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Modeling Photosynthesis and Carbon Partitioning: Introduction to the Workshop

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This workshop was organized to provide concise guidelines for those contemplating modeling photosynthesis or C partitioning and a useful reference for those already involved in modeling.

The concept of modeling to provide a simplified representation of a real-world process is not new. The complex nature of plant and soil systems, however, made their description through models difficult until the advent of modern computers. During the last 3 decades, interest in developing crop models has gradually intensified, and models to evaluate plant and soil systems are now available. Simulation models have been developed to quantify physiological processes in several crops and determine the effects of environmental and management factors on these processes. Models have been used to test hypotheses, plan experiments, and identify areas where knowledge is lacking. They are also useful for practical purposes such as controlling insects and disease, scheduling irrigation, and making other crop-management decisions. Simulation models that predict the growth and development of diverse crops such as citrus, grains, and feed crops have been developed during the past decade.

Practically all dry matter of higher plants originates from photosynthesis. The oxidation-reduction reaction of H_2O and CO_2 during photosynthesis to produce carbohydrate occurs against existing energy gradients. Leaf chlorophyll absorbs energy from certain wavelengths of solar radiation to provide the additional energy needed to reduce CO_2 . The extent to which a plant absorbs the incident solar radiation depends on its leaf area index and on leaf age, turgidity, shape, size, and positioning. In the visible wavelengths, a typical leaf absorbs 75%, reflects 15%, and transmits 10% of incident sunlight (Gates, 1965). Leaves are usually at an angle that permits some radiation energy to reach the lower canopy without being intercepted by the top leaves. Competition for solar energy may occur between plants, when one plant casts a shadow on another, or within a plant,

when top leaves shade the bottom leaves.

Earth's atmospheric CO_2 concentration is not optimal for the maximum photosynthesis rate (Bonner, 1962). It is difficult to increase the CO_2 level in a field crop canopy, but CO_2 fertilization in greenhouses has been used advantageously in high-value vegetable and flower production. In a CO_2 -stable crop canopy, the internal leaf CO_2 concentration may vary considerably as a result of differing resistance to CO_2 diffusion into the leaves. Leaf stomatal resistance to diffusion is affected by such factors as leaf temperature, air vapor pressure, and plant water status.

Not all C fixed by photosynthesis is converted to dry matter. Part of it is lost through respiration to provide energy to maintain the living complex and synthesize compounds that form the final dry matter. Also, in agricultural crops, much of the synthesized dry matter is translocated to the plant organ harvested for use.

Most photosynthesis and C-partitioning models have been developed to establish quantitative relationships between the environmental factors, crop canopy characteristics, ontogeny, and the rates of photosynthesis and photosynthate partitioning to various plant organs. These relationships are then used to describe how photosynthesis rate and the amount of dry-matter production and translocation to yield-producing organs would be affected in particular situations. Whisler et al. (1986) have tabulated the names of prominent research groups and institutions that have developed models dealing with photosynthesis and C partitioning, their test species, and the names of these models.

Since there are fewer models available for horticultural crops than agronomic crops, it is our hope that this workshop will generate interest in developing crop-simulation models for photosynthesis, C partitioning, and other yield-determining processes in horticultural crops. Because most horticultural crops are intensively managed and of high value, models of these crops may be a valuable tool in selecting cultural options that produce the highest economic yield.

McKinion and Sequeira discuss the requirements for building a sound model: an appropriate database, adherence to a minimum set of design features, calibration and validation of the model, and continued

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subsequent validations. Boote and Pickering describe the essential components of a row crop photosynthesis model. The available C supply and the demand by different plant C sinks are used by DeJong and Grossman to develop a model for annual vegetative and reproductive growth in deciduous fruit trees.

The CO₂ level in the atmosphere is expected to double in the next 50 to 100 years, resulting in a 2 to 3°C increase in Earth's temperature (Gates, 1983). How this will affect life processes, including photosynthesis, is of great concern. Reddy, Pachepsky, and Acock describe a model that can be used to simulate the effect of CO₂ and temperature on canopy photosynthesis.

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Mechanics of Model Building

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In the late 1960s, with the advent of wide availability of the digital computer, it became possible by applying systems theory to build simulation models of biological entities. In production agriculture, scientists have built models for various field crops: cotton (*Gossypium hirsutum* L.), corn (*Zea mays* L.), wheat (*Triticum aestivum* L.), soybean [*Glycine max* (L.) Merr.], and alfalfa (*Medicago sativa* L.). In most of the models built to date, crop phenology is simulated directly with detailed aspects of crop physiology. Some models also rely on principles of soil physics to some degree. This paper addresses the methodology of constructing process-level, physiologically based crop simulation models that possess detailed descriptions of plant physiological and soil physical mechanisms and proposes a minimum set of design features.

THE DATABASE

Data availability largely determines the type of model of a physiological process, or an entire crop, that a modeler can develop. Unfortunately, most field-crop experiments are designed to determine either differences between means or the significance of specific treatments, not an understanding of the cause of treatment differences. As a result, one cannot determine from field data which external events caused responses in the biological–physical system. If a model is developed from such a data set, that model will be valid only for data conditions at that site for the years over which the data were collected and cannot reliably be extended to other sites or other years.

In a simulation model, detailed information must be available on all exogenous variables that can affect the process or crop being studied. For example, if one were modeling leaf growth and development, many variables would have to be known to build a comprehensive leaf model: date the leaf was initiated and the change in leaf size, N concentration, water potential, temperature, exposure to solar radiation, dry weight, stomatal conductance, and photosynthesis rate. Of course, most of these variables would have to be measured from leaf initiation through senescence. If significant information is missing from this data set, the type of model one can construct is limited. If temperature data were missing, the job would become very difficult. If leaf N concentration data are missing, a leaf model could be built, but the model would be confounded by the unknown leaf N status under which the data set was collected.

In applying systems methodology to modeling biological systems, experiments are designed to determine cause and effect and measure external variables pertinent to the system being studied. Even when one strives to be comprehensive in field research experiments, certain classes of experiments cannot be conducted in the field. For example,

determining the isolated effect of temperature on the rate of single leaf area expansion would be almost impossible to do in the field. The first problem is the range of temperatures the leaf would experience at a particular site. The second problem is the confounding effect of N variation under field conditions. A third problem is the confounding effect of water stress on a field crop. Any model built describing leaf area development from such a set of field-collected data would have these confounding effects built into the model.

If one had enough resources, land, and time, field experiments could be conducted across the ecological range of the crop under variable conditions of temperature, solar radiation, water regimes, and plant nutrition so that one could unravel cause and effect in field-collected data sets. These would have to be replicated over sites and years in hundreds of locations for each crop being modeled. However, there is a better way that is much more efficient and much more accurate for collecting data for building process-level models.

Naturally sunlit-controlled-environment plant growth chambers have been used to collect data for constructing process-level crop models since the mid-1970s (McKinion, 1986; Phene et al., 1978). These soil–plant–atmosphere–research (SPAR) chambers are used to control all external independent variables except solar radiation.

Methodology has been developed with these SPAR chambers to run appropriate experiments and collect process data to parameterize process-level crop growth models that require only 3 years of experiments. Such models have all primary and secondary plant processes described and calibrated. Some tertiary effects may also be addressed, but additional controlled-environment experiments are required to address crop-specific processes to complete the model.

MODEL-BUILDING METHODOLOGY

The methodology we have developed for calculating photosynthesis in cotton, wheat, and soybean is based on plant canopy geometry. The experimental method for acquiring these data involves using SPAR chambers in which these crops have been grown in a row-crop configuration (McKinion, 1986; Parson et al., 1980; Phene et al., 1978). Solar radiation is allowed to vary naturally, but air temperature, CO₂ concentration, and soil conditions are controlled. Thus, we measure apparent photosynthesis under various air temperature, soil moisture, and soil N regimes (McKinion and Baker, 1982; Reddy et al., 1992). We also measure light, maintenance, and growth respiration rates so that, given crop biomass, we can calculate net photosynthesis. Statistically, the equations derived from this experimental approach and database have an *R*² of 0.92 or better for cotton and wheat.

The methodology we use for building dynamic simulation models of field crops has led us to propose a minimum set of design features:

- 1) The model will be a materials balance accounting for dry-matter production and organ senescence.
- 2) The model will calculate photosynthate production separately from respiration (since the forcing functions in the two processes are different and the ratios change).

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