERIALS
	Plant Material and Treatments. 21 CO, Exchange Measurements. 24 Gröss Photosynthesis Estimation. 25 Total Daily Photosynthesis. 26 Dry Matter Sampling. 28 Respiration Cost Estimation. 29 Statistical Analysis. 33
IV. H	RESULTS AND DISCUSSION
	Weather and Irrigation

CHAPTER

PAGE

			oots. arbon											
v.	SUMMARY	AND	CONC	LUSIC	NS.		• • • •	•••	•••	• •	• • •	•••	 • • •	95
APPEN	DIX	••••		• • • • •	• • • •	••••		•••	•••	•••	• • •	••	 1	00
BIBLI	OGRAPHY.				• • • •			•••		•••	• • •	• • •	 1	.23
BIOGR	APHICAL	SKET	сн										 1	.28

LIST OF TABLES

TABLE	PAGL
1.	Treatments and subtreatments22
2.	Grams of glucose (CH ₂ O) required for synthesis of one gram product (protein, fat and structural carbohydrate
3.	Fraction of protein, fat and structural carbo- hydrate (Str. CH ₂ O) in soybean tissue as used in soybean tissue as used in SOYGRO32
4.	Reproductive growth stages for 'Cobb' soybean subjected to defoliation and irrigation treat- ments, expressed as days after planting on June 26, 1981, at Gainesville, Florida37
5.	Cumulative daily gross photosynthesis (CUMDPG) for the entire season and during the seed filling period in relation to relative final seed yield53
6.	Seasonal total, growth, and maintenance respiration estimated by SOYGRO for all the treatments67 $$
7.	Field measured and SOYGRO (model) estimated seed growth rate (SGR) on a land area basis for all treatments90
8.	Total seasonal carbon (CH ₂ O) available and respective total seasonal above-ground dry matter accumulation based on field measure- ments and SOYGRO simulation92
A.1.	Climatic data for the 1981 season101
A.2.	Parameters of the rectangular hyperbolae for instantaneous gross photosynthesis and percent of variation explained by the model
A.3.	Parameters of the rectangular hyperbolae for daily gross photosynthesis and percent of variation explained by the model

TABLE

A.4	Leaf area index (LAI) and dry matter accumu-
	lation throughout the season for all the
	treatments on 'Cobb' soybean, 1981,
	Gainesville, FL. Number of replicates vary
	from 1 to 4

PAGE

LIST OF FIGURES

FIGURE PAG	Е
 Rainfall, pan evaporation and irrigation distribution for the main treatments on 'Cobb' soybean planted June 26, 1981, at Gainesville, Florida	5
 Photosynthesis-light response curve of well- irrigated (non-defoliated) treatment at 39 and 91 days after planting (DAP). Points represent four and two replicate field locations measured at 39 and 91 DAP, respectively	8
 PG1500 for the three non-defoliated treatments. PG 1500 is the instantaneous PG predicted from rectangular hyperbolae equations at PAR of 1500 u mole/m²s	0
 Daily photosynthesis-daily PAR relationship for the well-irrigated (non-defoliated) treatment at 39 and 91 days after planting (DAP)4 	3
 Comparison of total daily photosynthesis (TDPG) between vegetative stage water deficit (non-defoliated) treatment and the well- irrigated (non-defoliated) treatment	5
 Comparison of total daily photosynthesis (TDPG) between vegetative stage water deficit (defoliated) treatment and the well-irrigated (non-defoliated) treatment4 	6
 Comparison of total daily photosynthesis (TDPG) between reproductive stage water deficit (non-defoliated) treatment and the well-irrigated (non-defoliated) treatment4 	7
 Comparison of total daily photosynthesis (TDPG) between reproductive stage water deficit (defoliated) and the well-irrigated (non-defoliated) treatment4 	8

FIGURE

PAGE

9.	Comparison of total daily photosynthesis (TDPG) between defoliated and non-defoliated plots in the well-irrigated treatment49
10.	Total, maintenance and growth respiration for the vegetative stage water deficit (non- defoliated) treatment
11.	Total, maintenance and growth respiration for the vegetative stage water deficit (defoliated) treatment
12.	Total, maintenance and growth respiration for the reproductive stage water deficit (non- defoliated) treatment60
13.	Total, maintenance and growth respiration for the reproductive stage water deficit (defoliated) treatment61
14.	Total, maintenance and growth respiration for the well-irrigated (non-defoliated) treatment62
15.	Total, maintenance and growth respiration for the well-irrigated (defoliated) treatment63
16.	Comparison of leaf dry matter accumulation between simulated (line) and field sampled (circles) for the vegetative stage water deficit (non-defoliated) treatment
17.	Comparison of leaf dry matter accumulation between simulated (line) and field sampled (circles) for the vegetative stage water deficit (defoliated) treatment
18.	Comparison of leaf dry matter accumulation between simulated (line) and field sampled (circles) for the reproductive stage water deficit (non-defoliated) treatment
19.	Comparison of leaf dry matter accumulation between simulated (line) and field sampled (circles) for the reproductive stage water deficit (defoliated) treatment
20.	Comparison of leaf dry matter accumulation between simulated (line) and field sampled (circles) for the well-irrigated (non- defoliated) treatment

FIGURE

21.	Comparison of leaf dry matter accumulation between simulated (line) and field sampled (circles) for the well-irrigated (defoliated) treatment74
22.	Comparison of stem dry matter accumulation between simulated (line) and field sampled (circles) for the vegetative stage water deficit (non-defoliated) treatment
23.	Comparison of stem dry matter accumulation between simulated (line) and field sampled (circles) for the vegetative stage water deficit (defoliated) treatment
24.	Comparison of stem dry matter accumulation between simulated (line) and field sampled (circles) for the reproductive stage water deficit (non-defoliated) treatment
25.	Comparison of stem dry matter accumulation between simulated (line) and field sampled (circles) for the reproductive stage water deficit (defoliated) treatment
26.	Comparison of stem dry matter accumulation between simulated (line) and field sampled (circles) for the well-irrigated (non- defoliated) treatment
27.	Comparison of stem dry matter accumulation between simulated (line) and field sampled (circles) for the well-irrigated (defoliated) treatment
28.	Comparison of seed dry matter accumulation between simulated (line) and field sampled (circles) for the vegetative stage water deficit (non-defoliated) treatment
29.	Comparison of seed dry matter accumulation between simulated (line) and field sampled (circles) for the vegetative stage water deficit (defoliated) treatment
30.	Comparison of seed dry matter accumulation between simulated (line) and field sampled (circles) for the reproductive stage water deficit (non-defoliated) treatment

PAGE

FIGURE

31.	Comparison of seed dry matter accumulation between simulated (line) and field sampled (circles) for the reproductive stage water deficit (defoliated) treatment
32.	Comparison of seed dry matter accumulation between simulated (line) and field sampled (circles) for the well-irrigated (non- defoliated) treatment
33.	Comparison of seed dry matter accumulation between simulated (line) and field sampled (circles) for the well-irrigated (defoliated) treatment
A.1	Comparison of daily gross photosynthesis simulated by SOYGRO versus field measured TDPG for the vegetative stage water deficit (non-defoliated) treatment
A.2	Comparison of daily gross photosynthesis simulated by SOYGRO versus field measured TDPG for the vegetative stage water deficit (defoliated) treatment
A.3	Comparison of daily gross photosynthesis simulated by SOYGRO versus field measured TDPG for the reproductive stage water deficit (non-defoliated) treatment19
A.4	Comparison of daily gross photosynthesis simulated by SOYGRO versus field measured TDPG for the reproductive stage water deficit (defoliated) treatment
A.5	Comparison of daily gross photosynthesis simulated by SOYGRO versus field measured TDPG for the well-irrigated (non-defoliated) treatment
A.6	Comparison of daily gross photosynthesis simulated by SOYGRO versus field measured TDPG for the well-irrigated (defoliated) treatment

Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

ESTIMATING CARBON BALANCE OF FIELD-GROWN SOYBEANS

By

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Daily total canopy photosynthesis estimated throughout the whole season in field-grown soybean (<u>Glycine max</u> (L.) Merr., 'Cobb'), was input into the Florida Soybean Crop Growth Simulator (SOYGRO) which was allowed to estimate respiration costs (growth and maintenance respiration) and allocate assimilate to dry matter production. Simulated results were compared with field dry-matter measurements.

The soybean crop was subjected to three water regimes (vegetative phase water deficit, reproductive phase water deficit, and well-irrigated) and two levels of insect defoliation (non-defoliated and approximately 30 percent defoliated), in a split-plot design with four field replications. These treatments provided a range in seasonal carbon input to compare with induced variations in dry matter production and yield.

хi

Carbon exchange rate was measured in the field once or twice weekly at mid-day, using a portable assimilation chamber. Efflux of CO₂ from crop and soil in darkness was also measured to allow calculation of total canopy photosynthesis. Photosynthesis-light response equations were developed and used with hourly values of photosynthetic photon flux to give daily integrated total canopy photosynthesis for every day of the season.

Total seasonal photosynthesis was reduced in all treatments when compared to the well-irrigated (nondefoliated) plants. Water deficit treatments reduced total seasonal photosynthesis by 16.2 and 12.5 percent, compared to the well-irrigated plants. Defoliation caused reductions of 4.8, 4.8 and 4.5 percent in total seasonal photosynthesis when compared within the respective main plot water treatments. Final seed yield was best correlated with the cumulative photosynthesis during the linear phase of the seed filling period.

Dry matter accumulation in plant parts estimated by SOYGRO (inputing field-measured photosynthesis) stayed within 15 percent of the equivalent field measured dry weights.

This study suggests the feasibility of using a portable chamber technique to measure canopy photosynthesis, making possible the study and validation of simulation model parameters, in soybeans.

xii

CHAPTER I

INTRODUCTION

In a simple analysis, carbon balance of a plant is regulated by the rate of carbon being fixed in photosynthesis, the rate of carbon being transformed to plant material, and the rate of carbon being given up by the respiratory processes.

The photosynthetic rate of leaves responds to external factors, and to plant factors. Under natural conditions the more important external factors are irradiance, temperature, water and mineral nutrients. Internal factors could be morphology, anatomy, age, stomatal behavior, and others.

The effects of those factors on photosynthesis and respiration can be studied in growth chambers or even in the field on single leaves to establish parameters and relationships; however, validity of such relationships needs to be tested under field conditions using whole plants, where many interactions occur which are not found in controlled conditions.

Crop modellers have access to powerful computers and to sophisticated computer programming, but the availability of field data for testing and validation is at best incomplete.

The overall objective of the present research was to estimate a carbon balance under field conditions for soybean growing under several combinations of insect defoliation and water deficit. Those treatments were utilized to obtain patterns of photosynthesis and growth, and not to study effects of defoliation or drought <u>per se</u>. Specific objectives were 1) the study of relationships between field measured photosynthesis and field measured dry matter and 2) validation of photosynthate partitioning and respiratory cost estimates by the Florida Soybean Crop Growth Model. (SOYGRO).

CHAPTER II

LITERATURE REVIEW

Carbon Dioxide Exchange Rate

The CO, assimilation in plants has been described as a process in which during the daytime photosynthate is progressively formed in the leaves of plants and then is translocated to growing tissues throughout the plant. Photosynthate is mainly sucrose, but also is in the form of other sugars and a considerable range of nitrogenous compounds. Photosynthate is utilized continuously in the synthesis of new plant biomass and in the maintenance of existing material. Phtosynthate in excess of the requirements is drawn upon during the subsequent nighttime to provide energy and carbon skeletons for synthesis (growth) and maintenance processes. As the night progresses, the concentration of stored substrate falls, and the rate of use decreases (Wilson et al., 1978). Any external or internal factor affecting either photosynthesis or respiration will affect growth and development and ultimately yield of a crop.

The photosynthetic rate of leaves respond to external factors, and to plant factors. Under natural conditions the more important external factors are light (intensity),

temperature, water and mineral nutrients. Internal factors could be morphology, anatomy, age, stomatal behavior, and others.

Study of those factors on photosynthesis and respiration on growing single leaves in growth chambers or even in the field are useful to establish parameters and relationships; however, validity of relationships need to be tested under field conditions using whole plants, where many interactions occur which are not found in controlled conditions.

Community canopy carbon exchange rate and dry matter accumulation were measured simultaneously for several plant species (Cartledge and Connor, 1972; Kanemasu and Hiebsch, 1975; Vietor and Musgrave, 1979). Effects of leaf carbon exchange rate (CER), plant geometry, leaf area, and other factors were naturally integrated within the light and temperature conditions of the canopy chambers to measure CO₂ uptake per unit soil area. Some agreement was observed between relative dry matter accumulation rate and CO₂ uptake among species, but substantial discrepancies were also found.

Larson <u>et al</u>. (1981) pointed out a disadvantage of using permanent enclosures for studying gas exchange of plant stands, in that a plant stand can acclimate to the enclosure conditions and in a short time become different physiologically from a plant in an undisturbed stand nearby.

Gifford (1974) observed that in a pure crop stand with a closed canopy many factors other than the potential photosynthesis of single leaves come into play to determine the net downward flux of CO_2 into the crop surface during the day. He cited factors of leaf area index and its distribution with height, leaf inclination, respiration by non-photosynthetic parts of the systems, and feedback control of leaf photosynthesis by sink utilization of assimilates.

Portable and temporary chambers for measurement of canopy carbon exchange rate have been widely used (Kanemasu and Hiebsch, 1975; Baker, 1965; Peters <u>et al</u>., 1974; Puckridge, 1971).

Respiratory Processes

Respiratory losses have been categorized into two components: growth respiration and maintenance respiration. The relevance of these processes in crop production and growth simulation has been recognized by crop and plant physiologists. McCree (1970, 1974 and 1976) used whole plant measurements to analyze growth and maintenance respiration.

Penning de Vries (1975 and 1976) and Penning de Vries <u>et al</u>. (1974) have applied a quantitative biochemical approach to study those processes.

Thornley (1970 and 1977), and Thornley and Hesketh (1972) made important mathematical contributions to the understanding of maintenance and growth respiration.

Maintenance, according to Penning de Vries (1976), includes the processes which maintain enzyme pools, cellular structures, gradients of ions and metabolites, and the process of physiological adaptation that maintains cells as active units in a changing environment.

According to Penning de Vries (1972 and 1976) the rate of maintenance respiration processes in higher plants is estimated to require 1 to 4 percent of the dry matter per day to be respired to produce the needed energy.

McCree (1974) reported a value of about 15 mg C/g C/24 hours for sorghum at 30 C. Higher values have been reported for other species grown at 30 C: sunflower (<u>Helianthus annuus</u> L.) 47 mg C/g C/24 hours (Penning de Vries, 1975; and Penning de Vries <u>et al</u>., 1974), white clover (<u>Trifolium repens</u> L.) 36 to 60 mg C/g C/24 hours (McCree and Kresovich, 1978; McCree and Silsbury, 1978), and subteranean clover (<u>Trifolium subterraneum</u> L.) 48 mg C/g C/24 hours (McCree and Silsbury, 1978).

Jones <u>et al</u>. (1978) observed a considerable drop in the maintenance efflux from a perennial ryegrass (<u>Lolium perenne</u> L.) crop as it matured. The drop was correlated with a large decrease in protein content.

Growth respiration is related to the synthesis processes occuring in plants. From theoretical considerations,

Penning de Vries (1972) provided estimates of the cost of synthesizing the major components of plant biomass (amino acids, protein, cellulose, lignin, lipids and others) in terms of glucose. In his studies, Penning de Vries considered maximum theoretical efficiency to produce ATP and NADH, but used stoichometric costs for ATP or reductant for biochemical pathways as estimated by biochemical studies.

Hunt and Loomis (1979) predicted respiration during sugar-beet growth simulation by assuming an intimate coupling to growth and maintenance processes. The predicted respiratory responses were complex, reflecting interaction between past and current synthetic activities, so that increases in either component of respiration (growth or maintenance) generally depressed the other, as either growth rate was lowered (reducing growth respiration) or less living biomass accumulated (reducing maintenance respiration). The ratio of maintenance to growth respiration ranged from 0.6 to 2.67, reflecting those changes.

Effects of Light on Carbon Balance

Classic studies have demonstrated that there is a photo saturation point in the light response curve of photosynthetic rate of single leaves exposed to full sunlight. However, leaves of a plant shade each other as the leaf area index (LAI) increases, and under such conditions, leaves at the top of the canopy could be at the saturation point, while many leaves inside the canopy receive light below the

saturation point. Thus an increase of light intensity at the top of the canopy beyond the saturation point could improve the photosynthetic rate of the canopy.

Bowes <u>et al</u>. (1972) showed that the saturating light intensity and maximum photosynthetic rate of field grown soybean leaves are a direct function of the light intensity received during growth. Also, Beurlein and Pendleton (1971) suggested that soybean leaves acclimate to the light environment.

Jeffers and Shibles (1969) found that light saturation did not occur in soybean canopies having LAI greater than 4.

Chalker (1980) studied the relationship between the rate of gross photosynthesis and irradiance, and found that the relationship could be simplified to the hyperbolic tangent function. Light response curves for photosynthesis exhibit similar shapes. Initially the rate of photosynthesis is nearly directly proportional to irradiance. Thereafter, photosynthesis approaches a horizontal asymptote which is defined as the photosynthetic capacity, photosynthetic maximum or assimilation number.

Rectangular hyperbolae derived by direct analogy to the Michaelis-Menten equation for enzyme kinetics, have been used to describe the relationship between photosynthesis and irradiance (Duncan, 1971; Ingran et al., 1981).

Kanemasu and Hiebsch (1975) determined canopy net carbon dioxide exchange rates of sorghum, soybean, and wheat

throughout a growing season. They observed an apparent light saturation in both soybeans and wheat.

McCree and Loomis (1969) studied photosynthetic rates in fluctuating light. Under the most extreme conditions, light at sunlight levels versus complete darkness once a second, the deviations from the steady-state rates were only 20 percent. Also they found that when light was reduced but not extinguished, the plants acted as nearly perfect integrators, for all periods of alternating light between 10^{-2} and 10^3 seconds.

Huxley (1969) grew cotton, mustard, radish, tobacco and tomato for 8-16 days under strips of shades and daylight. The shades were fixed or made to move laterally by a onestrip width, so as to subject any part of a leaf to alternate conditions of high and low light intensities for cycles of 86, 16 or 2.2 seconds. Huxley did not detect differences in dry weight among treatments.

McCree and Troughton (1966) found that plants added weight over the few days of their experiment, even those placed in light levels initially below their compensation point. The plants adapted their respiration rates (mostly from rate of synthesis of material) to low assimilate supply conditions. The rate of respiration was very dependent on light level and began to fall as soon as the light level was reduced. The drop in respiration was not due to the death of leaves, since the number of dead leaves was not

sufficient to explain the drop in respiration. Also the drop in respiration was not due to a drop in temperature. The respiration rates of the plants growing at various light levels were proportional to their photosynthesis rates.

de Wit (1959) in his model subtracted 20 percent from the total gross photosynthesis of the crop for respiration losses. This amounts to an assumption that the respiration rate is a constant proportion of the rate of gross photosynthesis.

Leafe (1972) measured ryegrass canopy CER at several irradiance levels and in darkness throughout the season. Cumulative CO_2 exchange for growth periods, estimated from the CER's and climatic data, were in approximate agreement with total dry matter accumulation for the growth period if root respiration estimates were assumed to be 15 to 20 percent of the sum of the CER in light and CO_2 efflux rate in darkness.

Wilson <u>et al</u>. (1978) compared the CO_2 balances of communities of subterraneum clover plants exposed to variable and constant photon fluxes. They monitored CER continuously during a 4-day test. During two of those days the communities were exposed to photosynthetic photon flux densities (PPFD) which were varied over the range 0.26 to 2.00 mE/m²/s in a pattern that emulated the diurnal pattern of a clear day at 30 C. During the other two days the PPFD was constant at 1.20 mE/m²/s. The photoperiod was 12 hours throughout. The PPFD was adjusted so that the integrated totals of CO_2 taken up during the daytime were identical for the two treatments. The patterns and the totals of CO_2 released during the nightime were found to be almost identical for the two treatments. Consequently, the diurnal CO_2 balance of the plants was not affected by different patterns of photon flux.

McCree (1982) discovered differences in maintenance requirements for white clover (Trifolium repens L.) growing at high versus low growth rates, in whole-plant assimilation chamber studies. After several days in high light, during which the growth rate was 30 grams of dry matter per meter square per day, the light level was reduced so that the plants were in a maintenance condition (zero growth rate). They were kept in this condition for 27 days. The maintenance requirement fell gradually from 39 to 23 mg C per gram of C per day, while the growth conversion efficiency remained constant at 0.67 g C per g C. The protein content also remained constant at 27 percent. McCree interpreted the results in terms of Thornley's dynamic model of plant growth. The model was modified to include starch storage. In Thornley's (1970 and 1976) model for the daily carbon balance of a plant, the maintenance requirement is first subtracted from the carbon input; then the remainder is converted into new biomass with an efficiency Yg (the yield of the growth processes). Typical values of Yg range from 0.6 to 0.8 g per g, while values of

m (maintenance requirement per unit biomass per 24 hours) fall in a much wider range, 15 to 50 mg per g per day (Hunt and Loomis, 1979). This is partly due to the fact that m has the dimensions of a rate, and therefore is a function of temperature, while Yg is a dimensionless ratio and is independent of temperature because biochemical stoichmetry of respiration and synthesis are not affected by temperature in the range of growth.

McCree and Kresovich (1978) monitored CER of white clover stands for several days at 30 C and at high light intensity level (2.0 mE/s/m²), and at different day/night lengths in the range of 6/18 to 18/6 hours. The plants were kept in continuous darkness for 2 days. Thornley's growth and maintenance coefficients were calculated from 24 hour CO, exchange rates (Thornley, 1970 and 1976). The yield of new biomass carbon per unit of carbon input into growth (Yg) was found to be independent of daylength, the average being 0.74. The maintenance loss rate of carbon per unit of biomass carbon present (m) increased from 36 to 53 mg/g/ 24 hours as the daylength increased from 6 to 18 hours. This was shown to be an indirect effect of the seven-fold increase in growth rate (24 hour net gain) from 12 to 90 g $CO_{\gamma}/m^2/24$ hour. They found no direct effect of daylength on either growth or maintenance requirements.

Effects of Temperature on Carbon Balance

Penning de Vries (1976) suggested that increase in temperature raises the cost of maintenance by stimulating protein turnover and active ion fluxes.

McCree and Silsbury (1978) reported that at 22.5 C and below, the CER for subterraneum clover was at a constant rate throughout the night, as previously reported for white clover at 20 C (McCree, 1974). At higher temperatures, in both species, the CER was consistently greater during the first half of the night. They attribute this to a greater initial rate of substrate use at higher temperatures. At lower temperatures, perhaps the plants were not capable of using substrate at a rate sufficient to show this effect; because carbon reserves were depleted less rapidly, the respiration rate could be maintained all night.

Also, according to McCree and Silsbury (1978), the net increase in CO_2 content over 24 hours is the equivalent of the rate of dry matter production of the stand. The net CO_2 uptake (daytime minus nighttime) was only slightly dependent on temperature in the range of 10 to 30 C. At 35 C, the daytime uptake was smaller and the nighttime efflux was larger than at 30 C. Since the maintenance component is a function of temperature, the net CO_2 gain would hypothetically be much more sensitive to increasing temperature in old stands than in young stands.

McCree (1974) developed equations for respiration in crops. The equations were developed from CER of whole

plants grown under constant conditions. The dark respiration rate was separated into two components. The maintenance component was taken to be the efflux of CO_2 after more than 48 hours in the dark at constant temperature. This component was proportional to the dry weight of the plant and was a strong function of temperature. The growth component was the difference between the maintenance component and the total efflux during a normal night period. This component was proportional to the total influx during the previous daytime period, and was independent of species and temperature.

McCree and Amthor (1982) determined the carbon balance of dense stands of white clover with the following diurnal cycles of temperature: constant temperatures of 10, 20, and 30 C; and day/night temperatures of 30/20 C and 30/10 C. They showed that carbon balance with a diurnal cycle of temperature could be predicted from the balances at constant temperature of 30, 20 and 10 C. With a 30 C day, the daily carbon gain (growth rate) increased as night temperature decreased. The gain with a 30/10 C diurnal cycle was less than that with a constant 20 C, although daily substrate input of carbon from photosynthesis was the same for both treatments. McCree and Amthor (1982) explained this by the geometric nature of the relationship between the maintenance requirement and temperature (it increased 100 percent from 20 to 30 C, but decreased only 50 percent from 20 to 10 C).

Vietor and Musgrave (1979), based on the CER in darkness at 10, 15 and 30 C, established a linear relationship between air temperature in the measurement chambers and dark respiration for the range of 10 to 30 C for maize canopies. Values of Q10, calculated from the regression equations, were greater than 3.4 if temperature was increased from 10 to 20 C and equal to 1.7 for a temperature change from 20 to 30 C.

Warrington <u>et al</u>. (1977) found that soybeans grown under constant day/night temperatures (23 C) had significantly more leaves and were taller at 22-day harvest than those grown in either of the fluctuating temperature regimes (26/20 and 29/17 C). Leaf, stem and total plant dry weights were higher in the 29/17 C treatment than in either of the two other thermoperiods. Dry weight differences were not large, however, ranging from 9 to 20 percent higher in the 29/17 C than in the 23/23 C plants. The largest increase was in stem dry weight (20 percent) with relatively little increase in leaf dry weight (9 percent) and a minor decrease in leaf area (2 percent). Photosynthetic rate differences were not detected between treatments.

Effects of Defoliation on Carbon Balance

Different types of pests (insects, pathogens, nematodes, and weeds) have various mechanisms by which they affect carbon flow processes of crop growth and thereby reduce yield: 1) pests reduce photosynthetic photon flux

absorbed by leaves; and 2) they affect crop process rates of C fixation, translocation, nitrogen fixation and tissue growth (Boote, 1981).

In the literature there are many studies showing the effects of artificial or natural defoliation on soybean yield and dry matter accumulation in various plant parts. However, few studies have shown the effects of defoliation on photosynthesis and respiration.

There is a consensus among researchers that soybean tolerates moderate defoliation without major yield loss (Turnipseed, 1972; Todd and Morgan, 1972). However, the effect of an equal level of defoliation is dependent upon crop growth stage. As crop development proceeds, soybean loses its ability to recover from defoliation injury (Hinson et al., 1978).

Many researchers agree that defoliation during pod set through seed filling poses the greatest yield reduction (Turnipseed, 1972; Todd and Morgan, 1972; Hinson <u>et al</u>., 1978; Caviness and Thomas, 1980).

Poston <u>et al</u>. (1976) studied the effects of artificial and insect defoliation on soybean net photosynthesis. Net carbon exchange rates were measured by using an excised leaflet technique. Cork-borer, paper-punch, and along-themidrib leaflet bisection adequately simulated defoliation of soybean leaflets by <u>Plathypena scabra</u> (F.) and <u>Cynthia</u> <u>cardui</u> (L.). Net carbon exchange rate was significantly reduced 12 hours post-defoliation but was not significantly different from the check 24 hours post-defoliation on a leaf area basis.

Jones <u>et al</u>. (1982) found that peanut plants manually defoliated 75 percent on different dates were initially reduced in canopy CER 45 to 70 percent due to loss of LAI and to a so-called 'shock effect' or the lack of adaptation of previously shaded leaves to higher light levels. After one or two weeks they observed a recovery of CER, which they attributed to increase in LAI and to photosynthetic adaptation of lower leaves to increased light penetration in the canopy.

Boote <u>et al</u>. (1980) found that artificial defoliation of upper leaves of peanuts (LAI reduction of 25 percent) reduced canopy CER by 35 percent, although it did not reduce light interception. They attributed the photosynthetic reduction to the inability of lower leaves to respond to the increased light reaching them.

Ingram <u>et al</u>. (1981) studied the relationships among insect-induced defoliation, CO_2 exchange rate, and reproductive growth in field grown soybean. They observed a reduction of 50 percent in LAI and 40 percent in leaf weight. Reduction of PN1500 (net canopy photosynthesis at 1500 uE/m²/s) was 6.8 mg CO_2/dm^2 /hour during the seed filling period due to defoliation treatments.

Hinson <u>et al</u>. (1978) artifically defoliated soybeans at rates of 33 and 67 percent on four dates: 3, 17, 31 and 42 days after flowering. They estimated that from 5.2 to

28.4 kg N/ha in the leaf tissues were lost and unavailable to developing seeds. The 28.4 kg N/ha loss would account for a seed yield reduction of 428 kg/ha (actual reduction was 913 kg/ha). They concluded that additional processes are involved, which include duration and rate of photosynthesis.

Caviness and Thomas (1980) measured the yield response of a determinate soybean cultivar to four different levels of defoliation under irrigated and non-irrigated conditions. They concluded that yield reductions under irrigated and non-irrigated conditions were proportionately similar because all interactions with irrigation treatments were non-significant.

Effects of Water Deficit on Carbon Balance

Daily rate of carbon accumulation per unit dry weight decreases as the mean daytime leaf water potential decreases (Boyer, 1970a, 1970b; Brix, 1962; Wilson <u>et al</u>., 1980).

Silvius <u>et al</u>. (1977) studied the effects of water stress on carbon dioxide exchange rate and assimilate distribution in chamber-grown soybean plants, during the vegetative, flowering, and pod-filling stages of development. They found that when water was withheld, the decrease in CER was correlated with the increase in stomatal resistance at leaf water potentials as low as -21 bars; however, CER and stomatal resistance recovered to predessication levels within 24 hours after rewatering. When leaf water

potentials were allowed to drop below -21 bars, recovery of CER lagged behind the return of stomatal resistance to predessication levels. They suggested that additional factors may be involved.

Penning de Vries (1974) and Yamaguchi (1978) reported that neither the biosynthetic pathways nor the chemical composition of dry matter formed was affected by water deficit.

Silvius <u>et al</u>. (1977) exposed whole plants to labeled CO₂ and determined its percent distribution. At leaf water potential of -15 bars to -20 bars, plants displayed alterations in labeled-C distribution among plant parts corresponding to alterations in dry weight distributions. They observed that compared to well-watered plants, relatively more labeled-C was found in the roots for water stressed plants before the pod filling stage. Less labeled-C was retained in the leaf blade of these plants, but this response was reversed during pod-filling. They suggested that drought decreased CER and altered assimilate distribution, producing growth modifications that favor efficient use of the limited supply of fixed carbon.

Wilson <u>et al</u>. (1980) offered two main reasons for the reduced rates of substrate production they observed in their water stress experiment. First, there was a decrease of leaf area, and thus photosynthetic capacity per plant. They attributed this decrease to the suppression of leaf expansion. Second, the rate of substrate production per unit of leaf area decreased as leaf water potential decreased. This decrease was primarily caused by partial stomatal closure.

Also Wilson <u>et al</u>. (1980), studying the carbon balance of water deficient grain sorghum plants, found that water deficits did not affect the efficiency of conversion of substrate used in growth synthesis of new plant dry-matter. As water deficits became more severe the maintenance coefficient (m) decreased from 60 to 30 mg/g/24 hours. They were not able to determine the cause of the decrease. Total C efflux rate from the plants in the dark was decreased by water deficit. Of the 58 percent reduction in C efflux rate, 22 percent was attributed to the reduction of the maintenance component and 36 percent was caused by the reduction of the growth component.

CHAPTER III

METHODS AND MATERIALS

Plant Material and Treatments

Soybeans, <u>Glycine max</u> (L.) Merr. c.v. 'Cobb', were planted 26 June 1981 at the Agronomy Farm of the University of Florida in Gainesville, Florida. The soil was an Arredondo fine sand (a loamy, siliceous, hyperthermic, Grossarenic Paleudult). Row spacing was 76.2 cm and average plant density as sampled throughout the season was 35.9 plants/m².

The field plots were fertilized, before planting, with 666 kg/ha of 0-17-24 (NPK) fertilizer. Weeds were controlled at planting by Lasso at a rate of 3.1 1/ha. During the season, weeds were further controlled by one cultivation and some hand-weeding. Diazinon (38%) was applied seven days after emergence in order to control corn stem borer. Seeds were not inoculated with <u>Rhizobium japonicum</u> since soybeans were grown in the same field in previous years. The experimental design was a split-plot with four field replications (Table 1). Main plot treatments were three irrigation regimes, while in the subplot treatments plants were allowed

Table 1

Treatments and subtreatments imposed upon 'Cobb' soybean planted June 26, 1981 at Gainesville, Florida.

Main treatments	Subtreatments
Vegetative stage water deficit ^a	non-defoliated defoliated
Reproductive stage water deficit ^b	non-defoliated defoliated
Well-irrigated	non-defoliated defoliated

aplants were subjected to two water deficit (wilting)
periods: 26-33 and 47-54 days after planting.

^bplants were subjected to one water deficit (wilting) period: 89-98 days after planting.

^Cactive leaf-eating period: 67-91 days after planting.

to be defoliated by velvetbean caterpillar (<u>Anticarsia</u> <u>gemmatalis</u> Hubner) or non-defoliated. Non-defoliation was achieved by the use of insecticides: Dipel (<u>Bacilis</u> <u>subtilis</u>) and Dimilin (difluorbenzuron). Main plot treatments were 16 rows wide and 13.7 m in length and were irrigated by overhead sprinklers positioned at the four corners of each plot. Split plots were 8 rows wide by 6.8 m in length, corresponding to one-quarter of a whole plot.

In the well-irrigated treatment the plants received irrigation whenever tensiometer readings at 15 cm depth in the soil reached 200 millibars (Hammond, 1981). Plants in the vegetative stage water deficit treatment were subjected to the same irrigation criteria as above except for two stress periods in which plants wilted for 8 days each period: from 26 to 33 days after planting (DAP)¹ and from 47 to 54 DAP. In the reproductive stage water deficit treatment, plants received the same treatment as the wellirrigated, except for one period of water stress, in which the plants wilted for 10 days: from 89 to 98 DAP.

Defoliation treatments started 67 DAP in all three main treatments and ended approximately by 91 DAP. The average percent leaf area eaten by the insects was visually estimated to be 37, 29, and 37 percent, respectively, for

¹ Throughout this research planting date is counted as 1 DAP. This criterion was used in order to match data obtained from field sampling to the simulation model SOYGRO, which counts planting date as day 1.

well-irrigated, vegetative stage water deficit and reproductive stage water deficit treatments. Actual leaf area reductions were subsequently evaluated by growth analysis sampling.

CO, Exchange Measurements

Canopy CO₂ exchange rate (CER) was measured approximately once or twice per week depending on the weather conditions beginning 13 DAP. Measurements were made starting at noon (EDT) and extending until approximately 2 pm. Due to the number of measurements all treatments were not necessarily measured in the same day.

The CO_2 analyzer used was a Beckman 865 Infrared Gas Analyzer (IRGA). The CER obtained was based on the rate of depletion of concentration of CO_2 inside a closed aluminumframed Mylar chamber during approximately one to two minutes. The chamber was composed of two parts: an upper portable chamber and a soil base which were joined at matching flanges. The system has been previously described by Boote <u>et al</u>. (1980) and Jones <u>et al</u>. (1982). The flanges were covered with foam rubber gaskets to assure a good seal. The base was placed in the row of soybeans and pushed 4 cm into the soil to make a tight seal. At the time of measurement the upper part was placed on the base and fastened together with vise-grip pliers. The length and width of the soil area covered was 1.090 m and 0.762 m, respectively. The volume of base plus chamber top was approximately 1.028 m³

when the base was pressed into the soil. Inside the chamber there was an electrical fan to mix the air, a shaded thermocouple, and a light sensor for measurement of incident photosynthetically active radiation (PAR). Connection from the chamber to the IRGA was made by 12 m of Tygon tubing (0.62 cm inner diameter). Air from the chamber was pumped through a dew point hygrometer at a rate of 10 1/min, then back to the chamber. A flow of 0.6 1/min was split from the original flow and sent through the IRGA. Each measurement took about two minutes from the placement of the chamber on the base. Temperature, PAR, dew point and CO₂ concentration were continuously recorded during the measurements on a paper chart recorder, at a speed of four centimeters per minute.

In order to estimate CER, the CO_2 slope on the chart was recorded over a one-minute period of the linear part of the curve. This value was transformed in milligrams of CO_2 per meter square land area per second, using the ideal gas equation and appropriate transformations for chamber dimensions, ground area, temperature and time.

Gross Photosynthesis Estimation

In order to obtain instantaneous canopy gross photosynthesis (PG) versus PAR, the value of CER obtained in the dark was added to the value of CER measured under several light levels (apparent canopy photosynthesis), since CO_2 efflux from the respiring plant parts and soil, and CO_2

uptake by photosynthesis is assumed to occur simultaneously under light. Zero light was achieved by covering the chamber with a white plastic tarp during the measurements.

A PG-light response curve was determined based on the CER obtained under four or more light intensities: darkness, one-eighth, one-fourth, half, and full sunlight. These light intensities were obtained by covering the chamber with one or more sheets of neutral shade cloth.

Values of PG obtained from the different light intensities were fit to a rectangular hyperbolae using the Statistical Analysis System (SAS) nonlinear least square parameters search (NLIN) procedure (Goodnight, 1979):

PG=(PGMAX) (PAR) / (K+PAR)

where PG is the instantaneous canopy photosynthesis (mg CO₂/m²/s). PGMAX (mgCO₂/m²/s) and K(umole PAR/m²/s) are Michaelis-Menten constants, and PAR is the photosynthetically active radiation (umole/m²/s).

Total Daily Photosynthesis

A primary objective was to estimate total daily gross photosynthesis, for every day of the season. An approach was devised to convert instantaneous PG-light response curves to curves of daily gross photosynthesis versus daily PAR, the latter to allow interpolation between measurement days and days when diurnal light distributions were not available. Instantaneous PAR was recorded hourly throughout the season using a Campbell CR5 data logger. Also, total integrated daily PAR was obtained from the Agronomy Weather Station, located close to the experimental site. The instantaneous PAR was integrated over each day (rectangular integration) and the results were compared with daily PAR from the weather station. Those days were selected in which integrated instantaneous PAR was within ten percent of the daily PAR from the weather station. This was done to screen out days in which the hourly readings had randomly sampled biased points which failed to integrate out to the same total PAR as the weather station. Hourly values were also not available on all dates due to malfunctioning of the CR5 data logger. From a total of 117 measured days, 58 days of instantaneous PAR were used. Hourly instantaneous PAR from the selected days was applied to each of the PG-light response equations to determine instantaneous hourly PG. Instantaneous hourly PG was integrated (rectangular integration) to give total daily gross photosynthesis (TDPG) versus the respective total daily PAR (TDPAR). A mathematical relationship was developed between TDPG and TDPAR. The rectangular hyperbolae were found to give a good fit. Thus for each sampling date a relationship was developed between total TDPAR and TDPG.

TDPG=(TDPGMAX) (TDPAR) / (TDK+TDPAR)

where TDPG is the total daily gross photosynthesis (mg $CO_2/m^2/day$), TDPGMAX (mg $CO_2/m^2/day$) and TDK (moles $PAR/m^2/day$) were Michaelis-Menten constants, and TDPAR is the total daily PAR (moles/m²/day).

In those days between photosynthetic samplings, a linear interpolation was made between the prior and posterior TDPG-TDPAR response curves at the specific total daily PAR (weather station values). The weather station daily PAR'S were used because 1) they were the only complete set, and 2) they were assumed more correct since the integration was continuous rather than from discrete hourly points in the case of the CR5 data logger.

This approach allowed TDPC estimates for the whole season in all treatments.

Dry Matter Sampling

Above-ground dry matter accumulation, LAI, and light interception at midday were estimated throughout the season by sampling the plants inside the CER assimilation chamber. Beginning at 57 DAP, 60 cm of row samples were taken once each week from four field replications outside the chamber. The intensified sampling was to evaluate effects of defoliating pests during the latter part of the season. A

subsample of the plants (3 to 5) was separated into leaves, stems (plus petioles), seeds, and pod walls. The dry weight of the non-subsampled portion was also recorded. Plant material was dried at 60 C in a forced draft oven until constant weight, in order to estimate dry matter weight. Dry weights of component parts were computed as g/m^2 land area, making use of the subsampled plants for respective ratios multiplied times the total phytomass (subsample + non-subsampled portion).

Respiration Cost Estimation

In order to estimate respiration costs and photosynthate allocation to the plant dry matter, the TDPG data estimated from the field measurements were input in the Florida Soybean Crop Growth Model (SOYGRO) (Wilkerson <u>et</u> <u>al</u>., 1981). The model was implemented on a PRIME 250 computer located in the Agricultural Engineering Department of the University of Florida.

Maintenance respiration was calculated by summing two separate functions of topweight and TDPG:

MR=(Ro) (Topwt)+(Rp) (TDPG)

where MR is total daily maintenance respiration (g $CH_20/m^2/day$), Ro is the daily maintenance respiration coefficient (g CH_20/g dry weight/day), Topwt is dry weight of the above

ground plant parts (g/m^2) , Rp is the daily maintenance coefficient (g CH_2O/g TDPG), and TDPG is daily gross photosynthesis (g $CH_2O/m^2/day$).

The Ro coefficient is a quadratic function of temperature as given by McCree (1974) for white clover and sorghum:

Ro=R30(0.044+0.0019t+0.001t²)

where R30 is maintenance respiration at 30 C (grams of CH_2O per gram of above ground dry weight per meter square), t is air temperature in degrees centigrade. Daily R30 in the model was estimated to be 0.0144 g CH_2O/g dry weight/day based on the calibration to data for Quincy, FL (Ingram <u>et al</u>., 1981). Temperature used in the daily model comes from a weighted sine function using daily maximum and minimum temperature.

Growth respiration calculated by the model is based on Penning de Vries (1976) synthesis costs and is expressed in grams of glucose (CH₂O) required per gram of product synthesized (Table 2). Three basic products are considered: protein, fat and structural carbohydrate. Table 3 presents the fixed fraction of these three components in each plant part as used by the SOYGRO model. At present, SOYGRO considers protein produced from nitrogen fixation to cost the same as protein produced as the result of NO₃ assimilation and reduction.

Ta		

Grams of glucose (CH_O) required for synthesis of one gram product (protein, fat and structural carbohydrate).

	<u>CH₂O Required per</u>	g Product Syn	nthesized
Product	Condensation	Respiration	Total
Protein NO ₃ Source Remobilized	1.33 0.00	1.14 0.26	2.47 0.26
Fat	1.94	1.09	3.03
Str. Carbohydrate	1.13	0.08	1.21

Source: Wilkerson et al. (1981).

Ta	b:	Le	3

Fraction of protein, fat and structural carbohydrate (Str. CH₂O) in soybean tissue as used in SOYGRO.

		Fraction	
Component	Protein	Fat	Str. CH ₂ 0
Leaves	0.294	0.025	0.587
Stems	0.188	0.004	0.762
Shells	0.250	0.015	0.656
Seeds Protein from NO ₃ Mined Protein	0.398 0.398	0.197 0.197	0.357 0.357
Roots	0.092	0.010	0.841

Source: Wilkerson et al. (1981).

Statistical Analysis

The goodness of fit for the rectangular hyperbolae, used for photosynthesis-light response equations, was indicated by the percentage of variation explained by the model (PVEM) (Ingram <u>et al</u>., 1981). PVEM was calculated from SAS-NLIN output (Goodnight et al., 1979) as follows:

PVEM = 100 x [1-(SSR/df R)/(SS CT/df CT)]

SS is the sum of squares, df is the degrees of freedom, R is the residual, and CT is the corrected total.

Probability levels were assigned from a table of significant values for correlation coefficients with residual degrees of freedom.

CHAPTER IV RESULTS AND DISCUSSION

Weather and Irrigation

The 1981 weather in Gainesville was characterized by very low rainfall compared to the 70-year normal. July and August received a total of 20.0 cm of rain (normal 41.4 cm) and pan evaporation was 32.9 cm. September and October received 4.9 cm of rain (normal 17.8 cm) and pan evaporation was 26.5 cm.

Even during years with average rainfall distribution, irrigation is commonly required during spring and late autumn in Florida, to achieve efficient crop production (Hammond, 1981). Also according to Hammond, two factors create the need for irrigation: 1) unfavorable rainfall distribution, and 2) predominance of sandy soils with low water storage capacity.

Total amounts of irrigation applied were 21.7, 25.6, and 30.7 cm of water for vegetative stage water deficit, reproductive stage water deficit and well-irrigated treatments, respectively (Figure 1). This was in addition to 26.9 cm of rainfall received by the plots during the season.

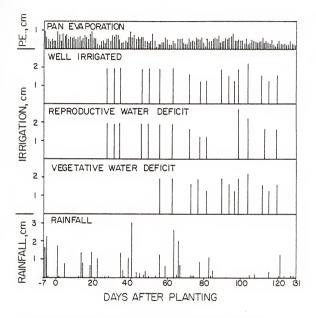


Figure 1: Rainfall, pan evaporation and irrigation distribution for the main treatments on 'Cobb' soybean planted June 26, 1981, at Gainesville, Florida.

Other climatic data of relevance for this study include daily photosynthetically active radiation (PAR), daily maximum and minimum air temperatures and are presented in Table Al in the Appendix.

Reproductive Growth Stages

Water deficit or defoliation affected reproductive development as measured by the reproductive growth stages according to Fehr and Caviness (1977). Table 4 shows the reproductive growth stages for all treatments, expressed as days after planting. Those reproductive stages were input in the SOYGRO model. The model uses the reproductive stages to control changes in partitioning of dry matter.

Emergence occurred at 7 DAP (days after planting) in all treatments. Vegetative stage water deficit caused a slight delay in reproductive development until R5, when compared to well-irrigated plants. Reproductive water deficit caused earlier occurrence of R7 and R8 stages. Defoliation treatments generally caused earlier R7 and R8 stages.

Carbon Exchange Rate

Figure 2 is an example of typical responses of total canopy photosynthesis (PG) in relation to incident PAR, obtained in this experiment on two different days, 39 and 91 DAP.

Treat.	R1	R2	R3	R4	R5	R6 ^C	R7	R8
v-o ^a	49 ^b	49	64	69	73	98	119	131
V-D	49	49	64	69	73	98	115	130
R-O	48	48	62	67	71	98	109	125
R-D	48	48	62	67	71	98	107	124
W-O	48	48	62	67	71	98	119	131
W-D	48	48	62	67	71	98	115	131

Table 4 Reproductive growth stages for 'Cobb' soybean subjected to defoliation and irrigation treatments, expressed as days after planting on June 26, 1981 at Gainesville, Florida.

^aV - vegetative stage water deficit

R - reproductive stage water deficit

W - well-irrigated
0 - non-defoliated

D - defoliated

D = deloilated

^bDays after planting

C_{Estimate}

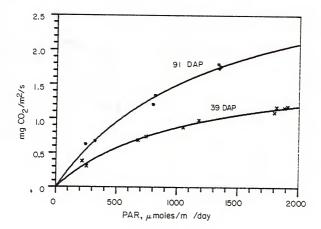


Figure 2. Photosynthesis-light response curve of wellirrigated (non-defoliated) treatment at 39 and 91 days after planting (DAP). Points represent four and two replicate field locations measured at 39 and 91 DAP, respectively.

Rectangular hyperbolae gave a good fit in all treatments throughout the season. The parameters of this equation, PGMAX, K, as well an estimate of goodness of fit, the PVEM (percentage variation explained by the model), are presented in Table A2 of the Appendix.

The curves varied throughout the season. For earlier measurements they were relatively flat but as LAI increased they became steeper. Then as leaves senesced, the curves again became flatter and the theoretical PGMAX became smaller.

PGMAX ranged from 0.18 mg $\text{CO}_2/\text{m}^2/\text{s}$ for vegetative stage water deficit plants at 32 DAP to 4.52 for well-irrigated plants at 81 DAP. K ranged from 69 umole PAR/m²/s for reproductive stage water deficit plants at 123 DAP to 2398 on vegetative water deficit plants at 85 DAP.

As a more realistic indication of the canopy photosynthetic capacity, the value of PG1500 was calculated as mg $CO_2/m^2/s$ with PAR at 1500 umoles/m²/s. Figure 3 shows the PG1500 for all non-defoliated treatments. PG1500 is the most realistic single parameter, because it was generally within 100 umole PAR/m²/s of the full sun intensities and was close to the actual measured gross photosynthesis; yet it co-variate adjusts for differences in PAR at mid-day observed during the season.

PG1500 for the well-irrigated plants started as low as 0.12 mg $\rm CO_2/m^2/s$ at 145 DAP and increased steadily reaching a maximum of 1.92 mg $\rm CO_2/m^2/s$ at 95 DAP, then declined

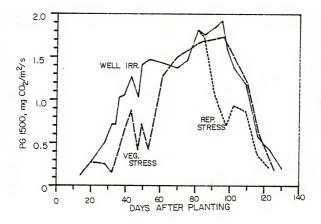


Figure 3: PG1500 for the three non-defoliated treatments. PG1500 is the instantaneous PG predicted from rectangular hyperbolae equations at PAR of 1500 u mole/m²/s.

again to 0.21 at 130 DAP due to loss of leaf area and senescence processes. When compared with the well-irrigated plants, PG1500 of the vegetatively water stressed plants was 50.3 percent less at 28 DAP and 78.6 percent less at 32 DAP. Rainfall terminated the stress on 34 DAP but PG 1500 continued 59.8 percent less at 36 DAP and 40.1 percent less at 39 DAP. This decrease in the PG1500 is attributed in part to the slow increase (even a loss) of LAI during the water deficit periods, and to the decrease in photosynthesis per unit of intercepted light during stress. However, 10 days after the stress was relieved, the canopy photosynthesis of the vegetatively stressed plants had recovered to within 10 percent of well-irrigated plants.

The average reduction of PG1500 due to water stress was 31.4 percent on vegetatively stressed plants compared to well-irrigated plants (average estimated over all common measurements dates from 29 to 117 DAP). Obviously there was a greater reduction during the water deficit periods (from 26 to 33 DAP inclusive and from 47 to 54 DAP inclusive).

In the reproductive stage water deficit plants, there was a 41.9 percent decrease in PG1500 at 91 DAP and a 55.6 percent decrease at 98 DAP compared to well-irrigated plants. Similar to what occurred on vegetatively water stressed plants, the decrease of PG1500 in reproductive stage water stressed plants was due to loss of leaf area and decrease of photosynthesis per unit of intercepted light.

However, contrary to vegetatively stressed plants, they did not recover their photosynthetic capacity, which remained 31.8 percent less than the well-irrigated plants at 102 DAP, because at this point in the season leaf growth had stopped.

The average reduction of PG1500 for the reproductive water stressed plants, estimated from 85 to 123 DAP reached 37.0 percent (water stressed from 89 to 98 DAP inclusive).

Defoliation treatments also caused a reduction of the photosynthetic capacity measured by PG1500, when compared with their respective main treatments without defoliation. Those reductions were 6.7, 7.9 and 22.3 percent, respectively, for well-irrigated, vegetative water stressed and reproductive stage water stressed plants (estimated from 85 to 116; 85 to 126; and 91 to 116 DAP, respectively)¹.

Canopy Gross Photosynthesis

Figure 4 is an example of two typical total daily gross photosynthesis (TDPG) response curves to total daily PAR as developed from two instantaneous light response equations shown earlier in Figure 2. A value for a given light condition day (point on curve) was derived by summing (rectangular integration) the output of a given equation for

¹These comparisons were made only when the CER measurements were made in the same day for the treatments being compared. In comparisons between well-irrigated plants and vegetative stressed plants, data on 61, 69 and 75 DAP were excluded, because on those dates the measurements for well-irrigated plants were underestimated due to the chamber top depressing the canopy (and altering its architecture).

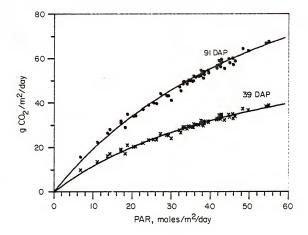


Figure 4. Daily photosynthesis-daily PAR relationship for the well-irrigated (non-defoliated) treatment at 39 and 91 days after planting (DAP).

instantaneous photosynthesis-light response versus diurnal light distribution. To obtain a range of daily PAR's, this was done by randomly selecting 58 days during the season (as previously described) for each instantaneous light response equation.

Rectangular hyperbolae also were found to provide a good fit for all treatments throughout the season. Parameters of the TDPG versus TDPAR equations are presented in Table A3 of the Appendix. Daily photosynthesis was expressed in terms of grams of CH_2O per meter square per day. Transformations from CO_2 to CH_2O were made by multiplying the CO, value by 30/44.

Figures 5 through 9 show the comparison of daily gross photosynthesis (TDPG) throughout the season, for each treatment versus the well-irrigated (non-defoliated) treatment. The sharp fluctuations represent cloudy versus sunny days, whereas the general shape of the upper points defines response to increasing crop LA1, water stress periods, defoliation stress and canopy senescence. These latter factors influence one equation to the next with interpolation between measurement dates. Water stress either early or late in the season caused a reduction in TDPG. The same effect resulted from the defoliation treatments.

Vegetative stage water deficit caused 63.7 and 57.0 percent reductions in the cumulative daily gross photosynthesis (CUMDPG) during the first stress period (26

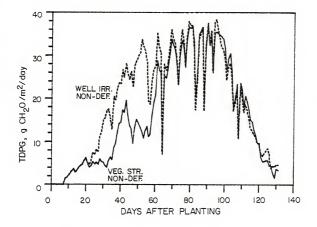


Figure 5: Comparison of total daily photosynthesis (TDPG) between vegetative stage water deficit (nondefoliated) treatment and the well-irrigated (non-defoliated) treatment.

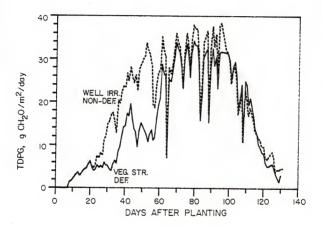


Figure 6. Comparison of total daily photosynthesis (TDPG) between vegetative stage water deficit (defoliated) treatment and the well-irrigated (non-defoliated) treatment.

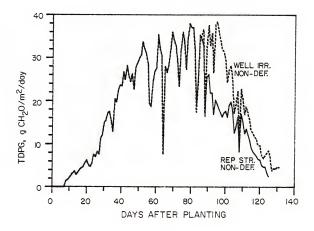


Figure 7. Comparison of total daily photosynthesis (TDPG) between reproductive stage water deficit (nondefoliated) treatment and the well-irrigated (non-defoliated) treatment.

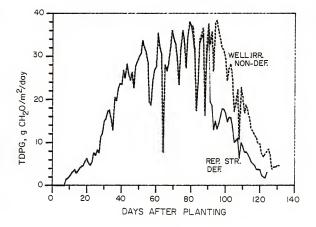


Figure 8. Comparison of total daily photosynthesis (TDPG) between reproductive stage water deficit (defoliated) and the well-irrigated (nondefoliated) treatment.

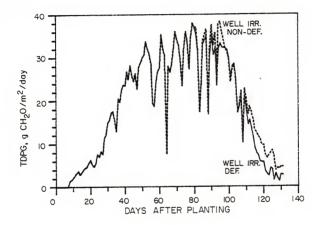


Figure 9. Comparison of total daily photosynthesis (TDPG) between defoliated and non-defoliated plots in the well-irrigated treatment.

to 33 DAP) and during the second stress period (47 to 54 DAP) as compared to well-irrigated plants. Cumulative daily gross photosynthesis (CUMDPG), as used in this section, represents daily gross photosynthesis summed up over a specific inclusive time period which will be given in each instance. Those cumulative effects over each 8 day stress period were represented by CUMDPG of 35.0 versus 96.2 g $\rm CH_2O/m^2$ and 91.9 versus 213.7 g $\rm CH_2O/m^2$ for stressed versus irrigated canopies, respectively. In between stress periods (from 33 to 47 DAP) there was an increase in the photosynthetic capacity of the water stressed plants, holding the reduction in CUMDPG (day 33 to 47) at 44.1 percent (from 317.3 to 177.3 g CH_2O/m^2). However, when water deficit was relieved by irrigation and rainfall after 57 DAP, the reduction in CUMDPG, 57 DAP until the end of the season was at only 2.6 percent compared to well-irrigated plants (from 1750.4 to 1704.5 g CH_2O/m^2). The latter is consistent with minimal reduction in seed yield as will be shown later.

Water deficit during the reproductive stages reduced CUMDPG by 42.7 percent during the stress period (89 to 98 DAP), compared to the well irrigated treatment. After stress was relieved, CUMDPG from 98 DAP until the end of the season was reduced by 36.7 percent. Although a partial recovery in photosynthetic capacity after the stress was observed, this recovery was not as dramatic as in the

vegetatively stressed plants and was responsible for greater reductions in yield for reproductive drought stress.

CUMDPG during the defoliation period (67 to 91 DAP), was reduced 7.6 percent due to the defoliation on plants previously drought stressed during vegetative growth compared to the respective non-defoliated water stressed plants. After the active leaf-eating period, CUMDPG from 91 DAP until the end of the season, was reduced 6.0 percent when compared with the respective non-defoliated treatment.

Defoliation in the reproductive water-stressed plants at the level and timing observed in this experiment did not cause reduction in CUMDPG during the active leaf-eating period compared to the respective nondefoliated water stressed plants (732.9 to 737.6 g CH_0O/m^2). However, after this period, CUMDPG from 92 DAP until the end of the season was 25.6 percent less for defoliated plants (434.0 to 322.8 g CH_O/m²). This pattern of CUMDPG could be explained by the fact that during the active leaf-eating period, the decrease in LAI by the insects was not enough to cause major reduction in TDPG, due to its gradative character and to the initially high LAI achieved by the plants. However, when the water stress was applied, the plants were about 10 days into the linear seed filling period, causing a premature senescence of leaves on defoliated plants, reducing their photosynthetic capacity.

Defoliation on well-irrigated plants caused a CUMDPG pattern similar to that observed in the reproductive stage

water stressed plants. During the active leaf-eating period there was a 1.7 percent reduction in CUMDPG from 762.7 to 749.4 g CH_2O/m^2 . After the active leaf-eating period until the end of the season, the reduction was 14.0 percent (from 720.4 to 619.4 g CH_2O/m^2) compared to well-irrigated non-defoliated plants.

Table 5 summarizes the total estimated seasonal canopy photosynthesis for all treatments and the respective reductions compared to the well-irrigated plants (nondefoliated) as 100 percent. Also in Table 5 is illustrated the reductions in canopy gross photosynthesis during the seed filling period² and the relative seed yields obtained.

Vegetative stage water deficit treatment (non-defoliated) caused a reduction in seasonal total canopy gross photosynthesis of 16.2 percent when compared to wellirrigated plants (non-defoliated). Reproductive stage water deficit caused a reduction of 12.5 percent reduction also compared to well-irrigated plants.

However, during the seed filling period the vegetative stage water deficit caused a reduction of only 5.3 percent in the CUMDPG compared to the well-irrigated treatment, while in the reproductive stage water deficit the decrease in the CUMDPG was 32.0 percent compared to well-irrigated

²The seed filling period was assumed to begin at the intercept of the x-axis (DAP) for the linear regression of the total seed weight on a land area basis versus DAP; the end of the filling period was considered as R7.

Table 5

Cumulative daily gross photosynthesis (CUMDPG) for the entire season and during

Treatment	En	Entire Season	Seed	Seed fil	Seed filling period	Relative
	CUMDPG	Relative CUMDPG	filling	CUMDPG	Relative CUMDPG	yıeld
	g CH ₂ O/m ²	 	DAP ^b	g CH ₂ O/m ²	049 	
v-o ^a	2120.0	83.8	85-119	863.4	94.8	95.3
V-D	2018.8	79.8	84-115	793.8	87.1	85.8
R-O	2212.7	87.5	81-109	574.2	63.0	73.7
R-D	2106.1	83.3	78-107	619.3	68.0	67.3
M-0	2528.8	100.0	82-119	911.2	100.0	100.0
M-D	2414.5	95.5	85-115	795.4	87.3	87.9

53

b_{DAP} - days after planting

plants. This contrasts to seed yield reductions of 4.7 and 26.3 percent for the vegetative and reproductive water deficit treatments, respectively.

Although insects caused considerable damage, eating between 20 and 30 percent of leaf weight, the consequences in terms of total seasonal gross photosynthesis were relatively minor considering that the reductions were less than 5 percent (4.8; 4.8; and 4.5 percent for vegetative stage water deficit, reproductive stage water deficit and wellirrigated, respectively).

Reductions in the CUMDPG during the seed filling period between defoliated and non-defoliated treatments were 8.1, -7.9, and 12.7 percent for the vegetative water stress, reproductive stress, and well-irrigated treatments, respectively. This compares with 10.0, 7.4, and 12.1 percent reductions in seed yield, respectively. Again, yield reductions are more closely associated with reductions in CUMDPG during seed fill than reductions over the entire season.

The percentage of CUMDPG occuring during the seed filling period compared to that for the entire season was higher in vegetative stressed plants (40.7 and 39.3 percent for non-defoliated and defoliated) compared to the wellirrigated plants (36.0 and 32.9); the reproductive stage water deficit caused this relationship to be reduced (26.0 and 29.4 percent).

Respiration Costs

Canopy gross photosynthesis data estimated from the field measurements were input in the Florida Soybean Crop Growth Model (SOYGRO). The model is implemented on a PRIME 250 computer located in the Agricultural Engineering Department, University of Florida. The model is written in FORTRAN computer language, using a modular subroutine approach.

SOYGRO is a process oriented soybean growth and yield model. Physiological processes of photosynthesis, respiration, tissue synthesis, nitrogen remobilization, and senescence in the model depend on weather, as well as soil and crop phenological conditions. These processes are linked mathematically by a series of differential equations that create partitioning of dry matter dependent on phenological phase of crop development.

The soybean plant is assumed to consist of leaf, stem (including petioles), shell, seed, and root tissue components. During growth, each tissue is assumed to be composed of constant fractions of protein, fat, and structural carbohydrates. Tissue biomass growth rates are described by the partitioning of carbohydrate (CH_2O) to each tissue component and the utilization of the carbohydrate in synthesis and respiration processes. During vegetative growth and up to the end of pod addition, growth of plant parts is source-limited (photosynthate driven, as set by

relative partitioning and respiration costs). Pod growth and seed growth is temperature dependent but is on an absolute (mg/day/seed) basis, not on a relative growth rate basis. Only after a pod load is set, is growth allowed to be sink limited if photosynthesis improves while fruits are removed or slowed down. The sink-limited feature was disabled for purposes of simulation in this research. Carbohydrate, supplied by photosynthesis, is assumed to be a limiting substrate for tissue synthesis. Therefore, growth is described by a basic carbon balance.

During vegetative growth, protein is a constant fraction of leaf, stem and shell mass. Some of this protein can be later remobilized for seed growth. It is assumed that nitrogen fixation is possible on demand, that nitrogen for protein synthesis is non-limiting provided that carbohydrate is available for either nitrogen fixation or growth.

Normally the model calculates gross photosynthesis using a quadratic equation that calculates the daily photosynthesis from daily PAR data; this daily photosynthesis is reduced by a multiplicative series of factors that account for LAI, soil water, leaf nitrogen concentration and temperature. Figures A-1 to A-6 in appendix illustrate how the original model-computed photosynthesis compares with the daily photosynthesis measured in this experiment. The model underestimated the total seasonal photosynthesis for all treatments by 3.9 to 16.2 percent. However, for the purpose of this experiment, these factors were not allowed to

influence the measured daily photosynthesis, since the model was modified to directly accept the daily canopy gross photosynthesis obtained from field measurements, already influenced by those factors.

Figures 10 through 15 show the total respiration and its components (maintenance and growth respiration). Sharp fluctuations in the maintenance respiration curve were due to changes in daily temperature, and to changes in daily gross photosynthesis. Seasonal changes in this curve were due to changes in above-ground dry matter accumulation. Sharp fluctuations in the growth respiration curve were due to changes in daily gross photosynthesis. Seasonal changes in this curve were due to seasonal changes in seasonal gross photosynthesis.

Maintenance and growth respiration estimated by SOYGRO were reduced in the vegetatively stressed plants compared to well-irrigated plants. During the first period of stress the reduction in the integrated maintenance respiration was 50.0 percent (from 10.0 to 5.0 g CH_2O/m^2); during this period integrated growth respiration was reduced 65.2 percent (from 17.2 to 6.0 g CH_2O/m^2) when compared to wellirrigated plants. During the second water stress period (47 to 54 DAP) integrated maintenance respiration was reduced 50.8 percent (from 30.1 to 14.8 g CH_2O/m^2) while integrated growth respiration was reduced 58.2 percent (from 37.0 to 15.5 g CH_2O/m^2). Between stress periods the reductions in integrated maintenance and growth respiration were

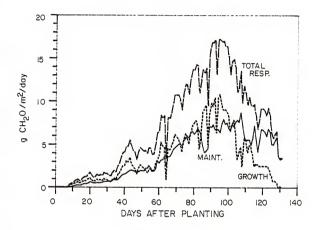


Figure 10. Total, maintenance and growth respiration for the vegetative stage water deficit (nondefoliated) treatment.

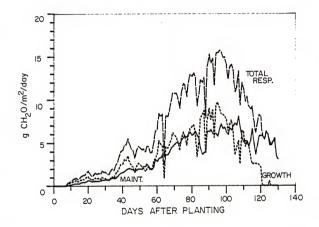


Figure 11. Total, maintenance and growth respiration for the vegetative stage water deficit (defoliated) treatment.

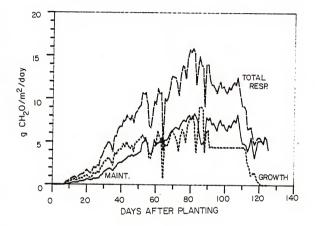


Figure 12. Total, maintenance and growth respiration for the reproductive stage water deficit (non-defoliated) treatment.

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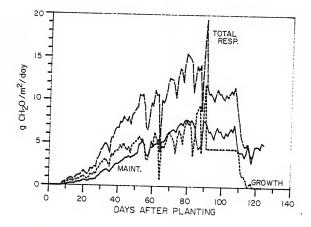


Figure 13. Total, maintenance and growth respiration for the reproductive stage water deficit (defoliated) treatment.

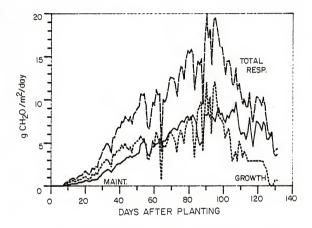


Figure 14. Total, maintenance and growth respiration for the well-irrigated (non-defoliated) treatment.

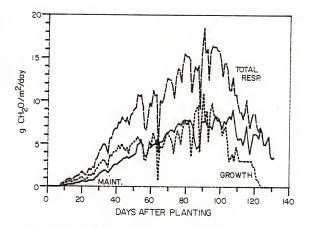


Figure 15. Total, maintenance and growth respiration for the well-irrigated (defoliated) treatment.

43.1 and 44.3 percent, respectively. After the end of water stress (54 DAP) until the end of the season, SOYGRO projected a reduction of 16.4 percent in integrated maintenance respiration (from 507.4 to 424.2 g CH_20/m^2) while integrated growth respiration was reduced by only 0.9 percent (from 393.6 to 390.1 g CH_20/m^2). This pattern could be explained because the vegetative stressed plants were smaller than the well-irrigated plants, allowing them to spend less in maintenance respiration. Although smaller, their photosynthetic capacity was reduced only by 2.6 percent during this period (as discussed earlier), reducing the growth respiration just slightly compared to well irrigated plants.

The integrated maintenance respiration of reproductively stressed plants, as estimated by SOYGRO, was reduced by 12.7 percent during the stress period (89 to 98 DAP), from 73.7 to 64.4 g CH_2O/m^2 . During this same period their integrated growth respiration was reduced by 48.1 percent (from 86.5 to 41.6 g CH_2O/m^2), compared to wellirrigated plants. The relatively lower reduction in the maintenance respiration was due to the fact that maintenance respiration is a function of both plant dry weight and gross photosynthesis; moreover, it is subtracted from gross photosynthesis prior to allocation of carbohydrates to growth. When the stress was relieved and until the end of the season, the reduction in integrated maintenance

respiration was 21.3 percent (from 192.8 to 151.8 g $(CH_2O)/m^2$), while the reduction in integrated growth respiration stayed at 32.4 percent (from 105.6 to 71.49 (CH_2O/m^2)) compared to well-irrigated plants.

SOYGRO estimated a reduction of 5.7 percent in integrated maintenance respiration during the active leaf-eating period for the vegetative stage water stressed plants. At the same time the reduction in integrated growth respiration was 8.0 percent, compared to the non-defoliated vegetatively stressed plants. After the end of the active leaf-eating period until the end of the season, the reductions in integrated maintenance and growth respiration were 9.9 and 9.7 percent, respectively.

SOYGRO estimated a decrease in integrated maintenance respiration of 3.6 percent, during the active leaf-eating period, in the reproductive stage water stressed plants, compared to non-defoliated water stressed plants. However, defoliated plants had a 4.4 percent higher integrated growth respiration during this same period. This was probably due to no significant loss in integrated gross photosynthesis during the same period for the defoliated plants, yet removal of biomass would have the effect of reducing maintenance respiration. Defoliated plants had 12.8 and 9.2 percent less biomass than non-defoliated plants, measured at 83 and 90 DAP, respectively.

Defoliation of well-irrigated plants caused a decrease of 1.7 percent for the integrated growth respiration during

the active leaf-eating period, compared to the wellirrigated non-defoliated plants. Also, 1.7 percent reduction was observed for the integrated maintenance respiration during this period. After the active leaf-eating period until the end of the season, the integrated maintenance respiration was 9.2 percent less, and integrated growth respiration, 13.4 percent less.

Table 6 presents the total seasonal respiration for all treatments.

Τa	ιb	1	e	6
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Seasonal total, growth, and maintenance respiration estimated by SOYGRO for all the treatments.

Treatment	Respiration Total Maintenance Growth				
		2			
		g CH ₂ 0/m ²			
v-o ^a	928.9	472.8	456.1		
V-D	865.6	440.2	425.4		
R-O	949.0	513.9	435.1		
R-D	912.0	483.8	428.2		
W-0	1112.0	593.1	518.8		
W-D	1053.5	560.6	492.7		

 ^{a}V - vegetative stage water deficit

R - reproductive stage water deficit

W - well-irrigated

- 0 non-defoliated
- D defoliated

Dry Matter Accumulation

Leaf

Figures 16 to 21 show leaf dry weight on a land area basis as estimated by the model and as measured by the field samples. Dry weight of plant parts are presented in Table A.4 of the Appendix.

Leaf dry weight simulated by the SOYGRO model (using TDPG inputs) was underestimated (compared to field measurements) for vegetative stage water deficit treatments (both defoliated and non-defoliated) (Figures 16 and 17). SOYGRO slightly overestimated (compared to field measured leaf dry weights) for reproductive stage water deficit and wellirrigated treatment (defoliated).

The field measurements show that vegetative stage water deficits reduced leaf growth rate and reduced the maximum amount of leaf on the plants. Although the reproductive stage water deficit treatment achieved the same leaf dry weight as the well-irrigated treatment before the water stress, leaf weight dropped more rapidly due to premature senescence as a consequence of the water deficit.

Defoliation treatments caused a reduction in the leaf weight. Defoliation started at 68 DAP in all treatments and finished approximately by 96 DAP in all treatments. Based on field measurements the average reduction in leaf dry weight on the defoliated treatments compared to the respective non-defoliated treatments was 21.7, 30.2 and 24.9 percent, measured from 75, 83 and 75 DAP until the end of

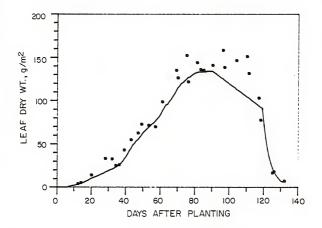


Figure 16. Comparison of leaf dry matter accumulation between simulated (line) and field sampled (circles) for the vegetative stage water deficit (non-defoliated) treatment.

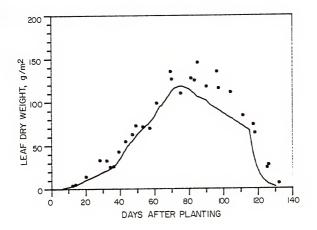


Figure 17. Comparison of leaf dry matter accumulation between simulated (line) and field sampled (circles) for the vegetative stage water deficit (defoliated) treatment.

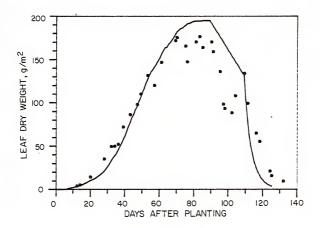


Figure 18. Comparison of leaf dry matter accumulation between simulated (line) and field sampled (circles) for the reproductive stage water deficit (non-defoliated) treatment.

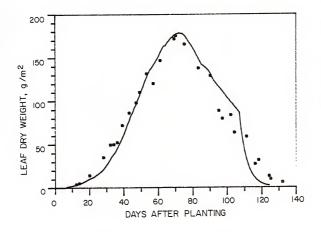


Figure 19. Comparison of leaf dry matter accumulation between simulated (line) and field sampled (circles) for the reproductive stage water deficit (defoliated) treatment.

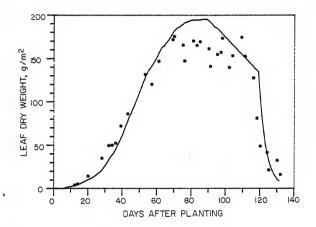


Figure 20. Comparison of leaf dry matter accumulation between simulated (line) and field sampled (circles) for the well-irrigated (nondefoliated) treatment.

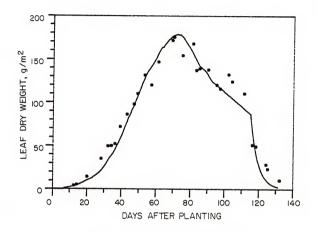


Figure 21. Comparison of leaf dry matter accumulation between simulated (line) and field sampled (circles) for the well-irrigated (defoliated) treatment.

the season, respectively, for vegetative stage water deficit, reproductive stage water deficit and well-irrigated treatments. The average reduction in LAI during the same period was 28.8, 39.8 and 23.2 percent, respectively.

Vegetative stage water deficit treatment caused an average reduction in LAI of 27.9 percent (estimated from 28 DAP until the end of the season) compared to the well irrigated treatment, based on the field measurements.

Reproductive stage water deficit caused an average reduction in LAI of 11.6 percent (estimated from 83 DAP to the end of the season).

As a consequence of the reduction in LAI there was less light interception; however, those reductions were smaller than the reductions in both leaf dry weight and LAI. Reductions in light interception (measured at midday) due to water deficit were 18.5 percent (from 28 DAP to the end of the season) and 11.0 percent (from 85 DAP until the end of the season) for vegetative and reproductive water deficit, respectively.

Reductions in light interception due to insect defoliation were 3.4 and 5.2 percent (from 75 DAP until the end of the season), for vegetative stage water stressed plants and well irrigated plants compared to their respective nondefoliated treatments. Light interception data for the reproductive stressed treatment were not reliable due to malfunctioning of the data logger.

Figures 22 through 27 show stem dry weight estimated by the model and field samples. SOYGRO, using TDPG input, underestimated stem dry weight early in the season and slightly overestimated later in the season for all treatments, this shows a consistent bias in SOYGRO regarding the partitioning toward stem and leaf for the growing conditions and variety used in this experiment. SOYGRO had been developed for a different cultivar 'Bragg' in different years.

Field measurements showed that vegetative stage water stress caused reduction of stem (plus petiole) dry weight on the plants throughout the season, as a consequence of smaller plants with shorter stems and petioles compared to well irrigated plants.

Reproductive stage water deficit caused a decrease in stem dry weight after the onset of water deficit, as measured by the field samples. This reduction was due to the premature leaf (and petiole) senescence and possibly to remobilization of assimilate to the seeds.

All defoliation treatments showed a decrease in stem dry weight as a consequence of defoliation, compared to their respective non-defoliated main treatment, based on field measurements. This could be attritubed to the dropping of the most severely damaged leaves and petioles by the insects. It could also include enhanced remobilization of assimilate from stems to seeds.

Stem

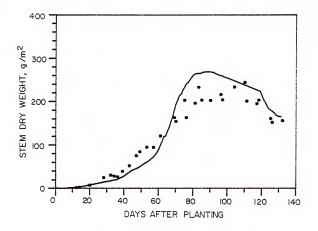


Figure 22. Comparison of stem dry matter accumulation between simulated (line) and field sampled (circles) for the vegetative stage water deficit (non-defoliated) treatment.

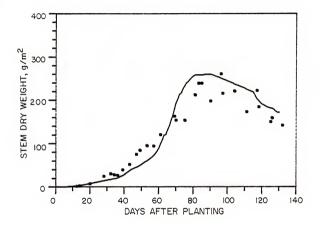


Figure 23. Comparison of stem dry matter accumulation between simulated (line) and field sampled (circles) for the vegetative stage water deficit (defoliated) treatment.

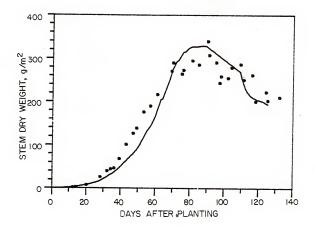


Figure 24. Comparison of stem dry matter accumulation between simulated (line) and field sampled (circles) for the reproductive stage water deficit (non-defoliated) treatment.

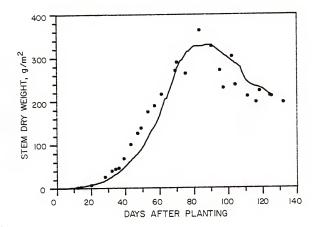


Figure 25. Comparison of stem dry matter accumulation between simulated (line) and field sampled (circles) for the reproductive stage water deficit (defoliated) treatment.

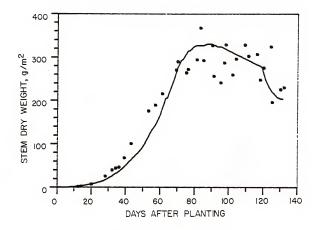


Figure 26. Comparison of stem dry matter accumulation between simulated (line) and field sampled (circles) for the well-irrigated (nondefoliated) treatment.

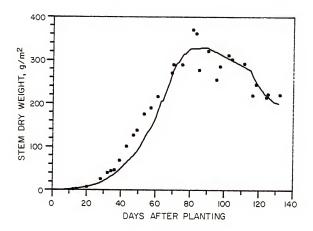


Figure 27. Comparison of stem dry matter accumulation between simulated (line) and field sampled (circles) for the well-irrigated (defoliated) treatment.

Pod walls

Pod wall dry weight on a land area basis (data not shown) was consistently overestimated by the SOYGRO model in all treatments. Dry weight increase started at the correct time but the rate of pod wall growth was too rapid. The problem resides in the coding of SOYGRO and suggests an area needing improvement.

The end of the season pod wall dry weight estimated by the model, when compared to the average of the three last field measurements resulted in the model overestimation by 20.3, 21.0, 23.5, 17.0, 24.1 and 16.6 percent respectively for treatments vegetative stage water deficit (nondefoliated and defoliated), reproductive stage water deficit (non-defoliated and defoliated) and well-irrigated (nondefoliated and defoliated).

Seeds

In relation to seed dry weight, the model overestimated for vegetative stage water deficit treatments (both defoliated and non-defoliated) and for the well-irrigated treatment (defoliated only), as shown in Figures 28 through 33. The overestimations appeared to occur for those situations which reduced biomass (and maintenance respiration), yet, where daily photosynthesis was good during the seed filling phase. This implies that maintenance respiration is not necessarily a function of biomass during seed fill.

Table 7 shows the effects of the treatments on the seed growth rates, based on field samples. Although total seed

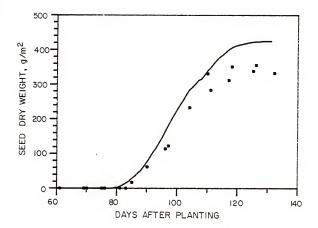


Figure 28. Comparison of seed dry matter accumulation between simulated (line) and field sampled (circles) for the vegetative stage water deficit (non-defoliated) treatment.

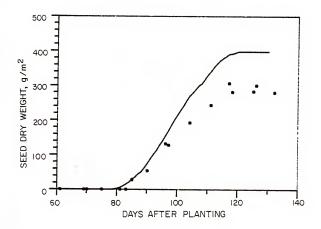


Figure 29. Comparison of seed dry matter accumulation between simulated (line) and field sampled (circles) for the vegetative stage water deficit (defoliated) treatment.

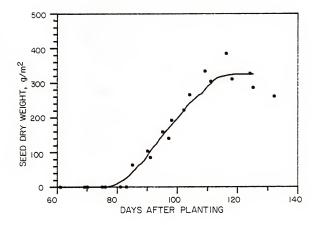


Figure 30. Comparison of seed dry matter accumulation between simulated (line) and field sampled (circles) for the reproductive stage water deficit (non-defoliated) treatment.

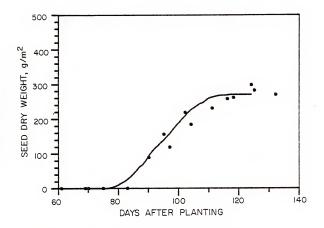


Figure 31. Comparison of seed dry matter accumulation between simulated (line) and field sampled (circles) for the reproductive stage water deficit (defoliated) treatment.

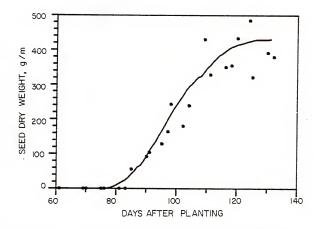


Figure 32. Comparison of seed dry matter accumulation between simulated (line) and field sampled (circles) for the well-irrigated (nondefoliated) treatments.

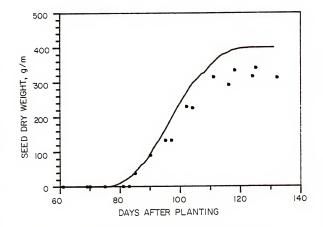


Figure 33. Comparison of seed dry matter accumulation between simulated (line) and field sampled (circles) for the well-irrigated (defoliated) treatment.

Table 7

Field measured and SOYGRO (model) estimated seed growth rate (SCR) on a land area basis for all treatments.

Treatment	SGR		r ²		x-intercept	
	Field	Model	Field	Model	Field	Model
g/m ² /day				DAP		
v-o ^a	11.04	13.15	0.990*	0.995**	84.6	83.6
V-D	9.06	12.90	0.997**	0.997**	83.4	83.9
R-O	10.38	9.95	0.972*	0.997**	80.9	80.4
R-D	7.01	8.29	0.991**	0.992**	78.3	78.1
₩-O	11.17	12.62	0.999**	0.994**	82.1	81.8
W-D	10.98	12.75	0.988*	0.993**	83.1	82.0

^aV - vegetative stage water deficit R - reproductive stage water deficit

W - well-irrigated

0 - non-defoliated

D - defoliated

* significant at 0.05 probability level. ** significant at 0.01 probability level.

growth rate varied by 37 percent between the well-irrigated (non-defoliated) treatment and the reproductive stage water deficit (defoliated) treatment, statistical analysis of the data showed no difference, at the 5 percent level of significance, among water regimes. Statistical differences in seed growth rate was detected between defoliated and nondefoliated treatments in the reproductive stage water deficit plants. Also no statistical difference was detected among the x-intercept (DAP) at the same level as above. Roots

During this experiment root samples were not available; however, SOYGRO estimates partitioning to root dry weight which will be briefly described here. The model was not programed to senesce roots; thus, the maximum root weight estimated by the SOYGRO was 163, 162, 258, 259, 259, and 258 g dry matter per meter square for vegetative stage water deficit (non-defoliated and defoliated), reproductive stage water deficit (non-defoliated and defoliated) and wellirrigated treatments (non-defoliated and defoliated), respectively.

Carbon Balance and Yield

Table 8 shows estimated total seasonal amount of carbon (CH₂O) available for biomass production, cumulative above-ground dry matter measured in the field, cumulative above-ground dry matter and roots estimated by SOYGRO, and final yield measured in the field.

Table 8

Total seasonal carbon (CH₂O) available and respective total seasonal above-ground² dry matter accumulation based on field measurement, and SOYGRO simulation.

Treat.		available ^b	Cumulat	Dry matter Cumulative tops				
		-	Field ^d	Model ^e	Root S (model)	eed yiel (field)		
v-o ^a								
	1191	424	790	888	163	325		
V-D	1153	403	718	851	162	293		
R-O	1264	237	914	876	258	251		
R-D	1248	266	755	836	259	233		
W-O	1417	496	985	1002	259	341		
W-D	1362	404	785	970	258	300		
R - re W - we O - no D - de	product 11-irri n-defol foliate	iated d	ter defi	cit				
^b gross	photosy	nthesis minu	s respir	ation				
^c see Ta	ble 5							
d averag for se	e of th nesced	e three last leaves and p	field metioles.	easureme	nts, adju	sted		
101 36	nesceu	reaves and p	ectores.					

The amount of CH_2O biomass was calculated by subtracting total seasonal respiration from total seasonal gross photosynthesis. The estimated fraction of total seasonal CH_2O for biomass production in relation to the total seasonal gross photosynthesis was similar in all treatments (56.0 to 57.8 percent).

Although estimated CH₂O available and cumulative aboveground dry weight (average of the three last field measurements) were lower for the vegetative stage water deficit treatments compared to the well-irrigated (nondefoliated) treatment, the percentage of the cumulative above-ground dry weight harvested as seed at the end of the season was higher for the vegetative stage water deficit treatments (41.3 and 40.8 percent) than for the wellirrigated (non-defoliated) treatment (34.7 percent).

On the reproductive stage water deficit treatments, the fraction of assimilate ending up in seeds was lower than the well-irrigated plants (27.5 and 30.9 percent against 34.7 and 38.3 percent).

Assuming the average carbon content in the dry matter to be 40 percent, the carbon available for biomass production was 9.8 to 12.3 percent overestimated compared to the carbon dry matter calculated by SOYGRO (tops plus roots). This overestimation could be attributed to the lack of condensation costs and root maintenance respiration in the model.

Final seed yield was correlated with both cumulative gross photosynthesis and cumulative available CH₂O (gross photosynthesis minus respiration) during the seed filling period (r^2 = 0.964 and r^2 = 0.957, respectively).

CHAPTER V

SUMMARY AND CONCLUSIONS

Canopy daily gross photosynthesis for the whole season was estimated for field-grown 'Cobb' soybeans, subjected to three water regimes (vegetative stage water deficit, reproductive stage water deficit, and well-irrigated), and two levels of insect defoliation (non-defoliated and approximately 30 percent of defoliation).

Canopy carbon exchange rate measurements were made once or twice weekly, between noon and 2 pm, using a portable mylar chamber with approximately 1 m³ of volume. An instantaneous photosynthesis-light response curve was developed by artificially shading the chamber during the measurements. Total or gross photosynthesis was estimated by adding the absolute value of CO_2 efflux from crop and soil in darkness to the values of apparent canopy carbon exchange response to light. Using a representative diurnal photosynthetic photon flux density distribution for the days of the season, a relationships were developed between total daily photosynthesis and total daily irradiance (photosynthetic active radiation), allowing the estimation of total canopy photosynthesis for every day of the season.

Daily photosynthesis was input in the Florida Soybean Crop Growth Model (SOYGRO), which estimated respiration costs (growth and maintenance) and allocated assimilate to dry matter production. Dry matter simulated by the model was compared with dry matter obtained from the field samples.

Total seasonal photosynthesis was reduced in all treatments when compared to the well irrigated plants (non-defoliated). However, final yield was best correlated $(r^2 = 0.964)$ with cumulative photosynthesis during the linear phase of the seed filling period.

Vegetative stage water deficit caused 63.7 and 57.0 percent reduction in cumulative daily gross photosynthesis (CUMDPG) during the two water deficit periods, compared to the well irrigated non-defoliated treatment, however, seasonal CUMDPG was only 16.2 percent less.

Water deficit during the reproductive stages reduced CUMDPG during the water deficit by 42.7 percent, and a seasonal CUMDPG by 12.5 percent compared to the well-irrigated non-defoliated treatment.

Defoliation reduced the seasonal CUMDPG in all treatments, compared to their respective main treatment non-defoliated. Those reductions were 4.8, 4.8 and 4.5 percent for vegetative stage water deficit, reproductive stage water deficit and well-irrigated treatment, respectively.

Dry matter accumulation in plant parts estimated by SOYGRO was compared to the equivalent field measurements. Overall simulated dry matter accumulation by SOYGRO was within 15 percent of field measured dry matter.

Leaf dry weight estimated by the model on a land area basis was underestimated for vegetative water deficit treatments (both defoliated and non-defoliated) and slightly overestimated for the reproductive water deficit and well irrigated treatments (non-defoliated). Vegetative water stressed plants produced less leaf dry matter for the whole season. Also the reproductive water stressed plants showed a premature leaf senescence after the stress.

Stem (plus petiole) dry matter was consistently underestimated early in the season and overestimated later in the season for all treatments. Vegetative water deficit plants had less stem dry weight during the season, because they were smaller and had shorter stems and petioles than well irrigated plants.

Pod wall dry matter also was consistently biased by the model in all treatments, being overestimated from 16.6 percent in well irrigated (defoliated) plants to 23.5 percent in reproductive water deficit (non-defoliated) treatment.

Seed weight on a land area basic was overestimated by the model for vegetative water deficit treatments (both defoliated and non-defoliated) and the well irrigated treatment (defoliated). Overestimation was due to both

97

increase in individual seed size and increase in seed number per meter square. This situation occurred primarily on treatments which had reduced biomass and less simulated maintenance respiration; yet had good photosynthesis during seed fill. The problem may be caused by the relationship of maintenance respiration to biomass.

In addition to some discrepancies between the model and field measurements for individual plant parts, the simulated top weight showed some consistent biases versus field observations. Initially, top dry weight was underestimated, but later it was overestimated by about 10 to 12 percent. This suggests that certain growth or maintenance respiration costs in SOYGRO may not be high enough. Alternatively, partitioning to root and shoot could be incorrect in SOYGRO. Alternatively, gross photosynthesis measurements could be slightly overestimated. It is also known that early leaf senescence occurs in the field; yet SOYGRO assumes no leaf loss until R4. This would give the appearance of an upward bias in leaf weight.

Finally it should be concluded, based on data obtained in this experiment, that the use of a portable chamber to measure canopy CER at mid-day, associated with the artificial shading to obtain different light levels for estimation of a photosynthesis-light response curve and subsequent daily photosynthesis over the season is satisfactory. Also that the input of this photosynthesis into a simulation model is a powerful tool to test and validate model parameters needed to better understand climatic and physiological factors affecting the carbon balance of a crop under field conditions. APPENDIX

Tab	le	Α.	1

		perature	Photosynthetic photon
DAP(1)	Maximum	Minimum	flux density
		c	moles/m ² /day
1	36.1	21.7	51.6
2	34.4	21.1	50.3
2 3 4	32.2	22.8	50.4
4	31.1	17.8	46.9
5	33.3	19.4	56.3
5 6	32.8	17.2	42.9
7	32.2	21.1	36.2
8	34.4	21.1	42.9
9	31.7	18.9	37.5
10	33.9	21.7	42.5
11	35.6	20.6	43.2
12	35.0	22.2	43.0
13	33.9	22.2	38.3
14	32.2	21.7	45.1
15	32.8	22.2	49.3
16	35.0	23.3	49.5
17	35.6	22.2	46.0
18	34.4	22.2	40.8
19	34.4	22.2	48.1
20	34.4	26.1	47.4
21	33.9	26.7	30.3
22	32.8	23.3	23.3
23	35.0	22.2	26.7
24	32.8	22.8	37.6
25	33.3	20.6	29.7
26	28.9	23.9	35.5
27	32.2	24.4	28.3
28	33.9	22.2	47.7
29	35.0	22.2	44.8
30	36.1	22.2	54.5
31	36.7	22.2	50.3
32	35.6	23.3	53.0
33	36.1	23.3	54.7
34	36.1	22.8	41.5
35	34.4	22.8	23.2
36	32.8	20.6	37.7
37	34.4	22.2	34.8
38	35.0	22.8	43.4
39	35.6	21.1	46.2
40	33.3	22.8	42.3

Table A.

Continued

		perature	Photosynthetic photon
DAP(1)	Maximum	Minimum	flux density
		c	moles/m ² /day
41	33.3	22.8	49.3
42	33.9	22.0	41.6
43	32.8	22.2	47.7
44	34.4	23.9	43.8
45	35.0	23.3	41.8
46	35.6	22.2	52.2
47	34.4	22.8	41.1
48	32.8	22.2	44.8
49	32.8	21.7	36.4
50	33.3	22.2	38.7
51	33.3	22.2	40.3
52	33.9	20.6	47.8
53	33.9	22.2	42.4
54	33.9	23.9	39.7
55	32.2	23.3	34.0
56	32.2	22.2	18.7
57	28.3	23.3	17.9
58	30.0	22.2	26.3
59	34.4	23.9	30.2
60	31.7	21.7	31.3
61	31.7	20.0	47.1
62	32.2	20.6	38.9
63	32.8	22.8	36.1
64	30.6	22.8	6.2
65	31.7	22.2	31.3
66	31.7	21.7	28.8
67	31.7	21.7	31.5
68	32.8	22.2	37.8
69	33.3	20.0	44.8
70	33.3	20.6	41.4
71	33.3	21.7	38.2
72	33.3	21.1	33.1
73	31.1	22.8	23.7
74	32.8	21.7	35.6
75	33.3	20.6	42.6
76	32.8	22.2	39.1
77	33.3	21.7	28.7
78	32.8	22.2	39.0
79	33.3	21.1	44.8

Table A.1

Continued

	Air temp		Photosynthetic photon
DAP(1)	Maximum	Minimum	flux density
		c	moles/m ² /day
80	32.8	18.9	42.8
81	33.3	18.9	42.6
82	33.9	20.6	35.0
83	33.3	22.2	16.6
84	30.0	21.7	24.2
85	26.7	16.7	38.8
86	26.1	11.7	40.7
87	28.3	9.4	41.8
88	27.8	15.0	15.0
89	31.7	21.1	33.6
90	32.2	17.2	41.0
91	32.2	20.0	32.6
92 93	30.6 30.0	17.2	36.0 22.6
93	31.1	20.6 16.7	37.3
95	32.2	18.3	37.3
96	32.8	16.7	36.4
97	31.7	20.0	37.3
98	31.7	16.7	38.1
99	32.2	17.2	38.7
100	32.8	13.3	36.0
101	30.0	15.6	27.3
102	31.1	17.8	34.3
103	31.7	14.4	38.5
104	31.7	17.2	32.1
105	31.7	20.0	18.1
106	30.0	19.4	22.0
107	32.8	20.6	29.4
108	30.6	20.0	10.8
109	26.1	16.1	33.3
110	25.6	14.4	31.8
111	26.1	15.6	15.2
112	27.2	14.4	35.5
113	28.3	8.9	36.3
114	30.0	11.7	35.4
115	33.9	15.0	31.7
116	29.4	11.7	36.8
117 118	26.7 28.3	6.7 13.3	35.0 32.6
118	28.3	13.3	32.6

Τa	b]	.e	А	•	1
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DAP(1)	Air temp Maximum	erature Minimum	Photosynthetic photon flux density
		c	moles/m ² /day
120	30.0	17.8	17.1
121	30.0	17.8	17.1
122	27.2	18.3	14.4
123	30.0	21.1	17.5
124	29.4	20.6	24.3
125	28.9	13.3	35.8
126	27.2	15.6	27.4
127	25.6	23.9	8.7
128	22.2	16.7	13.1
129	22.2	16.7	14.9
130	26.1	17.8	27.0
131	27.8	16.7	23.8
131	27.8	16.7	23.8

(1) DAP = 1 corresponds to planting date June 26, 1981.

Treatment	DAP	PGMAX	K	PVEM
		mg CO ₂ /m ² /s	PAR u mole/m ² /s	8
V-O	28 32 39 43 47 53 61 69 75 81 85 96 110 117 126	0.35 0.18 0.60 1.12 1.95 0.53 0.98 0.47 2.22 2.24 2.79 2.42 2.70 2.64 1.89 0.81 0.20	$\begin{array}{c} 581.76\\ 280.31\\ 672.40\\ 1151.92\\ 1820.74\\ 427.87\\ 545.25\\ 161.41\\ 1109.08\\ 744.54\\ 1162.16\\ 692.15\\ 898.02\\ 786.95\\ 856.57\\ 505.41\\ 124.11\\ \end{array}$	95.94*** 86.88*** 99.93*** 99.93*** 91.16*** 93.55*** 93.55*** 99.53*** 99.53*** 99.57*** 99.81*** 99.81*** 89.42*** 97.10***
V-D	85 96 110 117 126	4.15 2.08 1.75 0.50 0.26	2398.34 581.44 625.86 233.48 248.87	89.38** 98.35** 98.46** 99.77** 99.22**
R-O	85 91 95 98 102 109 116 123	2.80 1.43 1.02 0.85 1.32 1.28 0.43 0.22	937.33 500.91 317.17 309.07 616.50 705.13 305.49 69.13	99.55** 98.70** 96.93** 98.94** 79.15* 98.83** 92.74** 71.73*

Table A.2 Parameters of the rectangular hyperbolae for instantaneous gross photosynthesis and percent of variation explained by the model

Continued

Treatment	DAP	PGMAX	K	PVEM
		mg CO ₂ /m ² /s	PAR u mole/m ² /s	9
R-D	91	1.43	649.76	95.33**
	95	0.80	489.98	99.70**
	98	0.90	280.12	99.99*
	102	0.91	374.72	99.67*
	109 116	0.50	236.27 141.84	98.89*
	110	0.22	141.04	99.50*
W-O	14	0.19	773.90	73.57*
	20	0.51	1256.61	97.51*
	28	1.05	1607.02	89.48*
	32	1.30	1202.69	97.93*
	34	1.10	822.18	97.50*
	36	1.77	1082.27	91.99*
	39	1.83	1095.12	99.36*
	43	2.70	1696.95	98.40*
	47	1.47	639.79	97.57*
	49	2.07	709.98	98.64*
	53	2.29	845.09	97.29*
	61	2.19	800.64	99.70*
	69	1.92	607.05	98.01*
	75	2.21	767.10	98.64*
	81	4.52	2239.54	93.33**
	85	4.12	2014.05	99.91*
	91	3.47	1316.24	99.45*
	95	3.18	986.79	99.06*
	98	2.74	1080.26	98.99*
	102	2.04	723.02	98.90*
	109	1.76	751.61	96.28*
	116	0.75	452.53	92.29*
	120	0.60	387.90	73.22*
	123	0.49	237.84	98.85*
	130	0.23	153.01	94.94*
W-D	85	3.36	1509.95	99.80*
	91	3.01	1167.15	97.45*
	98	2.64	996.83	99.99*
	102	1.88	563.35	99.31*
	109	1.61	755.77	97.50*
	116	0.52	602.10	99.16*

* Significant at 0.05 probability level. ** Significant at 0.01 probability level.

Ta.	ble	A.3

Parameters of the rectangular hyperbolae for daily gross photosynthesis and percent of variation explained by the model

reatment	DAP	TDPGMAX	TDK	PVEM
		g CO ₂ /m ² /day	PAR mole/m ² /day	ġ
v-o	28	14.91	33.53	94.90**
	32	7.79	18.44	87.88**
	36	25.46	37.82	95.77**
	39	47.46	59.59	97.96**
	43	82.04	88.59	98.94**
	47	22.76	26.03	92.52**
	49 53	41.83 20.10	31.78	94.46** 78.37**
	53 61	93.97	11.82 57.69	/8.3/** 97.85**
	69	95.25	41.18	97.85**
	75	118.47	60.06	97.99**
	81	103.13	38.74	95.93**
	85	114.70	48.22	97.13**
	96	112.28	43.14	96.57**
	110	80.43	46.33	96.94**
	117	34.32	29.85	93.91**
	126	8.76	9.56	72.49**
V-D	85	174.44	112,98	99.30**
	96	88.70	33.52	94.90**
	110	74.43	35.63	95.36**
	117	21.49	15.91	85.10**
	126	11.06	16.75	86.08**
R-O	85	118.70	49,99	97.29**
	91	60.88	29.63	93.84**
	95	43.68	20.39	89.36**
	98	36.31	19.97	89.05**
	102	56.30	35.18	95.27**
	109	54.35	39.35	96.03**
	116	18.44	19.78	88.90**
	123	9.33	6.00	56.76**
R-D	91	60.64	36.76	95.58**
	95	33.91	29.10	93.67**
	98	38.39	17.90	87.27**

Continued

Treatment	DAP	TDPGMAX	TDK	PVEM
		g CO ₂ /m ² /day	PAR mole/m ² /day	Qi
R-D	102	39.01	23.36	91.24**
	109 116	21.53 9.32	16.06 10.64	85.28** 75.59**
W-0	14	7.94	42.54	96.49**
	20	21.54	64.21	98.20**
	28	44.41	79.44	98.73**
	32 34	54.89 46.60	61.83	98.08**
	34	46.60	44.76 56.50	96.76**
	39	77.61	57.07	97.78** 97.81**
	43	113.92	83.30	97.81**
	47	62.51	36.29	95.49**
	49	88.15	39,56	96.06**
	53	97.45	45.81	96.88**
	61	92.96	43.77	96.74**
	69	81.73	34.74	95.17**
	75	93.78	42.23	96.45**
	81	189.96	106.32	99.22**
	85	173.37	96.81	99.09**
	91	146.70	66.82	98.31**
	95	135.11	52.22	97.47**
	98 102	116.02 86.58	56.41 40.19	97.77**
	102	74.94	40.19	96.16** 96.35**
	116	31.87	27.26	93.01**
	120	25.53	24.02	91.59**
	123	20.95	16.15	85.39**
	130	9.66	11.30	77.25**
₩-D	85	141.99	75.25	98.61**
	91	127.39	60.26	98.00**
	98	112.18	52.07	97.51**
	102	80.24	32.65	94.69**
	109	68.45	41.70	96.38**
	116	22.05	34.50	95.12**

* Significant at 0.05 probability level. ** Significant at 0.01 probability level.

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Leaf area index (LAI) and dry matter accumulation throughout the season for all the treatments on 'Cobb' soybean, 1981, Gainesville, FL. Number of replicates vary from 1 to 4.

Vegetative stage water deficit (non-defoliated)

					Dry	Dry weight (g/m ²)	(g/m ²)			
		LAI	Le	Leaf	St	Stem	Se	Seed	Pod	Pod wall
DAP(1) mean	mean	st. d.	mean	st. d.	mean	st. d.	mean	st. d.	mean	st.d.
					-					
12	0.11	0.01	4.0	7.0	τ.α	T.U	ı	•	ı	
14	0.15	0.02	5.3	0.7	2.0	0.3	ı	ı	ı	,
20	0.37	0.04	14.4	0.5	7.0	0.2	ı	ı	ı	ı
28	1.20	0.07	3.31	0.2	25.0	3.3	I	ı	ı	I
32	0.97	0.16	32.9	5.0	30.6	5.9	I	ı	ı	•
34	0.85	0.10	25.1	5.2	28.4	4.9	ı	ı	ı	ı
36	0.77	0.01	25.9	0.7	26.6	1.3	I	ı	ı	ı
39	1.16	0.09	42.7	0.2	39.0	1.4	I	ı	ı	'
43	1.53	0.21	54.9	3.4	51.9	5.1	I	ı	ı	ı
47	2.01	0.03	62.7	6.0	74.9	0.3	ı	t.	ı	'
49	2.33	0.12	72.8	1.6	83.7	6.1	ı	1	ı	ı
53	2.18	0.06	71.7	3.6	95.3	4.9	I	ı	ı	ı
57+	2.19	0.08	70.0	3.6	94.8	4.8	ı	ı	ı	ı
61	2.89	0.60	98.9	20.7	120.5	20.9	ı	ı	0.1	÷,
.69	4.32	0.20	135.3	8.2	163.2	7.8	ı	ı	5.8	ı
70+	4.30	0.62	126.4	17.5	154.0	16.1	ı	ı	ı	ı
75	4.48	ı	152.5	ı	202.9	ı	ı	ı	34.4	ı
76 ⁺	3.94	0.27	122.0	7.0	163.4	16.2	ı	ı	ı	ı

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Continued

Vegetative stage water deficit (non-defoliated)

		I.A.I		Leaf		Stem	(m/p)	Seed	Pod	wall
(1) det	mean	st. d.	mean	st. d.	mean	st. d.	mean	st. d.	mean	st.d.
81.	4.19	ı	144.0	E	195.9	I	ł	I	61.6	
83+	4.09	0.49	136.0	14.4	232.5	34.2	ı	ı	ı	I
85	4.33	ı	135.0	,	202.9	ı	17.3	,	59.3	ı
+06	4.09	0.42	140.9	13.3	202.2	24.0	61.9	12.5	82.5	7.7
96	3.87	1	158.5	ı	216.0	ı	113.6	ı	97.4	I
+ 26	3.79	0.52	138.5	12.2	203.8	13.4	123.1	17.3	83.6	9.1
04+	3.73	0.29	146.5	8.1	233.5	26.1	233.0	37.1	100.7	8.1
10	3.66	ı	151.0	ı	244.0	,	330.6	ı	125.6	I
+11	3.17	0.32	131.5	15.2	201.0	15.2	289.9	21.4	86.4	6.0
17	2.52	ı	103.2	ı	195.6	ı	311.5	ı	86.7	ı
18+	2.10	0.77	77.7	30.5	203.5	20.1	350.7	35.7	103.7	15.8
25+	0.55	0.21	16.8	6.3	161.2	13.7	338.4	17.2	102.8	11.6
26.	0.57	ı	18.3	1	152.2	ı	354.7	ı	97.0	ı
132 ⁺	0.22	0.09	9.1	3.7	156.1	32.2	332.7	48.7	103.2	13.6

Continued

Vegetative stage water deficit (defoliated)

Wall	st. d	1	ı	ł	8.7	8.7	I	5.4	3.1	10.1	1	9.3	2.4	ł	9.8
Pod	mean	ı	ı	ı	63.1	79.6	108.3	91.3	93.0	79.1	101.9	94.2	92.5	93.2	94.8
Seed	st.d.	ı	ı	ı	ı	12.4	ı	25.2	18.1	36.2	,	33.1	8.6	ı	39.2
~ ~	mean	ı	ı	ı	28.0	54.1	132.0	128.1	192.6	243.9	306.5	280.9	283.4	300.3	280.0
Stem	st. d.	1	ı	19.9	ı	14.5	ı	14.4	23.5	16.2	ı	36.9	15.8	,	13.8
S	mean	153.3	212.3	239.2	239.2	198.8	260.7	216.4	220.5	173.9	222.4	185.0	150.6	159.4	142.8
Leaf	st. d.	1	'	17.7	ı	6.2	·	9.8	5.7	17.7	ı	19.4	8.3	,	1.3
	mean	110.2	127.7	125.4	145.8	118.1	135.4	116.2	111.0	84.4	74.1	64.3	24.6	27.7	6.3
AI	st.d.		ı	0.75	ı	0.31	ı	0.27	0.17	0.47	1	0.44	0.21	ı	0.02
T	mean	3.30	3.67	3.55	3.71	3.29	2.93	2.54	2.30	1.74	1.45	1.45	0.50	0.61	0 15
	DAP (1)	75	81	83+	85	+06	96	+ 26	104	111+	117	118+	125+	126	122+

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Continued

Reproductive stage water deficit (non-defoliated)

					ā	Dry weight	(_m/b)			
	1	LAI	1	Leaf		Stem		Seed	Pod	-
(1) AP(mean	st. d.	mean	st. d.	mean	st.d.	mean	st.d.	mean	st.d.
83+	5.11	0.53	176.4	20.7	404.5	72.0	1	I	1	1
	4.41		164.1	I	284.7	ı	64.1	ł	91.6	ı
+06	4.94	0.45	170.3	9.7	339.6	26.6	103.2	10.7	101.4	5.4
16	5.29	1	159.2	ı	307.3	ı	85.4	ı	85.0	ı
95	3.77	ı	135.9	ı	290.6	ı	158.9	ı	102.4	ı
+26	2.72	0.99	98.6	32.2	243.2	78.7	104.3	40.4	72.2	18.1
9.8	2.24	I	93.8	ı	258.4	ı	191.7	ı	84.5	ı
02	2.30	ı	88.5	I	254.5	ı	221.7	ı	91.2	ı
+ 10	2.65	0.74	108.1	31.0	278.8	36.6	265.9	32.8	1.66	9.7
60	3.05	1	134.2	ı	286.2	1	333.7	ı	115.8	ı
+ ;=	2.35	0.32	1.06	10.0	250.0	37.8	303.6	30.8	87.2	6.4
16	1.81	1	65.2	I	261.6	ı	384.8	ı	108.8	ı
+ 8	1.47	0.59	55.5	24.4	200.6	31.0	310.8	48.5	88.2	12.1
24	0.50	1	21.1	1	222.0	ı	326.8	ı	94.9	ı
25+	0.39	0.05	15.9	2.8	202.1	37.0	286.2	44.3	92.9	10.7
32+	0.21	0.10	9.8	4.3	199.5	21.7	269.6	53.9	84.1	11.0

Continued

Reproductive stage water deficit (defoliated)

					5	Dry weight	(m/b)				. 1
	-	LAI		Leaf	01	Stem		seed	Pod	wall	
(1) APC	mean	st. d.	mean	st. d.	mean	st. d.	mean	st. d.	mean	st.d.	
83+	3.71	0.37	138.1	17.0	363.4	45.2	ı	ı	1	ı	
+_	3.36	0.39	129.0	16.1	327.5	34.5	89.4	17.1	102.9	7.4	
	2.39	1	88.7	ı	271.1	;	155.9	1	103.2	ı	
+	1.83	0.70	79.6	25.8	230.4	67.8	118.6	28.4	71.4	15.9	
	1.59	ı	83.7	ı	303.3	,	218.5	,	103.2	ı	
+	1.19	0.44	63.7	18.9	236.6	32.7	183.5	29.0	82.4	10.1	
÷	1.07	0.48	58.9	21.1	211.0	13.3	231.3	24.3	75.3	7.6	
	0.55	1	27.0	1	197.8	ı	257.8	1	84.3	ı	
+	0.67	0.38	31.5	16.5	223.5	17.6	260.9	52.9	86.1	10.6	
	0.29		13.3	1	213.2	ı	298.4	ı	87.0	ı	
+	0.21	0.13	9.6	5.5	211.3	20.6	282.3	33.9	97.9	10.0	
+	0.17	0.06	7.7	2.6	191.7	12.9	300.2	33.6	101.8	11.1	

1

Continued

Well-irrigated (non-defoliated)

		I'AT		Leaf	500	Stem		Seed	Pod	wall
DAP (1)	mean	st. d.	mean	st. d.	mean	st.d.	mean	st. d.	mean	st. d.
12	0.11	0.01	4.0	0.2	1.8	0.1	ı	i	ł	ł
14	0.15	0.02	5.3	0.7	2.0	0.3	1	ı	ł	ı
20	0.37	0.04	14.4	0.5	7.0	0.2	1	ı	I	ı
28	1.27	0.33	35.0	7.4	25.4	5.5	1	1	ł	1
32	1.75	0.32	49.7	4.8	40.4	9.4	I	I	ł	ı
-34	1.75	0.28	49.9	6.0	43.7	8.9	I	ł	i	i
36	1.75	0.25	52.5	5.7	46.2	8.7	1	1	i	1
39	2.49	0.19	72.2	0.3	67.8	2.4	ı	ł	1	·
43	3.11	0.49	86.4	10.9	100.5	14.1	1	ł	ı	ı
47	3.48	0.08	98.0	1.6	126.0	3.8	I	ł	ı	ı
49	4.20	0.63	110.2	9.1	138.4	16.7	1	i	ı	ı
53	4.57	0.24	131.7	11.2	175.8	22.4	ı	i	ı	ı
57+	4.33	0.70	120.6	11.9	189.6	16.5	i	ı	ı	ı
61	5.01	0.04	146.9	7.1	216.3	3.1	ı	ı	0.4	1
69	5.87	0.27	171.7	11.9	270.4	2.7	I	1	8.9	i
70+	6.25	0.72	175.0	24.9	289.7	57.7	i	i	i	i
75	5.34	ł	165.7	ı	263.9	1	ł	ı	36.1	ł
76 ⁺	4.86	0.45	147.2	10.7	272.7	42.8	ł	1	ł	ı
81	4.49	ı	170.4	i	294.0	ı	ı	1	86.0	i
83+	5.06	0.51	165.1	13.6	367.4	25.1	ı	ı	i	ł
85	2.74	1	169.4	ı	292.8	ı	55.7	1	81.3	ı
+ 06	4.50	1.05	161.2	42.6	327.0	77.3	91.9	17.3	99.3	24.1
51	4.10	1	140.9	ł	256.6	ı	103.7	ı	94.6	ı
95	3.85	•	154.9	ı	241.9	:	129.4	ı	89.1	ı
97+	OL V	0 10	157 3	16 9	787 6	47 9	164 3	28 9	87 9	12.9

Continued

Well-irrigated (non-defoliated)

Dry weight (g/m²)

wall	st. d.	ı	ı	10.4	ı	11.1	I	6.8	ı	ı	9.0	ı	5.4
Pod	mean	112.3	89.1	98.3	126.4	97.0	93.2	93.7	120.2	117.0	90.06	99.3	107.9
Seed	st.d.	t	ı	17.8	ı	42.9	ı	18.9	I	ı	30.9	I	18.7
ŝ	mean	243.7	180.4	238.7	429.5	327.8	349.6	354.8	432.9	485.2	320.8	392.1	379.6
tem	nean st.d.	I	ı	26.4	I	17.9	ı	21.8	ı	ı	33.8	ı	26.0
S	mean	328.7	260.3	296.2	328.0	302.4	307.4	248.3	275.3	324.4	196.6	225.3	230.7
eaf	nean st.d.	1	ı	24.0	ı	11.4	1	34.7	ı	ı	5.2	ı	5.5
Ч	ທຣລກ	173.0	139.8	153.2	174.5	152.5	127.8	81.0	49.2	41.7	21.5	32.6	16.3
AI	mean st.d.	1	1	0.54	1	0.19	ı	0.99	ı	ī	0.13	ı	0.10
Ĥ	mean	4.33	3.17	3.96	4.60	3.83	3.43	2.18	1.38	1.03	0.61	0.88	0.44
	DAP (1)	86	102	104	109	+ 1 1 1	116	118+	120	124	125+	130	132+

Continued

115

Continued

. 2.

Well-irrigated (defoliated

		LAI		Leaf		Stem		Seed	Poc	Pod wall
DAP (1)	mean	st. d.	mean	st. d.	mean	st. d.	mean	st. d.	mean	st. d.
75	4.93	1	154.3	1	289.4	1	I	1	ı	ı
81	4.67	1	168.0	,	369.3	ı	ı	ı	I	ı
83+	3.96	0.35	137.1	9.1	360.8	33.3	I	I	I	ı
85	3.59	I	139.4	ı	276.6	ı	38.4	ı	70.9	ı
+06	4.05	1.03	138.0	27.6	321.2	73.0	90.2	31.2	92.4	18.5
95	3.08	1	120.5	ı	254.7	ı	132.5	,	89.3	ı
+ 26	2.55	0.51	115.9	14.8	285.6	33.3	132.6	21.3	83.7	13.6
102	2.79	1	132.4	ı	311.4	1	229.8	ı	96.5	ı
104	2.57	0.64	124.6	23.4	301.5	38.5	226.1	29.4	100.8	8.2
+	2.20	0.45	110.5	16.0	291.0	41.3	315.2	90.5	96.6	22.9
116	1.07	1	51.2	I	218.6	1	292.2	ı	96.8	ı
118	1.04	0.23	49.5	6.8	244.0	31.9	334.0	53.2	100.8	22.0
124	0.55	I	28.8	ı	214.1	ı	317.2	ı	97.3	ı
125+	0.55	0.37	23.6	16.0	221.3	17.0	341.1	45.3	104.7	13.1
132+	0.24	0.12	10.5	6.0	220.3	24.6	313.0	55.3	98.2	17.4

Designates sampling dates where four field replicates of 60 cm of row were sampled. All other dates pertain to samples taken from the assimilation chamber where 109 cm of row was sampled.

 $^{\mathrm{d}}\operatorname{For}$ dates not showing seed weight, pod wall includes a minus, but significant amount of seed.

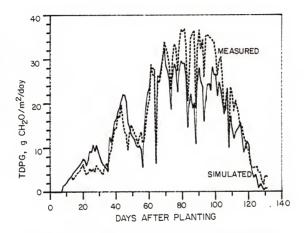


Figure A.1. Comparison of daily gross photosynthesis simulated by SOYGRO versus field measured TDPG for the vegetative stage water deficit (non-defoliated) treatment.

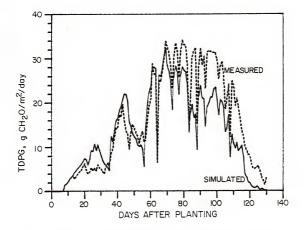


Figure A.2. Comparison of daily gross photosynthesis simulated by SOYGRO versus field measured TDPG for the vegetative stage water deficit (defoliated) treatment.

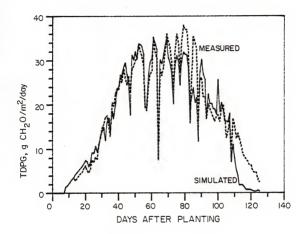


Figure A.3. Comparison of daily gross photosynthesis simulated by SOYGRO versus field measured TDPG for the reproductive stage water deficit (non-defoliated) treatment.

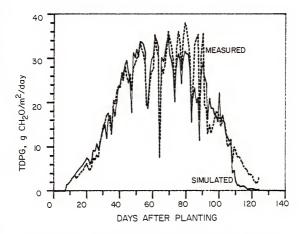


Figure A.4. Comparison of daily gross photosynthesis simulated by SOYGRO versus field measured TDPG for the reproductive stage water deficit (defoliated) treatment.

120

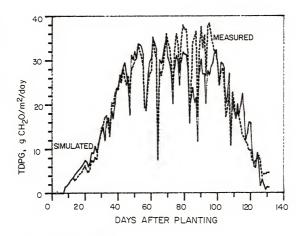


Figure A.5. Comparison of daily gross photosynthesis simulated by SOYGRO versus field measured TDPG for the well-irrigated (non-defoliated) treatment.

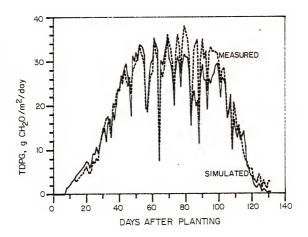


Figure A.6. Comparison of daily gross photosynthesis simulated by SOYGRO versus field measured TDPG for the well-irrigated (defoliated) treatment.

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Odair Alves Bovi was born October 4, 1947, in Piracicaba, Sao Paulo, Brazil. He enrolled in the Escola Superior de Agricultura Luiz de Queiroz (Universidade de Sao Paulo, Brazil) in 1968 and received a Bachelor of Science degree as Engenheiro Agronomo in 1972.

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Mr. Bovi is married and has two children.

128

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Dr. Kenneth J. Boote, Chairman Associate Professor of Agronomy

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August 1983

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