

EXPLORING THE USE OF THE ENVIRONMENTAL PRODUCTIVITY INDEX CONCEPT FOR CROP PRODUCTION AND MODELING

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ABSTRACT

Crops fail to achieve their genetic potential, even under the best crop husbandry, because of environmental constraints. Improvements in crop adaptation to environmental stresses and greater crop yield can be attained if the decrease in potential caused by each environmental factor is known. The objective of this chapter is to describe the concept of Environmental Productivity Index (EPI), and its effectiveness in quantifying stress effects on crop growth and in modeling. We used cotton (*Gossypium hirsutum* L) as a model crop and photosynthesis as an example process and experiments were conducted in a sunlit Soil-Plant-Atmosphere-Research facility. Temperature, solar radiation, atmospheric CO₂ [CO₂], water, ultraviolet-B radiation and nutrients were controlled and varied systematically and cotton canopy photosynthesis and abiotic variables were measured and quantified. Potential photosynthesis, defined as the rate of photosynthesis occurring under optimum environmental conditions, was measured and estimated. Then, algorithms were developed for simulating various stress factor effects, known as EPIs, to decrease the potential photosynthesis. The EPI indices for each environmental factor range from 0, when a given environmental stress is totally limiting a process, to 1, when it does not limit that process. These indices represent the fractional limitation due to the environmental stress effects on photosynthesis. The potential as well as the EPI functions for various environmental stresses on photosynthesis were used to simulate canopy photosynthesis in a dynamic cotton simulation model, GOSSYM. We also discuss various validation efforts of the GOSSYM cotton model with these concepts and its use in various applications such as identifying knowledge voids, hypothesis testing in research, farm management, climate change impacts, and in policy making decisions.

INTRODUCTION

Modern agricultural research with specialized disciplines has led to significant achievements in understanding the effects of environmental factors on crop production at field, plant, organ, cellular and biochemical levels. Integration of the knowledge gained from these specialized disciplines to develop a holistic understanding of crop production led to the development of crop models since the early 1960's (Sinclair and Seligman, 1996). Crop models developed vary from empirical models that are simple regression equations to dynamic mechanistic models that explain intricacies of crop growth, development and physiology (Thornley and Johnson, 1990; Passioura, 1996). Crop models are able to simulate the potential yield or biomass of a given crop; however, this is rarely achieved under field conditions due to combined abiotic and biotic stress effects on various growth and developmental processes. Therefore, attempts were made to incorporate the effects of various stresses on crop growth and development as new quantitative data become available with deeper understanding of physiological, growth and developmental processes of plants.

Abiotic stress conditions cause extensive losses to agricultural production worldwide (Boyer, 1982; Mooney et al., 1991). In addition, human activities are causing alarming changes to the environment (IPCC, 2007), on which we rely for ecosystem goods and services, which will exacerbate the yield-limiting factors even more in the coming decades. Breeders and producers have long known that a simultaneous occurrence of several abiotic stresses, as in the natural environment, can be more detrimental to crop performance than a single stress factor in any given environmental condition. Solar radiation, temperature, atmospheric [CO₂], soil water, and nutrients are the major abiotic factors influencing crop performance. Each of these environmental factors, when available at their optima, would result in achieving maximum potential yield or biomass. Any deviation from the defined optima would affect growth, development, and finally yield. Interactions between environmental factors are also necessary in crop models for correct prediction of growth and development (Ahuja and Ma, 2002; Ewert et al., 2002). For example, yield potential of cotton, based on numbers of potential fruiting sites, exceeds 9 bales per acre (K.R. Reddy and Hodges, 2006). However, current average world and US cotton yields are about 1.36 and 1.78 bales per acre, respectively (<http://www.fas.usda.gov>), much less than this potential. Thus, the effects of abiotic and biotic stresses need to be quantified and must be included in crop models to provide a realistic picture of yield under field conditions.

Controlled environment facilities have been extensively used in developing functional relationships between crop parameters and environmental factors (Wilkerson et al., 1983; K.R. Reddy et al., 1993, 1997a, 2001, 2003; Horie et al., 2000; Kim et al., 2006, 2007; Fleisher and Timlin, 2006; Fleisher et al., 2006a, b; Timlin et al., 2006). The potential of a given crop species can be achieved under controlled growth conditions, as the crop can be kept free from insects and diseases by isolating from the surroundings, and all environmental factors limiting to obtain the potential are optimally maintained. Also, controlled environmental facilities provide us with the ability to precisely simulate the effects of either single or multiple stresses on crop growth and development.

Crop models developed initially were either explanatory (de Wit et al., 1978; Duncan et al., 1967; van Keulen, 1975) or predictive (Fitzpatrick and Nix, 1969) of crop responses. Integration of these approaches has led to the development of complex and dynamic mechanistic models that are both explanatory and predictive in nature. Cropping system models that mimic production under field conditions have been developed for several crop species (Baker et al., 1983; Boote et al., 1997; Hodges et al., 1998; Jones et al., 2003; van Ittersum et al., 2003). Modeling the effects of environmental stresses is a challenging task in crop model development. Crop model developers differ in their approach in accounting for the effects of multiple stresses on crop growth, development and yield that may be independent (multiplicative function; Holt et al., 1975; Williams, 1995) or dependent (the most stressful factor remains; Godwin and Jones, 1991; Godwin and Singh, 1998).

The role of environmental stress factors and limiting factors to crop productivity has been discussed for centuries. Boyer (1982) touched on this topic and reminded the readers of the difficulty of quantifying the effects of limiting environmental factors on crop production. Little has been done quantifying the processes involved when one or several factors limit plant growth since the work of Sprengel-Liebig proposed the Law of Minimum (van der Ploeg et al., 2003). In the early 1960's, D. N. Baker (personal communication) recognized that with the coming availability of drastically improved computing capability and began holding informal seminars and discussions to assemble processes into comprehensive crop simulation models began employing a multiplicative approach in his conceptive cotton model. He, James McKinion, Jerry Lambert and others found it to be a satisfactory

method to predict crop responses to varying degrees of environmental stresses (for the details see Baker et al., 2004 and the references cited therein). The term environmental productivity index concept, however, was proposed and used by P. S. Nobel to account for both the independent and dependent nature of the stress factors on crop growth and development (Nobel 1984, 1988, 1991, 2000).

FACILITIES, EXPERIMENTAL CONDITIONS AND METHODS

1. Soil-Plant-Atmosphere-Research (SPAR) facility

The sunlit, controlled environment plant growth facility known as Soil-Plant-Atmosphere-Research (SPAR) is located outdoors on a 20 x 30 m concrete pad at Mississippi State University, Mississippi State (88.8 LONG., 33.5 LAT., and 85 MSL), Mississippi, USA was used to conduct the experiments and to generate the data presented in this chapter. Each unit has the capability for controlling air temperature, atmospheric [CO₂], and UV-B radiation at predetermined set points for studies of plant growth under natural solar radiation regimes (K.R. Reddy et al., 2001, 2003). The bottom third of each SPAR unit consists of a steel bin (1.0 m deep x 2.0 m long x 0.5 m wide) to contain rooting medium. The upper two-thirds is an airtight Plexiglas chamber 2.5 m height and 2.0 x 1.5 m in cross-section to accommodate the aerial plant parts. Variable-density shade cloths are positioned around the edges of the plant canopy inside each unit and are adjusted manually to match plant heights in order to simulate the presence of neighboring plants and to eliminate the need for border plants.

A door in the bottom of the aerial portion of each chamber is hinged for access to the soil surface and the aboveground portions of the plants. Ducts on the northern face connect to the cooling system. Conditioned air is introduced at the top of the Plexiglas chamber, flows down through the plant canopy, and is returned to ducts just above the soil surface. The northern face of the soil bin has many large holes closed with rubber stoppers to facilitate measuring soil environmental conditions. The southern face is constructed of reinforced glass to allow collection of data on root growth dynamics (V. R. Reddy et al., 1994).

The SPAR units provide a natural solar radiation environment (95% transmissive to photosynthetically active radiation, PAR) and have capabilities for controlling both the aerial and soil environment across a wide range of environmental set points. Controlled factors in each chamber include atmospheric [CO₂], air and dew point temperatures, and UV-B radiation. The environmental control system can be programmed to provide continuously changing values over a diurnal cycle to yield either a smooth sinusoidal or a square wave function. Similarly, a monitoring system consisting of sets of data acquisition/switching units (Agilent Technologies, Santa Clara, CA, USA) and in-house developed software system provides accurate measurement of the environmental conditions throughout an experiment. Set points can be programmed to change for short-term periods so that plant responses to short-term environmental conditions can be investigated during critical stages of crop development. In addition, [CO₂] can be maintained from sub-ambient to super-ambient levels in the SPAR system in a manner not possible with other types of field exposure systems. This capacity allows investigation of specific processes related to reduced carbon sources and sinks and their interactions that lead to widely varying growth, development, and fruiting patterns in cotton. Because the SPAR units provide continuous measurement of canopy photosynthesis and transpiration throughout the experimental period, these biophysical processes can be precisely determined and controlled as needed. Rate equations can be developed from these results to build new mechanistic models of growth and development and/or improve the existing models. In addition,

irrigation and nutrient media can be manipulated to deliver predetermined amounts into each SPAR unit by adjusting the provision of full-strength Hoagland's nutrient solution through a computer-controlled drip-irrigation system. In addition, the nutrient solution can be modified to study the effects of various nutrients on crop growth and development.

1. a. Measurement and control of environmental variables

Air temperature was monitored and adjusted automatically every 10 s. Temperature control was achieved using a dedicated computer that opens and closes a set of solenoid valves connected to a chilled water radiator and switches an electrical resistance heating system on and off as needed. Heat was provided by two 5.5 kilowatt heating elements mounted on either side of the air circulation unit. Air temperature was monitored using an aspirated, shielded thermocouple and maintained within ± 0.5 °C of the treatment set points over a daytime range of 18 to 40 °C and a nighttime range of 12 to 32 °C. Relative humidity in the SPAR chambers was measured at 10-s intervals and summarized over 900-s periods, but not controlled, with a Vaisala sensor (Vaisala, Inc. Tucson, AZ, USA) installed inside the return airline flow of the system.

Photosynthetic active radiation was monitored every 10 s using a pyranometer (Model, LI-200SA, LI-COR Inc, Lincoln, Nebraska, USA) placed above the canopy. Also, at an adjacent weather station, global radiation, and PAR were measured at 10 s intervals and those data were averaged separately over 900-s intervals. Similarly, canopy light interception was monitored using a dedicated line quantum sensor (Model, LI-1000, LI-COR Inc, Lincoln, Nebraska, USA) placed just above the soil-level.

The [CO₂] in each SPAR unit was monitored and adjusted every 10 s throughout the day and was maintained within 10 $\mu\text{L L}^{-1}$ of treatment set points during the daylight hours. A mass-balance approach based on output from a dedicated CO₂ analyzer for each unit (Model, LI 6200, LI-COR Inc, Lincoln, Nebraska, USA) was used to open and close the solenoid valves as needed to maintain constant [CO₂] in each chamber. To maintain that constant [CO₂], pure CO₂ was injected through a system that includes pressure regulators, solenoid and needle valves, and flowmeters. Flowmeters were calibrated with a gas displacement meter at the beginning and end of each experiment.

1. b. Measurement of photosynthesis and respiration

Each SPAR unit's growth chamber and fan-coil box formed a semi-closed system for the measurement of canopy CO₂ and water vapor exchange. The Plexiglas chamber containing the plants ducts, and cooling system was nearly airtight. A mass balance approach was used to calculate net CO₂ exchange rates (P_n) of the plant canopies throughout the experiment. Precise control of the [CO₂] at ± 10 $\mu\text{L L}^{-1}$ of the treatment-set point was achieved by using a calibrated infrared gas analyzer. Carbon dioxide flow rates were recorded three times a day and converted into mass quantity via gas law correction for temperature and pressure. The time intervals during which the solenoid valves are open were monitored by a computer, and thus the amount of CO₂ injected is known. A leakage test was performed each night to derive the plant growth chamber leakage rate and to correct canopy gas measurements (Acock and Acock, 1989; V.R. Reddy et al., 1995).

Using values for the mass of CO₂ injected to maintain treatment-set point, and the mass of CO₂ lost via leakage, one can calculate net canopy photosynthesis per unit ground area, P_n ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Rates of CO₂ fixation for cotton at full canopy are shown for a typical diurnal cycle in Fig. 1, and were closely coupled to the amount of solar radiation received. Respiration rates ($\text{mg CO}_2 \text{ m}^{-2}$

s⁻¹) were calculated in a similar manner by maintaining daytime temperatures one hour into the nighttime period. Consequently, gross canopy photosynthesis, P_g , was calculated and used to correct P_n data for daytime respiration rates (V.R. Reddy et al., 1995). Rates of typical canopy gross photosynthesis for cotton at full canopy as a function of PAR are shown in Fig. 2. Using photosynthesis and PAR response functions, canopy photosynthesis at a given light level was calculated.

EXPERIMENTS

Over the past 25 years, several experiments were conducted using the sunlit SPAR chambers to determine plant responses to a variety of environmental factors (K.R. Reddy et al., 1993, 2000, 2001) and provided a detailed database for model development. In this chapter, we present the studies describing quantitative relationships between photosynthetic process in cotton and abiotic stress factors. Unless otherwise mentioned, plants in all experiments were intercepting more than 95% of the incoming solar radiation with actively growing bolls.

2.1. Solar radiation studies

Cotton plants were grown at optimum temperature (30/22 °C), ambient [CO₂] and under optimum water and nutrient conditions until flowering. Using the mass-balance approach, carbon exchange rates were calculated as shown in Fig. 1 and canopy gross photosynthesis was calculated as described earlier (V.R. Reddy et al., 1995). Variability in natural solar radiation was used to generate relationships between estimated daily canopy photosynthesis and incoming daily solar radiation for several days using several SPAR chambers (Fig. 3A).

2.2. Atmospheric [CO₂] studies

In the experiments where atmospheric [CO₂] is a variable, plants were grown in optimum temperature (30/22 °C), water and nutrient conditions and at ambient atmospheric [CO₂] until plants reached first flower stage. Then, approximately for a one-week period, [CO₂] in the SPAR chambers were varied from 150 to 950 μL L⁻¹. Canopy photosynthesis was monitored and photosynthesis at 1200 μmol m⁻² s⁻¹ PAR estimated from the PAR-photosynthesis response functions were regressed against measured daytime [CO₂] as shown in Fig. 4A to quantify the effects of atmospheric [CO₂].

2.3. Temperature studies

Cotton plants were grown at optimum temperature (30/22 °C), water and nutrient conditions and in 360 μL L⁻¹ [CO₂] until first flower stage. Then, various temperature treatments were imposed for several days. Water and nutrients were supplied abundantly throughout the experimental period. Canopy photosynthesis was measured and quantified as shown in Fig. 1 using the photosynthesis and PAR response curves, canopy photosynthesis rates at 1200 μmol m⁻² s⁻¹ were estimated and regressed against measured average daytime temperature conditions (Fig. 5A) to quantify the effects of temperature on photosynthesis.

2.5. Ultraviolet-B radiation studies

In studies dealing with UV-B, five ultraviolet-B radiation treatments including a no UV-B control, and a total daily flux of biologically effective UV-B radiation of 4, 8, 12, and 16 kJ m⁻² d⁻¹ were imposed within a few days after emergence (K.R. Reddy et al., 2003). The SPAR Plexiglas is opaque to solar UV-B radiation and UV-B lamps placed inside the SPAR chambers were used to supply the desired UV-B radiation. Square-wave UV-B supplementation system was used in these studies. UV-B lamp power was adjusted, as needed, to maintain the respective UV-B radiation levels on a daily basis. The distance between the top of the plant canopy and the lamps was maintained at 0.5 m for the duration of the experiments. In the control units, unilluminated lamps mounted on frames were placed in control units to provide comparable shade similar to the UV-B treatments. Cotton plants

were grown at 30/22 °C, 360 μL L⁻¹ [CO₂] and under optimum water and nutrient conditions. As in the other experiments, canopy photosynthesis was measured daily. The imposed UV-B doses simulated 5, 10, 15, and 30% depletion of stratospheric ozone (Madronich et al., 1998). The 8 kJ m⁻² treatment is near natural solar UV-B levels during June-July months in Mississippi [(World Wide Web Site I (http://toms.gsfc.nasa.gov/ery_uv/ery_uv1.html)), and World Wide Web Site II (<http://uvb.nrel.colostate.edu/UVB/>)]. Using the PAR-photosynthesis response curves, canopy photosynthesis at 1200 μmol m⁻² s⁻¹ PAR was estimated and regressed against measured UV-B radiation (K.R. Reddy et al., 2003) and photosynthesis expressed as fractions of the zero UV-B levels is shown (Fig. 6).

2.7. Water deficit studies

Cotton plants were grown under optimal water and nutrient conditions until about one week before flowering with their full water requirements being met, and then 40 and 60% of previous day's transpiration from the well-watered plants was provided in each of water stress treatments. Transpiration was determined by measuring the cooling-coil condensate collected over 900-s intervals (K.R. Reddy et al., 2001). After two weeks in those conditions, the water supplied was progressively reduced to a lower percentage of the previous day's transpiration from the well-watered plants. In all treatments, complete nutrient solutions were provided and plants were grown at near optimum temperature (30/22 °C, day/night) and in ambient atmospheric [CO₂]. Excess water was allowed to drain from the fine sandy soil. Leaf water potential was measured near solar noon from recently fully expanded, mature, sunlit leaves at frequent intervals using the Scholander pressure chamber technique (Scholander et al., 1965). Canopy photosynthesis at 1200 μmol m⁻² s⁻¹ PAR estimated from the PAR-photosynthesis response curves were regressed as function of midday leaf water potential (Fig. 7A).

2.6. Nutrient deficiency studies

Nitrogen and potassium deficit experiments were conducted by growing plants at near-optimum day/night temperatures (30/22 °C) throughout the experimental period and at ambient atmospheric [CO₂]. A computer-controlled timing device applied a complete nutrient solution to each row of plants via a drip irrigation system in each SPAR unit. When nitrogen was a variable in the experiment, selected treatments provided an altered solution in which calcium chloride was used to replace varying amounts of calcium nitrate (A.R. Reddy et al., 1996). Cotton plants were grown until first flower stage with all nutrients provided in sufficient quantities after which solutions were changed so that one treatment received no N and other treatments were provided varying levels of N based on plant sufficiency. This provided two very similar canopies of healthy plants to begin the comparisons of plants with sufficient N and those with varying degrees of less than adequate N. Leaf N was determined weekly and canopy photosynthesis was measured daily. Canopy photosynthesis at 1200 μmol m⁻² s⁻¹ PAR estimated from the photosynthesis-PAR response functions were expressed as a function of leaf N as determined by the micro-Kjeldal technique, not the amounts of nitrogen fertilizer applied (Fig. 8A).

Potassium deficit studies were conducted in a similar manner as that of nitrogen deficit study (K.R. Reddy and Zhao, 2005). Ten treatments, including two levels of [CO₂], 360 μL L⁻¹ (ambient) and 720 μL L⁻¹ (elevated), and five levels of K supply at each [CO₂] were utilized. The [CO₂] treatments were imposed from emergence through final harvest, 85 days after emergence (DAE). The five K treatments were initiated around first square stage (23 DAE) and included: (1) a full K supply (Control, 100% K) irrigated with full-strength Hoagland's nutrient solution containing 0.234 g K L⁻¹ throughout the experiment; (2) K reduction to 40% of the control level (40% K); (3) 20% K of the control (20% K); (4) 5% K of the control (5% K); and (5) 0% K of the control (0%

K), until final harvest (85 DAE). All plants in the reduced (40, 20, and 5% K) and withheld K (the 0% K) treatments received full-strength Hoagland's nutrient solution before K stress treatments were initiated. Removing or reducing K from the nutrient solution resulted in dilution of K in the plant tissues because of subsequent crop growth and development. Canopy photosynthesis was determined using a mass balance approach in each chamber throughout the experiment (K.R. Reddy and Zhao, 2005) and expressed as $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PAR as a function of leaf K at each $[\text{CO}_2]$ (Fig. 9A).

ENVIRONMENTAL PRODUCTIVITY INDEX CONCEPT

The term, environmental productivity index (EPI), was first introduced by Nobel (1984) and later he used it to describe environmental limitations on cactus productivity (Nobel, 1988, 1991, 2000). However, we have been using the EPI concept in developing mechanistic crop simulation models for more than three decades (Baker et al., 1983, K.R. Reddy et al., 1997a, Hodges et al., 1998). The EPI is based on the fact that environmental factors affect crop growth, development and physiological processes multiplicatively, not additively. The environmental stresses are parameterized in the form of environmental stress indices, whose numerical value ranges from 0 to 1, where stress index of 1 indicates zero stress and a stress index of 0 indicates total stress.

A given individual environmental stress "i" can be characterized by a stress index S_i . Individual stress (S) due to solar radiation stress or light limitation (S_L), water stress or drought (S_D), temperature stress (S_T), carbon stress (S_C), ultraviolet-B stress (S_{UV-B}) and nutrient (N, P, K) stresses (S_N , S_P , S_K) represent the fractional limitation imposed on plant growth and development due to given individual stresses, such that the process rate decreases as the stresses become more severe. The EPI for each stress can be calculated for a given process and thus total EPI (T_{EPI}) can be calculated as show below:

$$T_{EPI} = S_L * S_D * S_T * S_C * S_{UV-B} * S_N * S_P * S_K; \quad [\text{Eq.1}]$$

If P_P is the potential growth or development rate, the actual rate of growth or development (P_A) can be calculated as represented below:

$$P_A = P_P * T_{EPI}; \quad [\text{Eq.2}]$$

Therefore, the EPI concept can be used to quantify environmental stress effects on crop growth and development and the algorithms dealing with these factors can be used in developing process-level crop models.

APPLYING ENVIRONMENTAL PRODUCTIVITY INDICES (EPI) CONCEPT FOR COTTON PHOTOSYNTHESIS

Photosynthesis, a vital physiological process, supplies raw material for food, fiber and other plant products. The photosynthesis algorithm in crop models should consider the effects of various environmental factors as the amount of assimilate produced controls biomass accumulation and it's partitioning to various organs, and finally yield. Potential photosynthesis is defined as the rate of photosynthesis that takes place at the maximum solar radiation levels under optimum environmental conditions (optimum water, nutrient, temperature, zero UV-B levels), and in an actively growing young canopy with optimum leaf area index intercepting maximum solar radiation. The potential canopy gross photosynthesis can be estimated from photosynthesis and solar radiation response functions as shown in Fig. 3 and 4 by summing up all daily values. The equation describing the potential photosynthesis is as follows (Fig. 3A; Eq. 3):

$$\text{Potential photosynthesis (g CO}_2 \text{ m}^{-2} \text{ d}^{-1}) = 10.7803 * X - 0.1767 * X^2; \quad r^2 = 0.73 \quad [\text{Eq. 3}]$$

where $X = 25 \text{ MJ m}^{-2} \text{ d}^{-1}$.

Once potential photosynthesis is calculated, then we have to account for all environmental factors that limit the crop from obtaining that potential. From experiments conducted over the past 30 years using the SPAR facility (K.R. Reddy et al., 2000, 2001), the EPI functions were derived for each of these environmental factors affecting photosynthesis potential (Figs. 3 to 9). As discussed earlier, individual environmental factors affect the potential photosynthesis multiplicatively, not additively. For instance, if prolonged drought causes daily stomatal opening to cease, then no photosynthesis will occur, regardless of whether or not light, temperature or other factors are optimal for photosynthesis. All the indices, ranging from 0 when it is totally limiting photosynthesis to 1 when it does not limit photosynthesis, represent the fractional limitation due to that particular environmental factor. Therefore, photosynthesis decreases as the effect of that particular stress becomes more severe. Using this approach, we can quantify the effect of most/many environmental factors limiting crop photosynthesis in multi-stress environments or in field conditions.

The influence of limited radiation due to insufficient canopy cover or due to cloud cover can be calculated as follows (Fig. 3B; Eq. 4):

$$\text{EPI for solar radiation} = 0.06665 * X - 0.06665 * X^2; \quad r^2 = 0.73; \quad [\text{Eq. 4}]$$

where $X =$ intercepted solar radiation.

Limitations due to lower than ambient $[\text{CO}_2]$ and enhanced photosynthesis due to elevated $[\text{CO}_2]$ can be best described by a cubic function as shown in [Eq. 5] (Fig. 4).

$$\text{EPI for } [\text{CO}_2] = 0.004050 * X - 0.000004006 * X^2 + 0.00000001303 * X^3; \quad r^2 = 0.78; \quad [\text{Eq. 5}]$$

where $X =$ atmospheric $[\text{CO}_2]$.

Increase in $[\text{CO}_2]$ from ambient ($360 \mu\text{L L}^{-1}$) to predicted future concentrations of $900 \mu\text{L L}^{-1}$ resulted in a 37% increase in photosynthesis, which is in agreement with predictions for C_3 crop plants (Kimball, 1983; K. R. Reddy and Hodges, 2000). The EPI values for $360 \mu\text{L L}^{-1}$ of $[\text{CO}_2]$ was set to 1, values lower than 1 are used to estimate the effects of sub-ambient levels where as values more than 1 are used to estimate the stimulation of carbon fixation due to elevated $[\text{CO}_2]$. A cubic function best described the response of canopy photosynthesis to temperature (Fig. 5A). Maximum potential was observed at 27°C , and any increase or decrease in temperature reduced that potential (Fig. 5B). The EPI relationship describing photosynthesis and temperature function is shown in [Eq. 6].

$$\text{EPI for temperature} = -2.2122 + 0.2302 * X - 0.004116 * X^2; \quad r^2 = 0.96 \quad [\text{Eq. 6}]$$

where $X =$ temperature.

A small component of solar radiation, UV-B radiation (290-320 nm), has large photomorphogenetic effects on cotton growth and development (Kakani et al., 2003; K.R. Reddy et al., 2003; Zhao et al., 2003). The effects of UV-B are usually incorporated into one of the calibration terms of many crop models. Spatial and temporal variability exists for UV-B radiation. UV-B radiation greater than $0 \text{ kJ m}^{-2} \text{ d}^{-1}$ causes reduction in cotton photosynthesis through direct (effect on PS II) and indirect (reduction of chlorophyll, etc.) effects (Fig. 6). Many of the current crop simulation models lack algorithms to account for the effects of UV-B radiation, which if incorporated, could increase the precision of growth, development, and yield predictions under field conditions and reduce the amount of calibration needed to adapt the model to new locations (http://www.toms.gsfc.nasa.gov/ery_uv/ery_uv1.html). The functional relationship describing UV-B effects on photosynthesis is described by [Fig. 6; Eq. 7].

$$\text{EPI for UV-B} = 0.9835 - 0.0002563 * X - 0.002163 * X^2; r^2 = 0.86 \quad [\text{Eq. 7}]$$

where X = biologically effective UV-B radiation.

Soil water deficit, another important factor, affects functions, which can reduce photosynthesis regardless of the light level, temperature, or whether other factors are optimal for photosynthesis. Midday leaf water potential less than -1.25 MPa (well watered condition) resulted in reduced photosynthesis (Fig. 7). A linear relationship between midday leaf water potential and photosynthesis best describes this response (Fig. 7B; Eq. 8). The lower r^2 values for photosynthesis and midday leaf water potential are most likely caused by numerous interactions of limited hydration on several biological processes (Kramer and Boyer, 1995).

$$\text{EPI for water stress} = 1.3129 + 0.2608 * X; r^2 = 0.64; \quad [\text{Eq. 8}]$$

where X = midday leaf water potential in MPa.

Cotton, being a C_3 plant, responds to various nutrient deficiencies in a similar manner to water deficit conditions (K.R. Reddy et al., 1997a, b). Leaf N concentration below 4.5% (Fig. 8A) and leaf K less than 1.5% (Fig. 9A) inhibited plants from achieving potential photosynthesis. The functional relationships describing photosynthesis and leaf N or K levels are described in Eq. 9 and 10 (Fig. 8B and 9B), respectively.

$$\text{EPI for N} = -0.7435 + 0.8624 * X - 0.1066 * X^2; r^2 = 0.71; \quad [\text{Eq. 9}]$$

where X is leaf N in percentages.

$$\text{EPI for K} = 1.0028 * (1 - \exp(-1.4577 * X)); r^2 = 0.96; \quad [\text{Eq. 10}]$$

where X is leaf K in percentages.

Therefore, the actual photosynthesis can be estimated on a daily basis as described in [Eq. 11] as discussed under the EPI concept.

$$\text{Photosynthesis (Actual)} = \text{Potential} * \text{EPI Solar} * \text{EPI temperature} * \text{EPI UV-B} * \text{EPI water} * \text{EPI nutrients as described in Eq. 4 to 10} \quad [\text{Eq. 11}]$$

The influence of individual environmental factors affects potential photosynthesis multiplicatively, not additively. The advantages of this parameterization are that multiple stress interactions (positive, negative, additive or null) are recognized (except under totally limiting conditions), and the total EPI value is restricted with the range of 0 to 1, such that $0 < P_A < P_p$. Alternative theories to the EPI concept include Sprengel-Liebig Law of Minimum (Liebig, 1840; van der Ploeg et al., 1999, and references cited therein) which states that process or yield is proportional to the amount of the most limiting factor, whichever factor it may be, and the effect of moderately limiting factors is zero in the presence of a dominating factor, thus neglecting the multi-stress interactions.

In this section, we have used a simplistic canopy photosynthesis model to demonstrate the utility of the EPI concept in cotton. There may be other factors that affect canopy photosynthesis in cotton. When new data becomes available, new EPI factors need to be calculated and incorporated into the equation.

MODEL DEVELOPMENT AND INTEGRATION

In this chapter, we have demonstrated the EPI concept which allows a way to quantify the effects of environmental stress factors on photosynthesis and thus productivity of cotton. The EPI concept allows one to interpret and to understand stresses in field situations. If we know the factor that is most limiting at any point of time during the growing season, then we may make appropriate management decisions to correct that limitation. The EPI concept can be applied to various facets of crop growth and development and be used to determine how environmental stress factors can be

quantified to provide appropriate functional algorithms for modeling. For cotton, functional algorithms describing the potential crop growth and development, as well as various environmental stress indices, were studied extensively and summarized earlier (K.R. Reddy et al., 1993, 1997a, 1997b, 2001, 1999, 2003). From this database, functional algorithms using EPI concepts have been developed and used for various growth, development and photosynthesis processes and have been incorporated into a dynamic cotton crop simulation model, GOSSYM.

The development, characteristics, and some applications of GOSSYM have been previously described (Baker et al., 1983; McKinion et al., 1989; Boone et al., 1995; K.R. Reddy et al., 1997a; Hodges et al., 1998). GOSSYM is a mass balance dynamic simulation model that accounts for carbon, nitrogen, and water in the plant and soil root-zone. GOSSYM simulates crop responses to environmental variables such as solar radiation, temperature, rain/irrigation, and wind, as well as to variation in soil properties and cultural practices. The model estimates growth and development rates by calculating potential rates for the observed daily temperatures assuming other conditions are not limiting, and then it corrects the potential rates by intensity of environmental stresses (Baker et al., 1983; K.R. Reddy et al., 1997a; Hodges et al., 1998). Each day, the model provides the user with the plant size and growth stage as well as growth rate and the intensity of the stress factors. A grower can assume certain future weather conditions (days and weeks) to determine yield estimates and impact of alternative cultural practices on the productivity and maturity of the crop.

A flow chart of GOSSYM shows the general organization of the model and program flow (Fig. 10). GOSSYM is the main program from which all of the subroutines vertically below it in the diagram are called. CLYMAT reads the daily weather information and calls DATES, which keeps track of both day of the year and the calendar date being simulated; and calls TMPSOL, which calculates the soil temperatures by soil layer. SOIL is a mini-main program, which calls the soil sub-programs (Boone et al., 1995). The soil routines provide the plant model with estimates of soil water potential in each grid cell as described below, in both the rooted and non-rooted portion of the soil profile, an estimate of the nitrogen entrained in the transpiration stream available for growth, and an estimate of metabolic sink strength in the root system. The belowground processes are treated in a two dimensional grid. The mass balances of roots in three age categories, water, nitrate and ammonia, and organic matter are maintained and updated several times per day (Hodges et al., 1998).

The validity of the model with EPI concepts for various growth and developmental concepts has been field tested by validating across a wide range of environmental conditions and management practices over years (Fye et al., 1984; V.R. Reddy et al., 1985; 1987, V.R. Reddy and Baker, 1988, 1990; Boone et al., 1993; V.R. Reddy, 1995; K.R. Reddy and Boone, 2002; Gowda et al., 2007). The validation data for the model came from areas of the USA cotton belt, and also from other cotton growing countries such as Israel (Marani and Baker, 1978), China (Pan et al., 1994) and Greece (Gertsis and Symeonakis, 1998). The improved cotton model has been used to help identify knowledge voids, hypothesis testing in research, farm management, climate change impacts, and in policy decisions (K.R. Reddy et al., 2002a, b, V.R. Reddy et al., 2007, and references cited therein).

CONCLUSIONS

In this chapter, we have demonstrated how to calculate the potential crop growth and developmental processes rates using photosynthesis as a model process and cotton as a model crop. We have shown how to model the effects of environmental factors that

crops encounter in real-world environments to decrease that potential. Even though we used a simplistic canopy photosynthesis model for defining the potential and studying the effects of various environmental stresses on it, the same concepts will be valid with increasing levels of complexity in simulation of this process (Boote and Pickering, 1994; Farquhar et al., 2001). Similar concepts can be used to quantify other biotic/abiotic stress factors that affect various growth and developmental processes in crops. Improved and mechanistic plant models can only be used to simulate complex plant and environmental interactions whereas as simple models fail to capture the necessary complexity.

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FIGURE LEGENDS:

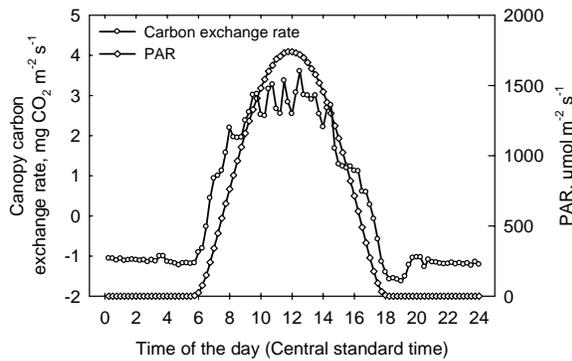


Fig. 1. Carbon exchange rate of cotton canopies at 80 days after emergence grown in $360 \mu\text{L L}^{-1}$ $[\text{CO}_2]$ and at optimum temperature ($30/22^\circ\text{C}$ day/night) for growth. During this time, plants were intercepting almost all of the incoming solar radiation. Variation in solar radiation, expressed as photosynthetically active radiation (PAR), on that day is also shown. Data for both photosynthesis and solar radiation were collected at 10-s intervals and integrated over 900 s.

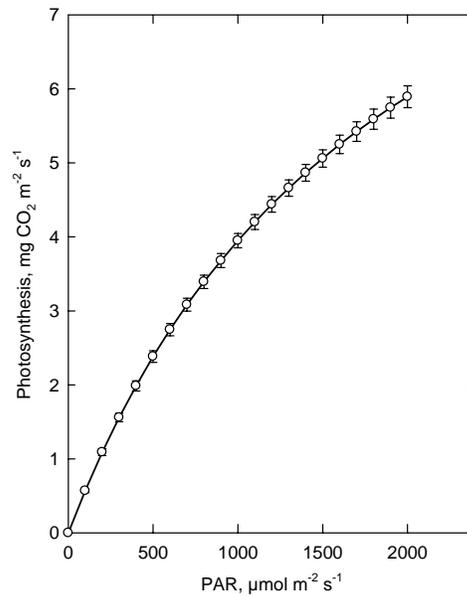


Fig. 2. Net photosynthesis of cotton as described in Fig. 1 and as a function of photosynthetically active radiation (PAR). Data were collected at 10-s intervals and integrated over 900 s. The data were means \pm S.E. of three observations for plants grown at similar conditions.

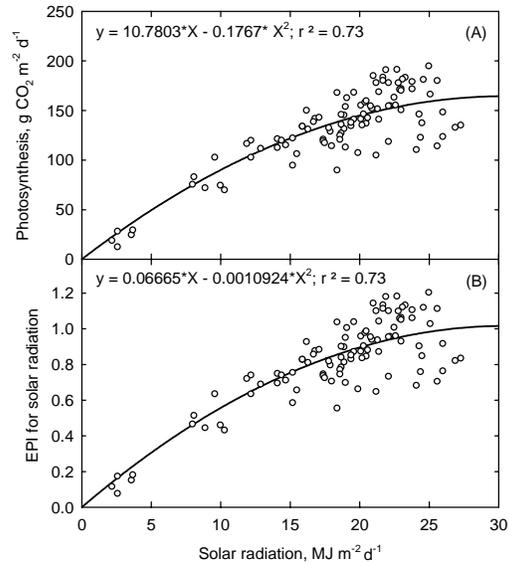


Fig. 3. Interrelationships between (A) photosynthesis as a function of integrated solar radiation and (B) environmental productivity index of photosynthesis expressed as fractions of the maximum for solar radiation. The data were collected from cotton plants grown in $360 \mu\text{L L}^{-1}$ $[\text{CO}_2]$, $30/22^\circ\text{C}$ temperature and at optimum water and nutrient conditions when the cotton canopies were intercepting more than 95% of the incoming solar radiation during flowering period.

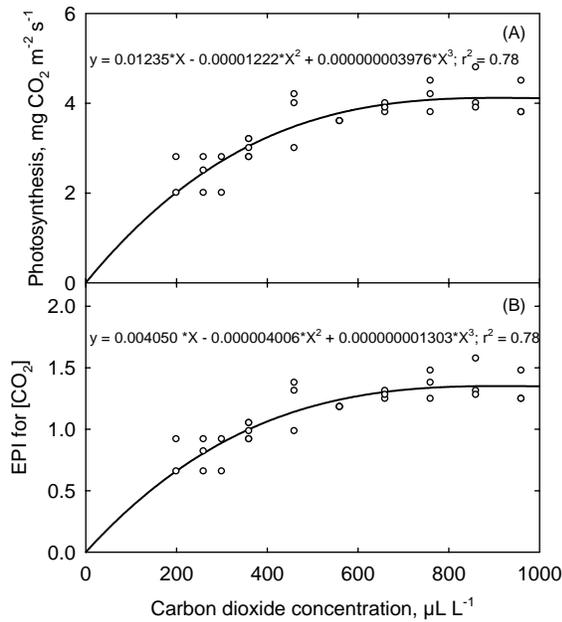


Fig. 4. Interrelationships between (A) photosynthesis as a function of atmospheric carbon dioxide concentrations and (B) environmental productivity index of photosynthesis expressed as fractions of the ambient CO_2 concentration ($360 \mu\text{L L}^{-1}$). The data were collected from cotton plants grown in $30/22 \text{ }^\circ\text{C}$ temperature and at optimum water and nutrient conditions when the cotton canopies were intercepting more than 95% of the incoming solar radiation during flowering period.

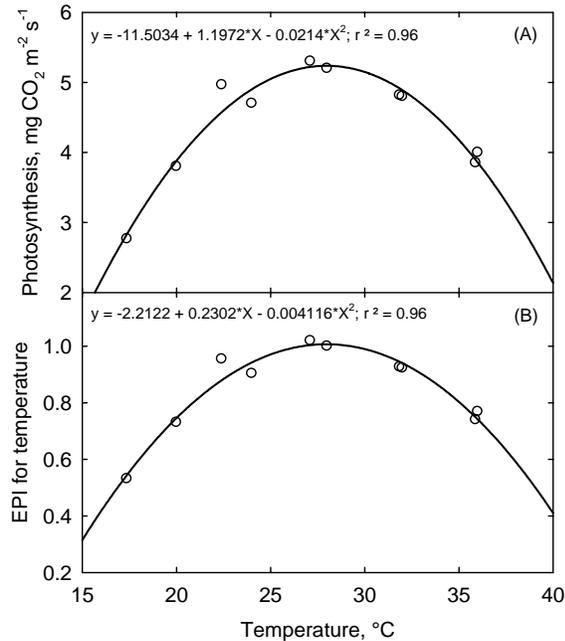


Fig. 5. Interrelationships between (A) photosynthesis as a function of temperature and (B) environmental productivity index of photosynthesis expressed as fractions of the optimum

temperature, $28 \text{ }^\circ\text{C}$. The data were collected from cotton plants grown in $360 \mu\text{L L}^{-1} [\text{CO}_2]$ and at optimum water and nutrient conditions when the cotton canopies were intercepting more than 95% of the incoming solar radiation during flowering period.

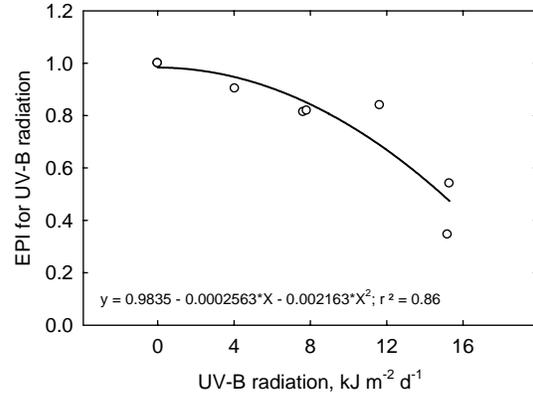


Fig. 6. Interrelationship between cotton photosynthesis expressed environmental productivity index (fraction of zero UV-B radiation). The data were collected from cotton plants grown in $360 \mu\text{L L}^{-1} [\text{CO}_2]$, $30/22 \text{ }^\circ\text{C}$ temperature and at optimum water and nutrient conditions (Adapted from K.R. Reddy et al., 2003).

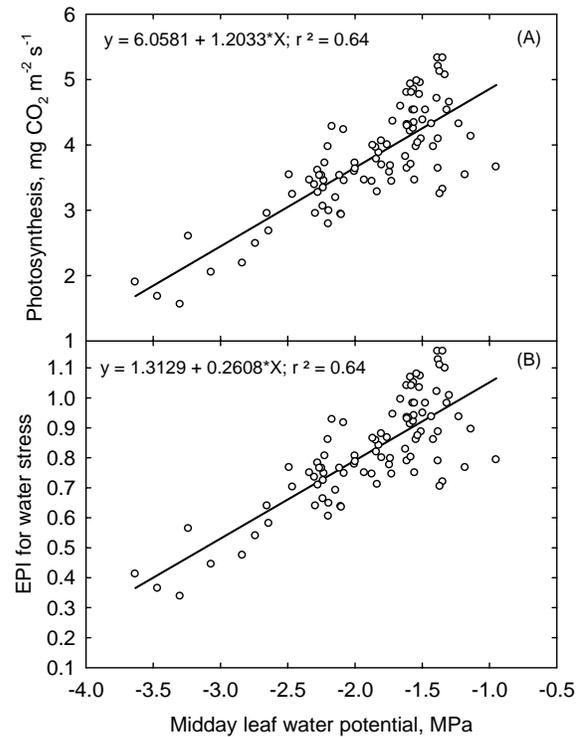


Fig. 7. Interrelationships between (A) photosynthesis as a function of midday leaf water potential and (B) environmental productivity index of photosynthesis expressed as fractions of the optimum leaf water potential. The data were collected from cotton plants grown in $360 \mu\text{L L}^{-1} [\text{CO}_2]$, $30/22 \text{ }^\circ\text{C}$ temperature and at optimum nutrient conditions when the cotton canopies were intercepting more than 95% of the incoming solar radiation during flowering period.

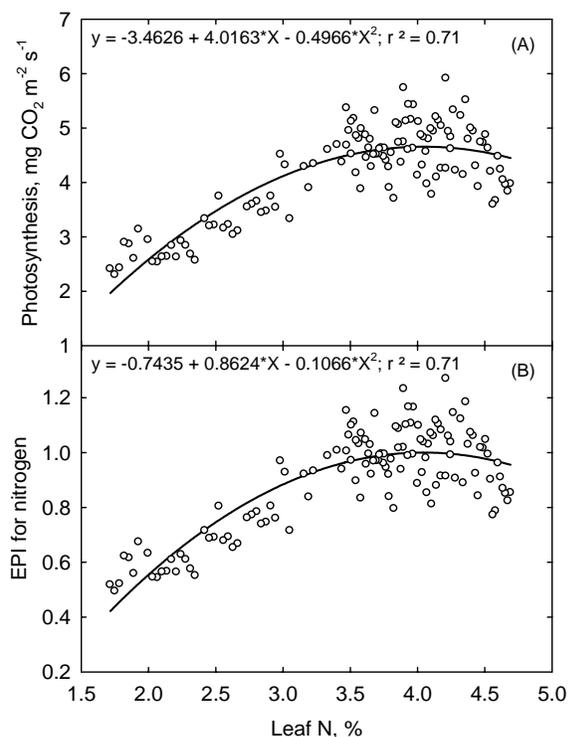


Fig. 8. Interrelationships between (A) photosynthesis as a function of leaf N concentration and (B) environmental productivity index of photosynthesis expressed as fractions of the optimum leaf N. The data were collected from cotton plants grown in $360 \mu\text{L L}^{-1}$ $[\text{CO}_2]$, $30/22^\circ\text{C}$ temperature and at optimum water and other nutrient conditions when the cotton canopies were intercepting more than 95% of the incoming solar radiation during flowering period.

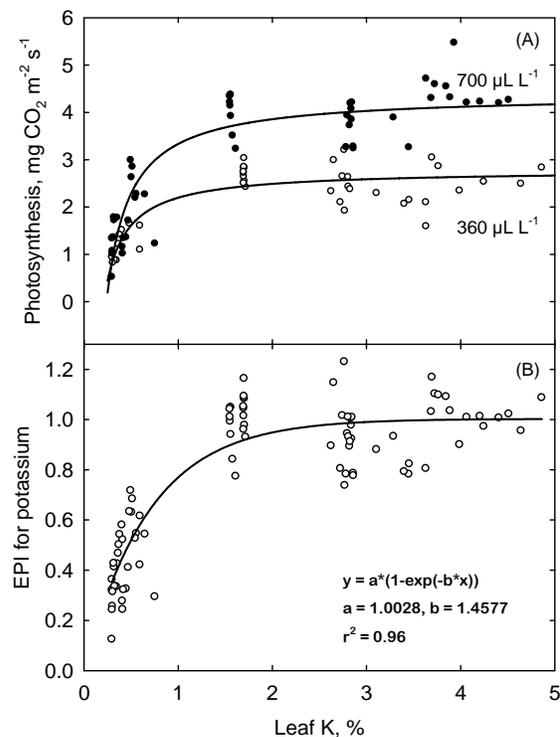


Fig. 9. Interrelationships between (A) photosynthesis as a function of leaf K concentration and (B) environmental productivity index of photosynthesis expressed as fractions of the optimum leaf K. The data were collected from cotton plants grown in ambient ($360 \mu\text{L L}^{-1}$) and elevated ($720 \mu\text{L L}^{-1}$) $[\text{CO}_2]$, $30/22^\circ\text{C}$ temperature and at optimum water and other nutrient conditions when the cotton canopies were intercepting more than 95% of the incoming solar radiation during flowering period. There were no significant interactions between $[\text{CO}_2]$ levels and therefore, one function best described the response of photosynthesis to leaf K.

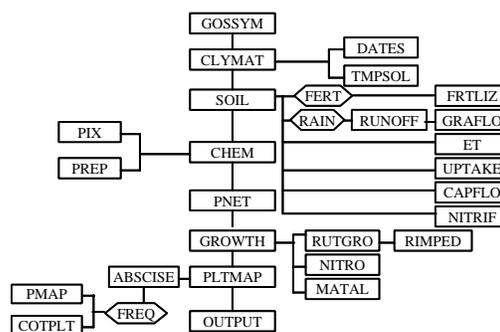


Figure 10. Flow diagram of the subroutines and structure of GOSSYM, a cotton crop simulator with organization and program flow of the model. See text for details.