

**MODELING LEAF PHOTOSYNTHESIS  
AS A FUNCTION OF AGE  
AND LIGHT ENVIRONMENT**

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**Abstract**

A mathematical description for the relationship between the rate of cotton leaf net photosynthesis at saturating light and differential light environment and leaf age is developed. Model calibration accounted for more than 90% of the total uncorrected sum of squares. Finally, the model provides a tool for the prediction of photosynthesis rates for leaves growing in canopy.

**Introduction**

Mathematical model provides important tools for optimizing production practices for cotton (Reddy et al., 1997a). Typical model simulates cotton growth and development in response to environmental factors and management practices. This paper describes the development of one component for a cotton crop model: a net leaf photosynthesis at saturating light model responsive to light environment and leaf age.

Photosynthesis is the primary production process that determines yield potential. The obtainable cotton yield could reach approximately 3 times the normal yield under optimal environmental conditions with natural light (Reddy et al., 1995, 1997b). Manipulating photosynthetic factory by crop management can substantially alter the cotton plant's ability to produce and retain fruiting forms during the reproductive cycle (Wells, 1997) and thus yield. The contribution of leaf senescence to declining canopy photosynthesis and to carbon availability for yield has been identified as a potential limitation in crop production (Wullschlegler and Oosterhuis, 1992). In addition, modifications of leaf longevity and photosynthesis rates have potential to increase net carbon production by individual leaf and thus increase the potential for cotton yield (Landivar et al, 1983; Wullschlegler and Oosterhuis, 1990a).

The possibility of restructuring the canopy to alter light environment in order to reduce the physiological deterioration of photosynthetic activity during leaf senescence has long been proposed. Sassenrath-Cole (1997), however, showed that varying light environment of

main stem leaf from 15% to 100% of full sun levels using artificial, individual leaf shading did not obtain photosynthetic responses other than physiological changes within the aging leaf. In contrast, we (Kasemsap et al., 1998) found positive correlation between  $P_{max}$  and differential light environment at various leaf ages under natural conditions. This evidenced photosynthetic adaptation of cotton leaves to growth light environment, in addition to physiological changes with leaf aging.

The objectives of this study were to: 1) supplement leaf age and photosynthesis rate to our earlier data (Kasemsap et al., 1998); 2) formulate a mathematical model for net photosynthesis at saturating light incorporating leaf age and light environment; and 3) calibrate this model.

**Material and Method**

**Field Experiment : Photosynthesis and Leaf Age**

Cotton plants (*Gossypium hirsutum* L., cv Srisumrong60) were grown during rainy growing season from seed planted on May 29, 1996 at research field in Suwan Station, Kasetsart University (latitude 14.7°N, longitude 101.2°E). Between row spacing was 1.25 m and within row spacing was 0.40 m. The experiment was conducted under well-watered conditions to eliminate the influence of water stress on photosynthesis. Irrigation was applied 4 times in growing season using a sprinkler system. Pre-plant fertilizer (formula 15-15-15 at 250 kg ha<sup>-1</sup>) was applied 2 weeks before planting.

**Photosynthesis Measurement**

Single leaf net photosynthesis rates at saturating light ( $P_{max}$ ) were measured using portable photosynthesis system model LI-6400 (Li-Cor, Lincoln, NE), using optional red LED light source that provided photosynthetically active photon flux (PPF) at 1800  $\mu\text{mol m}^{-2}\text{s}^{-1}$ . Leaf temperature was not controlled. Air humidity was 50%  $\pm$ 5%. Carbon dioxide concentration of entering air was set at 400  $\mu\text{l l}^{-1}$ .

**$P_{max}$  and Light Environment**

Data for relationship between  $P_{max}$  and light environment were taken from the study presented by Kasemsap et al. (1998). In brief, light sensors, made of amorphous silicon (Solems, ZI Les Glaises, Palaiseau, France) and calibrated with SKP 215 Quantum Sensor (Skye Instruments Ltd., U.K.), were attached to leaf surfaces to continuously monitor light environment. The analog signals were recorded by data logger model CR10 with multiplexer AM416 (Campbell Scientific Ltd., Logan, UT). Light sensors were attached to the center of upper leaf surfaces using double-sided tape when leaves were 10 DAU. Daily integration of PPF was used to quantitatively express light environment of the leaves being studied.

**Statistical Procedure**

The models were calibrated to  $P_{max}$  data using a non-linear regression procedure by Statistical Analysis System (SAS

Institute Inc., North Carolina). The selected method was by multivariate secant or false position analysis with a default convergence criterion.

## **Results and Discussion**

### **Effect of Leaf Age**

Relationship between  $P_{max}$  and leaf ages (Fig.1a) of leaves from all categories (main stem, sympodial, monopodial positions) clearly showed the physiological limitation that leaf age imposed on photosynthesis. Upper limit of  $P_{max}$  of at particular age increased with leaf age to the maximum of approximately  $36 \mu\text{mol m}^{-2}\text{s}^{-1}$  at approximately 20 days after it unfolded, remained constant for a few days, then gradually declined until it abscised from the plant. Observed  $P_{max}$  at each leaf age ranged from the upper limit to near zero (Fig.1).  $P_{max}$  of main stem leaves (Fig.1b) and F1 sympodial leaves (Fig.2a) were closed to the upper limit.  $P_{max}$  of leaves on monopodial branches (Fig.1c) were closed to upper limit at 8-20 days after unfolding (DAU) but ranged from 50% to 80% of the upper limit at ages greater than 20 DAU.  $P_{max}$  of leaves on sympodial positions on monopodial branches did not reach upper limit and showed a lot of variations. On the contrary,  $P_{max}$  of F1 F2 and F3 leaves reached the upper limit over greater range of leaf ages than monopodial leaves. The more further away from main stem, the greater variations in  $P_{max}$  of sympodial leaves (Fig.2).

### **Model Development**

**Leaf Age Function.** A function proposed by Reed et al. (1976) was fit to relationship between leaf age and the upper limit of  $P_{max}$  (defined as  $P_{age}$ ) selected from the obvious greatest observed  $P_{max}$  at certain leaf age (Fig.3).

$$P_{age} = P_{maxage} * \frac{(A - A_{min}) * (A_{max} - A)^{\beta}}{(A_{peak} - A_{min}) * (A_{max} - A_{peak})^{\beta}} \quad (1)$$

where  $P_{maxage}$  is the greatest  $P_{max}$  which is obtainable at leaf age equals  $A_{peak}$ ,  $A_{min}$  and  $A_{max}$  is the minimum and the maximum leaf age at which  $P_{age}$  reach zero, and

$$\beta = \frac{A_{max} - A_{peak}}{A_{peak} - A_{min}} \quad (2)$$

This fit is highly significant with 99% of the total uncorrected sum of squares being accounted for by the model (Table 1). All parameters are significantly different from zero (Table 2).

**Light Environment Function.** At certain leaf age,  $P_{max}$  was positively related to light environment ( $PPF_{leaf}$ ) under which leaves had been growing (Kasemsap et al., 1998). To describe the relationship between  $P_{max}$  and light

environment, several functions were tested and the modified rectangular hyperbola was selected. Furthermore, the upper limit of observed  $P_{max}$  at high light environment was prescribed to be proportional to  $P_{age}$ .  $P_{max}$  can be represented as:

$$P_{max} = \frac{s * (PPF_{leaf} + i) * c * P_{age}}{s * (PPF_{leaf} + i) + c * P_{age}} \quad (3)$$

where  $s$  is the initial slope of the response,  $i$  and  $c$  are constants, and  $PPF_{leaf}$  is the light environment each leaf experienced ( $\text{mol m}^{-2}\text{d}^{-1}$ ).

The fitting utilized  $P_{age}$  from equation (1) and (2). The data used included  $P_{max}$  observed when leaves were 25, 32, 39, 44, and 46 days after unfolding and light environment at 0, 1, and 2 days before  $P_{max}$  measurement (Kasemsap et al., 1998). This fit accounted for more than 90% of the total uncorrected sum of squares (Table 1). All three parameters are significantly different from zero (Table 2).

On the whole, the model predicts all observed light environment response data satisfactorily (Fig.4), although substantial overestimation occurs for 39-day-old leaves. Such deviation is not unexpected because the model assumes uniform environmental conditions and plant material, while the data includes daily light environment variations attributable to subtropical climate and inter-plant variability.

A three-dimensional plot (Fig.5) illustrates the changes in photosynthetic response to differential light environment and leaf age. At high light environment,  $P_{max}$  is remarkably responsive to leaf age similar to the observed response of main stem leaves. At low light environment,  $P_{max}$  response to leaf age is fairly flat between 10-40 DAU. This is coincided with the observed response of sympodial leaves on monopodial branches (Fig.1d) that initiated late in the growing season inside rather well developed canopy and received only about 50% of light compared to main stem leaves (Kasemsap et al., 1998). It is important to note that the model could be overestimating  $P_{max}$  at older leaf age because the data set used for calibration did not possibly include  $P_{max}$  of 4 shed leaves at 44 DAU).

Additional factors such as leaf temperature, specific leaf mass (SLM), and leaf nitrogen content can be incorporated into this model by letting  $P_{maxage}$  or  $P_{age}$  vary with these factors (Lieth and Pasian, 1990). The effects of SLM and leaf nitrogen content on photosynthesis could have already been inadvertently incorporated in the current model through the existing light environment variable because the typical response of leaf to differential light environment is to adjust SLM and leaf nitrogen content (Loomis and Connor, 1992). Furthermore, model extension to include the response to instantaneous PPF and respiration with

subsequent recalibration would allow the prediction of net leaf photosynthesis rate.

### Summary

The relationship between upper limit of cotton leaf net photosynthesis at saturating light and leaf age was described mathematically. Reduction of  $P_{max}$  from this upper limit was attributed to the effect of differential growth light environment. The developed mathematical model accounted for more than 90% of the total uncorrected sum of squares in the data set. The model can be extended to include additional factors in the future.

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Table 1. Nonlinear least-squares summary statistics from fitting the leaf age model and the light environment model to data set.

Source	Analysis of Variance			
	Leaf age model		Light Environment	
	df	Sum of Squares	df	Sum of Squares
Regression	4	21278.7	3	57492.8
Residual	24	69.7	170	6440.2
Uncorrected total	28	21348.4	173	63933.0

Table 2. Parameter estimates from nonlinear least-squares fitting of the leaf age model and the light environment model to data set.

Parameter	Unit	Value
Leaf age model		
$A_{min}$	Day	-5.15 ±1.53
$A_{peak}$	Day	20.9 ±2.46
$A_{max}$	Day	54.3 ±1.61
$P_{maxage}$	$\mu\text{mol m}^{-2}\text{s}^{-1}$	36.5 ±0.60
Light environment model		
s	Unitless	3.87 ±1.22
i	$\mu\text{mol m}^{-2}\text{s}^{-1}$	2.03 ±1.58
c	Unitless	1.09 ±0.12

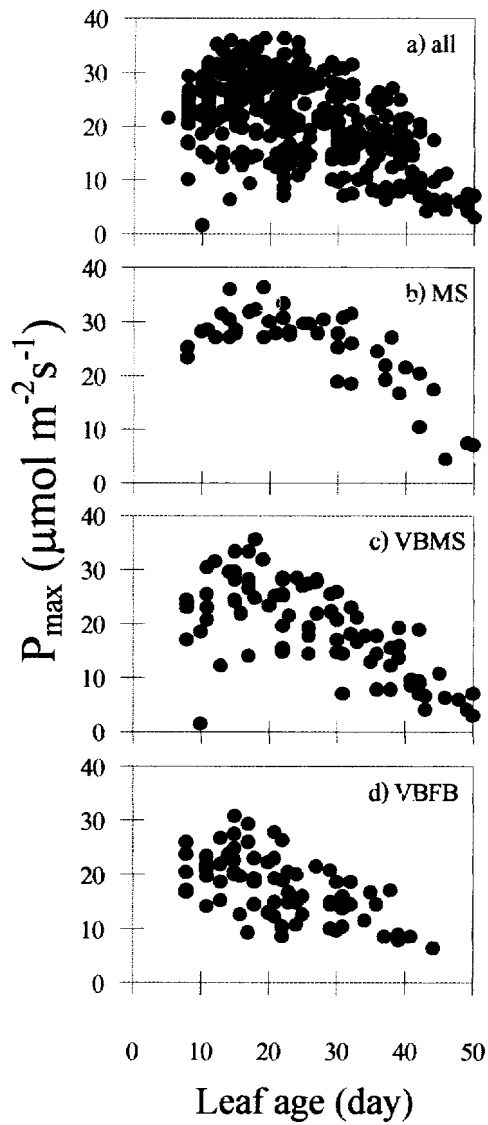


Figure 1. Relationship between cotton leaf net photosynthesis rates at saturating light ( $P_{\max}$ ) and leaf ages for: a) all leaves (including sympodial leaves); b) leaves on main stem (MS); c) leaves on monopodial branches (VBMS); and d) sympodial leaves on monopodial branches (VBFB).

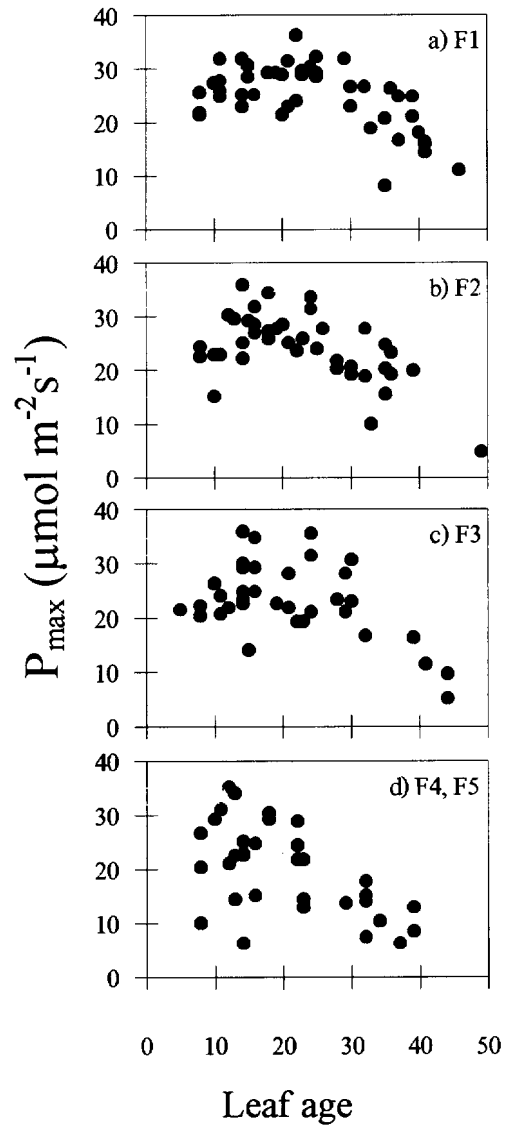


Figure 2. Relationship between cotton leaf net photosynthesis rates at saturating light ( $P_{\max}$ ) and ages for leaves at different positions on sympodial branches.

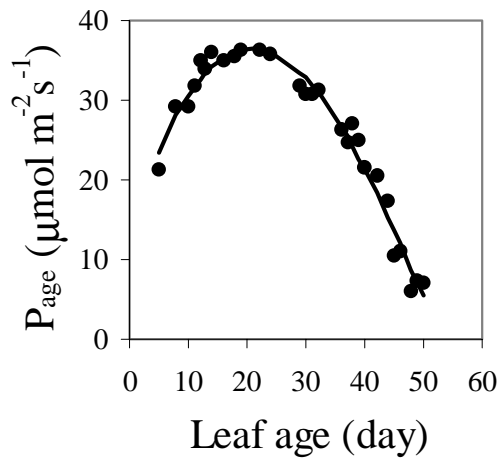


Figure 3. Relationship between upper limit of leaf net photosynthesis rates measured at saturating light at specific leaf age ( $P_{age}$ ) and leaf ages. Line was fitted using Reed's function with parameters shown in Table 1.

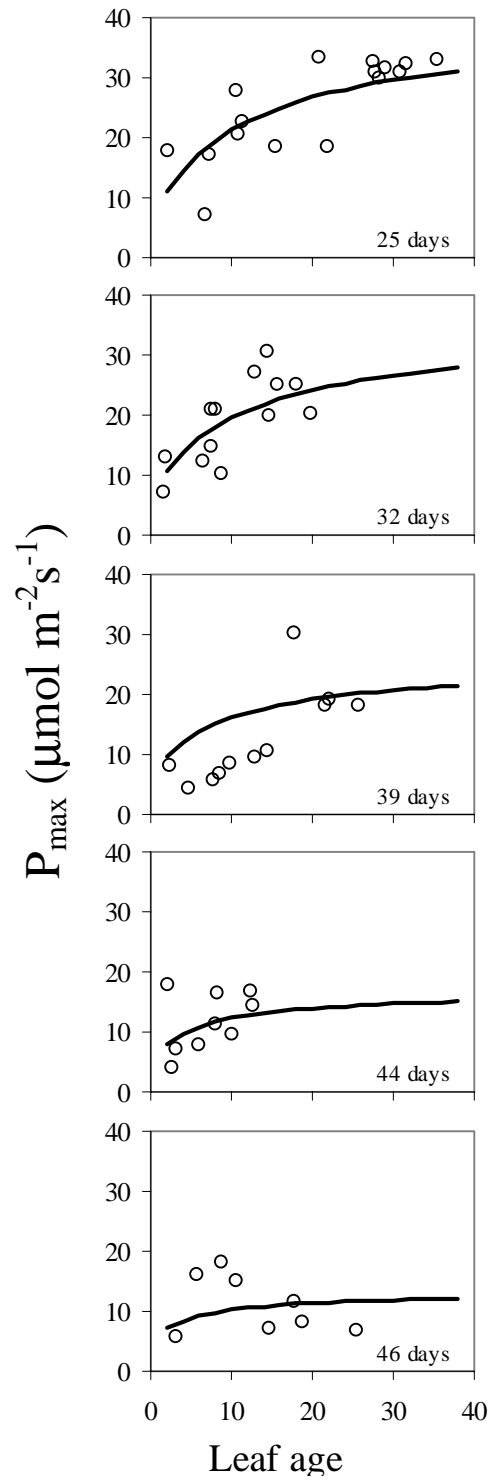


Figure 4. Predicted (curves) and observed (circles) cotton leaf net photosynthesis rates at saturating light ( $P_{max}$ ) as function of differential light environments of leaves recorded one day before photosynthesis measurement at leaf ages 25, 32, 39, 44, 46 days after leaf unfolding.

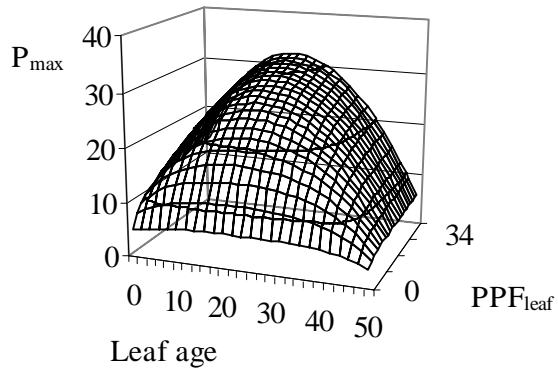


Figure 5. Predicted three dimensional response surface of cotton leaf net photosynthesis rates at saturating light ( $P_{\max}$ ,  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) as functions of differential light environment ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) and leaf age (days after leaf unfolding).