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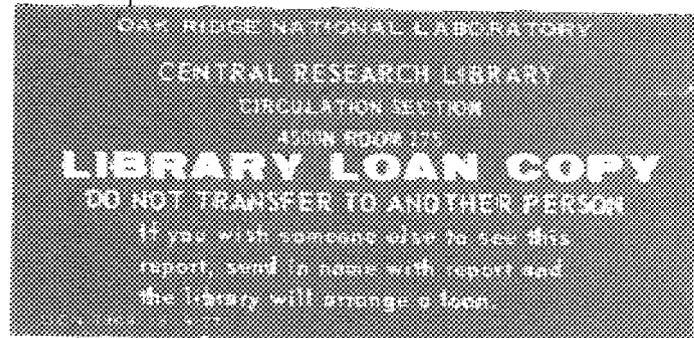
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## Information for Seasonal Models of Carbon Fluxes in Agroecosystems

A. W. King  
D. L. DeAngelis

Environmental Sciences Division  
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ENVIRONMENTAL SCIENCES DIVISION

INFORMATION FOR SEASONAL MODELS OF  
CARBON FLUXES IN AGROECOSYSTEMS

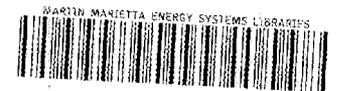
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## ABSTRACT

KING, A. W., and D. L. DeANGELIS. 1987. Information for seasonal models of carbon fluxes in agroecosystems. ORNL/TM-9935. Oak Ridge National Laboratory, Oak Ridge, Tennessee. 98 pp.

This report is a compilation of available simulation models and empirical data describing the seasonal carbon fluxes of the Earth's principal agricultural crops. Along with its two companion reports (King and DeAngelis 1985; King and DeAngelis 1986), this report will be a useful source of information for constructing the terrestrial source/sink component of a global model of atmospheric carbon dioxide (CO<sub>2</sub>). The report excludes pasture systems and permanent crops such as orchards, but it includes the crops that occupy most of the arable land: (1) cereals (wheat, rice, corn or maize, sorghum, and barley); (2) tubers (potatoes and sugar beets); (3) pulses (soybeans); and (4) others (cotton, tobacco, and a general crop model).

The objective of this compilation is to describe the models and empirical data in sufficient detail to allow prospective users to determine if these will meet their specific needs. The report also points out some areas of deficiency in crop modeling (at least where seasonal CO<sub>2</sub> flux is concerned), such as the absence of decomposition processes in crop models. Because of these deficiencies, the models currently available will not be sufficient to meet the needs of seasonal CO<sub>2</sub> flux predictions, and more work must be done, particularly in modeling decomposition in agricultural systems.



## INTRODUCTION

Man has dedicated considerable tracts of the terrestrial landscape to the managed production of food, fiber, and building materials. These conversions of natural ecosystems to agroecosystems have for centuries affected carbon dynamics on local, regional, and global scales. Over much of the Northern Hemisphere, forests have been replaced by croplands, with drastic reductions in carbon storage capacity per unit land area. Where temperate grassland is converted to forage grass production or upland grain crops, growth rates (grams per square meter per day) and aboveground net production (tons per hectare per year) generally increase, often dramatically (Mitchell 1984). Domesticated rice has displaced natural marshes over large areas of the world and, while respective growth rates and aboveground net production generally overlap, seasonal growth rate patterns may differ (Mitchell 1984). Additionally, there is evidence that many modern cultivars have lower rates of leaf photosynthesis than do their wild relatives (Mitchell 1984).

Of perhaps greater consequence are changes in the deposition and fate of litter and soil organic matter. Harvesting of croplands and intensive grazing of pastures may result in the exporting of plant materials that under more natural circumstances would become part of the surface litter. Plowing, a major aspect of conventional crop production, distinguishes between natural and agricultural systems. Recent investigations have focused on the effects of these management practices on nutrient cycling [e.g., on nitrogen, see House et al. (1984); Coleman, Cole, and Elliott (1984)], but the impact of harvesting and tilling on carbon dynamics is almost certainly comparable (Coleman, Cole, and Elliott 1984) and worthy of attention. On a small scale, tillage increases the rate of decomposition of buried organic matter, and carbon:nitrogen ratios in litter and other plant residues are narrowed (Woodmansee 1984). On larger scales, cultivation may promote the loss of soil organic matter, affecting the soil carbon reservoir of the global carbon cycle (Odum 1971; Houghton et al. 1983; Kohlmaier et al. 1983; Coleman, Cole, and Elliott 1984).

Differences between the carbon dynamics of natural ecosystems and those of agroecosystems, and the impact of conversion from the former to the latter, have been recognized for long-term carbon dynamics. These differences have been the focus of studies relating land-use change to the global carbon cycle and increases in atmospheric CO<sub>2</sub> (Bolin 1977; Houghton et al. 1983; Emanuel et al. 1984a, b; and Goudriaan and Ketner 1984). The influence of agroecosystems on the global carbon cycle may, however, be more demonstrable at finer spatial and temporal scales. The pronounced seasonal cycle in the records of atmospheric CO<sub>2</sub> (Keeling 1983) is generally attributed to regional and monthly variations in net CO<sub>2</sub> exchange between the atmosphere and terrestrial vegetation. At these scales, the carbon dynamics of agroecosystems may directly influence the atmospheric concentration of CO<sub>2</sub>.

This report is a compilation of information useful for constructing regionally differentiated models of seasonal carbon fluxes in the terrestrial biosphere. Such models can aid in understanding the global carbon cycle, and they may be applied towards the multidimensional models objective of the U.S. Department of Energy's (DOE's) Carbon Cycle Research Plan (Dahlman 1984). Two companion reports (King and DeAngelis 1985; King and DeAngelis 1986) describe information for seasonal carbon flux models of natural, relatively undisturbed ecosystems. Here we concentrate on models for agroecosystems, since, for the reasons outlined above, successful modeling of regional carbon dynamics may require consideration of carbon fluxes in agroecosystems.

Two classes of information are presented. First, extant agroecosystem models that simulate the flux of carbon in a stand or whole field are reviewed. Second, empirical data on seasonal carbon fluxes are compiled. These reviews and compilations are extensive, but not exhaustive. They simply introduce the available information. They should be useful, however, in guiding the incorporation of agroecosystems into regional models of seasonal carbon flux, in highlighting deficiencies in the available models of agroecosystem carbon flux, and in documenting the assumptions that will go into the development of seasonal models.

There is much potentially relevant information that is not presented here. The enormous mass of literature describing studies which relate various environmental factors to the carbon flux physiology of agricultural plant species is not reviewed. When models are based upon these studies, the sources used by the model developers are referenced. Crop yield models are not considered, and annual models and data are not reviewed (see Loomis and Gerakis 1975). We are concerned here with seasonal information. Models of agricultural production systems that involve energy subsidy and marketing (see Van Dyne and Abramsky 1975) also are not included. Models and empirical data for grazing systems and pastures are not reviewed, neither are orchard systems and managed timber stands considered. These managed systems, which can rightly be called agroecosystems, were excluded because of limitations of space and effort. Furthermore, the grazing systems are often modeled in conjunction with grasslands, and these models are dealt with by King and DeAngelis (1985). Managed orchards and timber stands may be modeled using appropriately modified forest stand models, also reviewed by King and DeAngelis (1985). The compilation reported here deals with cropland systems, generally tilled or cultivated, which, for the most part, occupy extensive, nearly contiguous tracts of land.

Finally, this document does not attempt to evaluate in any definitive manner the usefulness of available seasonal models and data. It is, instead, an introduction to information that may be used according to the needs specific to constructing models of seasonal carbon dynamics in agroecosystems.

## 1. SEASONAL CARBON DIOXIDE ASSIMILATION AND RESPIRATION

Agroecosystems remove  $\text{CO}_2$  from the atmosphere through photosynthesis. Some of this assimilate is returned to the atmosphere by the process of respiration as the plants consume photosynthates in maintenance and growth metabolism. The remaining photosynthate contributes to net primary production or dry matter production. Crop

production, particularly in the temperate latitudes, is a seasonal phenomenon. However, the extent to which this seasonality influences the seasonal concentration of atmospheric  $\text{CO}_2$  is unknown. Any attempt to model the seasonal exchange of  $\text{CO}_2$  between cropland and the atmosphere will require some consideration of seasonal dry matter production and will probably involve explicit consideration of photosynthesis and respiration. These factors are dealt with in Sect. 1.1. The release of  $\text{CO}_2$  during decomposition also influences seasonal  $\text{CO}_2$  exchange between cropland and the atmosphere; this influence is addressed in Sect. 2.0.

### 1.1 Crop Growth Models

Models that simulate the seasonal course of dry matter production in croplands are generally referred to as crop growth models. These models frequently involve submodels of photosynthesis, respiration, and translocation. These processes, and sometimes growth itself, are driven by environmental variables such as light, temperature, and available water, which may vary seasonally. Another characteristic of crop growth models is their simulation of canopy microclimate. This simulation may be a very complex micrometeorological simulation, or a rather simple one limited to considering the distribution of light within the canopy. In either case, the canopy microclimate influences canopy photosynthesis, and canopy growth can feed back to affect the microclimate. Crop growth models, then, may represent a major contribution to the modeling of cropland-atmosphere interactions.

In the descriptions of crop growth models that follow, we concentrate on the processes of photosynthesis and respiration. These are the live plant fluxes most critical in simulating seasonal  $\text{CO}_2$  exchange between the atmosphere and the terrestrial biosphere. Canopy influences are referred to, and the role of environmental driving variables in the processes of photosynthesis and respiration are considered explicitly. The descriptions also include comparisons of model results and empirical observations.

### 1.1.1 Wheat Models

Adapting earlier models of community photosynthesis, Connor and Cartledge simulated the photosynthesis of a wheat community under conditions of optimum nutrient and water supply (Connor and Cartledge 1970, 1971). Three models were used. The first, SIMPLE, considers the canopy as a continuous horizontal foliage plane; the other two are geometrical treatments which consider a number of foliage layers, each specified by its foliage area index and a characteristic foliage angle. In one model, 4M, this angle is a measured mean value; in the other, 6M, there is a distribution of measured foliage angle values. These latter models relate the photosynthetic-light response of individual leaves to the distribution of radiation in the model canopies. The distribution of incident radiation through the layered canopies follows the work of Warren Wilson (1965, 1967), Anderson (1966), and de Wit (1965).

The wheat leaf photosynthesis-light response curves are from Angus (1970; also see Angus and Wilson 1976). These curves include the effect of leaf age. Hence, net photosynthesis during the daylight hours is a function of irradiance and leaf age, or

$$P_n = f(I, a) \quad , \quad (1)$$

where  $P_n$  is net photosynthesis ( $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ ),  $I$  is incident radiation ( $\text{mW cm}^{-2}$ ), and  $a$  is leaf age.

Connor and Cartledge (1971) compared observed and simulated diurnal patterns of hourly community photosynthesis ( $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ ) for all three models and total daily photosynthesis for the layered canopy models (4M and 6M). The diurnal pattern predicted by SIMPLE deviated seriously from observed patterns. The geometric models generated values in fair agreement with observed values for both hourly rates and daily rates. No real differences in agreement could be resolved between the mean angle treatment (4M) and the angle distribution

treatment (6M). The fact that 4M is simpler and equally adequate recommends 4M over 6M. Interestingly, while SIMPLE failed to simulate diurnal patterns of photosynthesis in a wheat community, it did as well as 4M and 6M in simulations of a Rhodes grass community (Connor and Cartledge 1970), except when leaf area was low. This leads to the not unreasonable conclusion that canopy architecture is important to canopy photosynthesis in some community types but not in others.

Lupton (1972) developed a model relating photosynthesis to light intensity in successive layers of a wheat crop canopy. The distribution of incident light in the canopy is affected by leaf angle and leaf area of each canopy layer. Total crop photosynthesis is the sum of contributions of each layer. The layers are largely defined by wheat plant anatomy, for example, the ear zone, the flag leaf laminae zone, etc.

The rate of photosynthesis per unit ground area of the uppermost zone is given by

$$P_0 = \frac{m_0 I_0}{q_0 + (r_0 I_0 / L_0)} + \frac{(2 - m_0) I_1}{q_0 + (r_0 I_1 / L_0)}, \quad (2)$$

where

- $P_0$  = photosynthesis (mg starch  $\text{dm}^{-2}$  ground area  $\text{h}^{-1}$ ),
- $L_0$  = leaf area index of top layer,
- $m_0$  = chance of light encountering a leaf in the top layer,
- $I_0$  = total incident radiation ( $\text{cal cm}^{-2} \text{h}^{-1}$ ),
- $I_1$  = total diffuse radiation ( $\text{cal cm}^{-2} \text{h}^{-1}$ ),
- $q_0, r_0$  = constants in the general relationship between photosynthesis and light (after Monteith 1965).

Similar equations are derived for the other layers. Respiration is not considered and environmental factors other than light are implicitly assumed to be nonlimiting.

The 'constants'  $r_0$  and  $q_0$  of Eq. (2) (and their counterparts for other layers) were found to vary with plant age (Lupton 1972). This information, combined with observations on translocation, allowed model predictions of the contribution of particular layers (i.e., plant parts) to grain yield over time (up to 35 d after anthesis). The predictions generally did not compare well with observations (Lupton 1969). Lupton (1972) discussed possible causes of these discrepancies, such as error in observations due to disturbance of the canopy, or failure to allow for curvature of leaves in the model.

Rickman, Ramig, and Allanaras (1975) described a model of daily dry matter accumulation in winter wheat. The model involves environmental driving variables but does not consider photosynthesis or respiration. Osman (1971) predicted dry matter production in wheat using measured rates of gross photosynthesis and dark respiration, but he did not explicitly model these processes. These latter approaches do not, in themselves, represent the dynamic, mechanistic growth simulation models called for to predict seasonal carbon dynamics in wheat fields. The models of Connor and Cartledge (1971) and Lupton (1972), outlined above, are potentially more applicable, although they both lack considerations of respiration and dry matter production. They also fall short of modeling the seasonal carbon budget for an entire wheat field agroecosystem under a variety of environmental conditions.

### 1.1.2 Rice Models

Perhaps the only dynamic simulation model of rice growth is one developed by Iwaki (1975) during the Japanese International Biological Program. Iwaki's model was designed to simulate dry matter growth of rice plants during the vegetative period (about 120 d after seedlings are transplanted). The model involves the processes of photosynthesis, respiration, and synthate allocation. These processes of plant growth are related to daily illumination, temperature, and age of plants. The model divides the rice plant into four parts: living leaves; dead leaves; ears, culms, and leaf sheaths; and roots. The crop canopy

affects the distribution of light in the manners suggested by Saeki (1960), but other aspects of canopy microclimate are not considered.

Gross canopy photosynthesis ( $P_G$ , g dw m<sup>-2</sup> ground area d<sup>-1</sup>) is modeled using an equation developed by Kuroiwa (1968):

$$P_G = \frac{2BD}{AK} \ln \left\{ \frac{1 + \sqrt{[(1 + AKI)/(1 - M)]}}{1 + \sqrt{[(1 + AKI \exp(-KF))/(1 - M)]}} \right\}, \quad (3)$$

where

I = daily maximum of solar illumination at noon (Klux h),

D = daylength (hours),

F = leaf area index,

K = canopy light extinction coefficient,

M = light transmissibility of a single leaf,

A, B = constants characterizing the light  
photosynthesis curve of single leaves.

The leaf area index (F) varies with a time-dependent specific leaf area (m<sup>2</sup> g<sup>-1</sup> leaf weight) and simulated leaf weight.

Whole plant respiration (RSP, g m<sup>-2</sup> ground area d<sup>-1</sup>) is the sum of leaf respiration and respiration from nonphotosynthetic organs. The average rate of leaf respiration (RF, mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup>) is calculated using

$$RF = 0.1P_0(1 - 0.0625LAI), \quad (4)$$

where  $P_0$  (mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup>) is the photosynthetic activity of single leaves, and LAI is leaf area index. The parameter  $P_0$  is constant during the growing period, but the value of  $P_0$ , chosen from the reported range of values (Iwaki 1975), may vary with model run. Iwaki (1975) made several runs using different values of  $P_0$ , to explore the effect on growth processes.

Daily rates of respiration of nonphotosynthetic organs involve a time-dependent (seasonal), 'standardized' [sic] respiratory rate ( $RC$ ,  $\text{mg CO}_2 \text{ g}^{-1} \text{ organ dw h}^{-1}$ ), corrected for organ type. This formulation assumes a maintenance-type respiration that is dependent on organ dry weight. The 'standardized' [sic] respiratory rates (measured at  $30^\circ\text{C}$ ) are corrected for average air temperature, assuming a  $Q_{10}$  relationship with a  $Q_{10}$  parameter of 2.0.

Daily net production ( $P_N$ ) is calculated as gross photosynthesis ( $P_G$ ) minus whole-plant respiration (RSP). The resulting assimilate is partitioned to the three live plant organs according to empirically derived, time-dependent distribution ratios. Leaves receive the greatest proportion of the synthate [see Iwaki (1975) for details].

Simulation results were compared with field measurements of total plant weight ( $\text{g m}^{-2}$ ). A leaf photosynthetic rate ( $P_0$ ) of about  $30 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$  provided the best fit between observation and simulation. The model tended to overestimate growth in the early stages of vegetative growth (the first 40 to 60 d). Iwaki (1975) suggested that this was attributable to the lack of a temperature-dependent growth rate in the model. Agreement between observations and simulations, while generally good, varied with rice paddy location and year. The accuracy of photosynthesis and respiration predictions was not discussed.

Van Keulen (1976) has approached the problem of calculating potential rice production using the BACROS model of de Wit et al. (1978). His efforts are not widely referenced, and the details are not clear. We do not believe, however, that van Keulen goes much beyond the approach followed by Iwaki (1975). As is the case for the wheat models of Sect. 1.1.1, the available rice models do not simulate the carbon dynamics of the whole rice paddy over an entire year.

### 1.1.3 Corn Models

The preeminent model of  $\text{CO}_2$  exchange in a cornfield is the model SPAM developed by Stewart (1970) and Stewart and Lemon (1969), and

modified by Sinclair, Allen, and Stewart (1971). The model is also discussed by Lemon, Stewart, and Shawcroft (1971) and Sinclair, Murphy, and Knoerr (1976). In SPAM, a micrometeorological model, the canopy vegetation is divided into several horizontal layers of equal leaf area. The model simulates the micrometeorological conditions of each layer, determined principally by the interception and partitioning of solar and thermal radiation, and constructs a balanced energy budget for all foliage layers. Determination of canopy microclimate requires definition of top boundary conditions in the canopy aerodynamic boundary layer. The required boundary conditions include incident direct and diffuse radiation [both photosynthetically active radiation (PAR) and total solar radiation], wind speed, air temperature, water vapor content of the air, and atmospheric CO<sub>2</sub> concentration. A bottom boundary at the soil surface is also defined by further boundary conditions relating soil conditions to solar radiation, heat, CO<sub>2</sub> and moisture. In addition to these physical factors, several vegetation characteristics are also required. Various aspects of canopy architecture, including vertical distribution of leaf area and leaf angle and the interaction between leaf surface and the reflectance and transmittance of radiation, are involved. Physiological factors such as stomatal resistance, mesophyll resistance, and dark respiration rates are also required.

Through a series of rather involved and detailed functions, SPAM determines the microclimate of each layer. In turn, the layer microclimate is used to calculate the specific leaf and soil surface responses to variations in radiation, temperature, CO<sub>2</sub> concentration, and water vapor content. The photosynthetic response to incident light of individual leaves is modeled using a modification of Chartier's biochemically oriented leaf model (1970). According to Chartier, the relationship between net assimilation per unit leaf area ( $F$ , mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup>) and incident radiation ( $E$ , W m<sup>-2</sup>; 400 to 700 nm)

is described by a nonrectangular hyperbola. The maximum rate of net assimilation (FMAX) is given by

$$FMAX = \frac{C - R[r_x - (nr_m)]}{r_a + r_s + r_m + r_x} \quad (5)$$

where C is atmospheric CO<sub>2</sub> (ppm); R is the respiration flux (mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup>); n is the fraction of R mixed in intercellular spaces, and r<sub>a</sub>, r<sub>s</sub>, r<sub>m</sub>, and r<sub>x</sub> are boundary layer, stomatal, mesophyll, and carboxylation CO<sub>2</sub> diffusion resistances (s m<sup>-1</sup>) respectively. The photosynthesis submodel relates stomatal resistance to CO<sub>2</sub> concentration, light, and water deficit; boundary layer resistance is related to air turbulence. Respiration (R, mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup>) as a function of leaf temperature is modeled following Waggoner (1969):

$$R = R_x \exp[9000 \ln(Q)(1/293 - 1/T)] \quad (6)$$

where R<sub>x</sub> is respiration at 20°C; Q is the Q<sub>10</sub> coefficient (approximately 2), and T is temperature (°C). Total canopy gas exchange (e.g., CO<sub>2</sub>) is calculated by summing the photosynthesis and transpiration of each foliage layer. These responses feed back to affect layer microclimate.

The scale of responses modeled by SPAM permits simulation of diurnal patterns in microclimate, photosynthesis, and transpiration. Comparisons between simulated and observed microclimate were "good enough for many applications" (Lemon, Stewart, and Shawcroft 1971, p. 378). Comparisons between observed and simulated patterns of transpiration and net photosynthesis of a maize crop were generally very good (Sinclair, Murphy, and Knoerr 1976). These results are important, but as has been stressed by Lemon, Stewart, and Shawcroft (1971), SPAM is not a model for plant growth or crop yield. We are unaware of any comparisons between observations and SPAM simulations over a growing season.

Sinclair, Murphy, and Knoerr (1976) reported on a simplified SPAM. In this model vertical exchange coefficients between layers are assumed to be infinite; consequently, there are no vertical gradients in temperature, water vapor, and  $\text{CO}_2$  concentration (upper boundary values are used in the simulations). Only radiation varies in its distribution through the canopy. The model assumes that canopy microenvironment (except for radiation) is unimportant. The net photosynthesis submodel (Sinclair 1972) follows the biochemical approach of Chartier (1970) and is very similar to the submodel in the more complex SPAM. Simplified SPAM produces a predicted diurnal pattern of net photosynthesis nearly identical to that of the original SPAM simulations. However, predictions of transpiration patterns differed (were lower) when transpiration rates were high (e.g., air temperature was high).

Sinclair, Murphy, and Knoerr (1976) also discussed the so-called "big leaf" model, which treats the canopy as a condensed single plane, a single large leaf. This model assumes no differences in intracanopy microenvironment, but the leaf environment differs from ambient conditions above the canopy. The single-plane canopy is apportioned into sunfleck and shade leaves, and separate  $\text{CO}_2$  assimilation rates are calculated for each class. The leaf photosynthesis submodel is the same as in the simplified SPAM. Canopy photosynthesis in the submodel is the sum of the sunfleck and shade rates. This model gave results similar to those given by the simplified SPAM model. Predicted photosynthetic rates were similar to those of the complex SPAM, but transpiration rates differed. The big leaf model generated transpiration rates greater than those predicted by SPAM.

The results from the simplified models that do not consider gradients in canopy microenvironment lead to the interesting conclusion that, for corn fields at least, nothing much is gained in the prediction of canopy photosynthesis by laboriously modeling intracanopy differences in microenvironment. This may recommend these models over SPAM in certain applications.

Duncan et al. (1967) developed a general model of photosynthesis in a foliage canopy. Their model assumes a canopy of many small leaves

dispersed in space and arranged in horizontal layers. The model simulates the fate and distribution of incident solar radiation within the canopy. Canopy architecture (e.g., leaf area, leaf angle) and light transmission and reflection properties of the leaves affect this distribution. Photosynthetic rates ( $P$ ,  $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ ) vary only in response to illumination, following the light response curve for single leaves. This response curve is described by a rectangular hyperbolic function

$$P = \frac{P_{\max} I}{I + k} - R \quad , \quad (7)$$

where  $P_{\max}$  is the asymptotic photosynthetic rate,  $I$  is light intensity,  $R$  is dark respiration ( $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ ), and  $k$  is a constant equal to  $I$  at  $P_{\max}/2$ . Dark respiration rates are incorporated in adjustments of light response curves. Duncan et al. (1967) applied this model to maize populations at several population densities and found close agreement between simulations and observations over a 45-d period from 30 d after planting to maturity. The model tended to overestimate dry matter production at maturity, and agreement between simulation and observation tended to decrease with increasing plant density. Duncan et al. (1967) provide possible explanations for these discrepancies. The model did not deal with other aspects of carbon flux in the field, such as decomposition or soil respiration.

De Wit, Brouwer, and Penning de Vries (1970) applied the crop simulation model ELCROS (Brouwer and de Wit 1969) to a maize crop. ELCROS concentrates on the increase of root, stem, and leaf weights under the influences of tissue age, reserve synthate, water, and temperature. Photosynthesis is modeled as a function of light incident on individual leaves. The distribution of light within the canopy is determined by canopy leaf area and the height of the sun at hourly intervals (de Wit 1965). Leaf photosynthesis at 23°C ( $P$ ,  $\text{kg CH}_2\text{O ha}^{-1} \text{ h}^{-1}$ ) is given by

$$P = [LI/(0.356 + LI)]84.5 \quad , \quad (8)$$

where LI is visible light intensity ( $\text{cal cm}^{-2} \text{min}^{-1}$ ). Temperature is assumed to affect the photosynthetic rate in fixed proportions over the range from 0° to 45°C. Optimal temperatures are at 30° and 35°C. Photosynthesis decreases with temperatures above or below these values. Hourly air temperatures at a single fixed height are used. Canopy photosynthesis is the sum of individual leaf rates.

Respiration is the sum of growth respiration and maintenance respiration. Growth respiration ( $\text{GR}$ ,  $\text{kg CH}_2\text{O ha}^{-1} \text{d}^{-1}$ ) is a fixed proportion of plant growth and is described by the equation

$$\text{GR} = 0.33(\text{GLW} + \text{GRW} + \text{GS1}) \quad , \quad (9)$$

where GLW, GRW, and GS1 are the weight growth rates ( $\text{kg ha}^{-1} \text{d}^{-1}$ ) of the leaves, roots, and stems respectively. Maintenance respiration ( $\text{MR}$ ,  $\text{kg CH}_2\text{O ha}^{-1} \text{d}^{-1}$ ) is a more complicated function:

$$\text{MR} = 0.08\text{URRC} \quad , \quad (10)$$

where URRC, the uncoupled respiration rate of the whole crop, is the air- and soil-temperature-weighted sum of leaf, stem, and root respiration rates. These rates are age dependent and vary with tissue nitrogen content [see de Wit, Brouwer, and Penning de Vries (1970) for details].

When simulated results were compared with actual experiments, growth trends over 100 d postemergence were reasonably comparable, but the quantitative ( $\text{kg shoot/ha}$ ) simulation results tended to overestimate field observations from California and Iowa. Production in a Netherlands field was underestimated. Driving variables were altered in these simulations, but parameter values were unchanged. The authors related the differences between simulation and observation to temperature effects. Simulated photosynthesis and respiration showed the appropriate response to changes in leaf area, but comparisons with observed quantitative values were not discussed.

Baker and Horrocks (1976) have reported on another dynamic corn growth model. The model simulates an entire corn production system: planting, crop growth, and harvesting. The canopy and plant growth components are comparable to those of SPAM, and the photosynthesis and respiration submodels are very similar. However, in contrast to SPAM, the crop growth simulations proceed on a daily basis and involve a chronological clock of growing-degree days. Also, the stomatal resistance values are constants rather than variables. Baker and Horrocks (1976) did not discuss seasonal carbon or growth dynamics, although the structure of their model, CORNMOD, makes such simulations feasible.

Other simulations of carbon flux in corn fields include an application of de Wit's (1959) canopy model by Williams, Loomis, and Leply (1965) (the model tends to underestimate experimental values for photosynthesis) and applications of the SPAM model by Shawcroft (1970, 1971), Stewart (1970), Shawcroft and Lemon (1972), Lemon et al. (1973), Allen, Jensen, and Lemon (1971), Sinclair (1971), and Allen (1973). Terjung, Louie, and O'Rourke (1976) simulated the diurnal pattern of net photosynthesis ( $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ ) for maize using their general layered leaf canopy, energy budget model of photosynthesis (see Sect. 1.2). Photosynthesis was modeled as a function of leaf temperature and solar radiation. The model BACROS, a successor to ELCROS, described earlier, was used to simulate the seasonal growth of a corn crop (de Wit et al. 1978). Wright and Keener (1982) reported a test of a corn model (Stapper and Arkin 1980) in which photosynthate production is a function of average daily temperature and daily solar radiation. To our knowledge, none of these models simulates the whole cornfield's carbon budget over an entire year. Crop models are characteristically designed to simulate growing seasons, not entire annual cycles.

#### 1.1.4 Barley Models

Kallis and Tooming (1974) described a model designed to evaluate the impact of photosynthesis, respiration, specific leaf weight, and organ growth functions on crop yield. The model was applied to the

growth of barley. In the model, the barley plants are divided into four different organs: leaves, stems, roots, and reproductive organs. Empirically derived growth functions that describe changes in relative organ weight [increase in dry weight of organ  $i$  ( $\Delta m_i$ )/increase in dry weight of whole plant ( $\Delta M$ )] during vegetative and reproductive growth periods are combined with models of photosynthesis and respiration. The resulting model allows simulation of changes in organ and whole plant weight over time.

Gross photosynthesis ( $P_g$ ,  $\text{mg CO}_2 \text{ dm}^{-2} \text{ leaf area h}^{-1}$ ) is modeled after Tooming (1967):

$$P_g = (KI)/[K(a + I)] \quad , \quad (11)$$

where  $a$  is the derivative of the photosynthesis light curve at low irradiance (PAR),  $I$  is absorbed irradiance ( $\text{cal cm}^{-2} \text{ min}^{-1}$ ), and  $K$  is the gross photosynthetic rate at light saturation. This light-saturated gross photosynthetic rate is given by

$$K = a[(1 - \sqrt{c})/\sqrt{c}]I' \quad , \quad (12)$$

where  $c$  is a loss factor and  $I'$  is the irradiation density of adaptation (Tooming 1967). The distribution of  $I$  in the crop canopy, assuming a random leaf arrangement, is a function of time and leaf area (Tooming and Ross 1965).

Leaf respiration and the respiration of other, nonleaf organs are treated differently. Leaf respiration ( $R_l$ ,  $\text{mg CO}_2 \text{ dm}^{-2} \text{ leaf area h}^{-1}$ ) is related to the gross photosynthetic rate (Tooming 1967) such that

$$R_l = cK \quad , \quad (13)$$

where  $c$  and  $K$  are as in Eqs. (11) and (12). The respiration rate of all the other organs ( $\sum_{i=2}^4 R_i$ ,  $\text{mg CO}_2 \text{ d}^{-1}$ ) is proportional to the

dry weight of the organs, or

$$\sum_{i=1}^4 R_i = 0.015 \left( \sum_{i=2}^4 m_i \right), \quad (14)$$

where  $m_i$  is the weight of the  $i$ th organ. Daily photosynthesis and respiration of the whole crop is obtained by integrating Eq. (12) minus Eq. (13) over time and leaf area, and subtracting Eq. (14) from the result. The model goes on to consider the effects of variations in specific leaf weight (SLW).

Kallis and Tooming (1974) compared crop yield characteristics of simulated barley using experimentally derived parameters and modified or hypothetical parameters. The growth dynamics of the hypothetical barley over an 80 d period suggested that an increased photosynthetic activity could result in increased ear and total plant yield. The authors did not report comparisons of observations and simulation results.

Biscoe, Scott, and Monteith (1975), in conjunction with the development of a micrometeorological model (Biscoe, Clark, et al. 1975), described a barley stand's seasonal carbon budget. While not actually implemented as a simulation model, determination of the carbon budget involved models of  $\text{CO}_2$  exchange in the estimates of carbon flux. According to Biscoe, Scott, and Monteith (1975), net canopy photosynthesis [ $P(n)$ ,  $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ ] over a 24-h period is

$$P(n) = \sum (P_a - R_a) + \sum R_s, \quad (15)$$

where  $\sum (P_a - R_a)$  is the net exchange of  $\text{CO}_2$  between the canopy and the atmosphere over 24 h,  $P_a$  is hourly net canopy photosynthesis ( $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ),  $R_a$  is hourly night canopy respiration ( $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ), and  $\sum R_s$  ( $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ ) is the total amount of  $\text{CO}_2$  evolved by soil microorganisms over 24 h. Gross photosynthesis [ $P(g)$ ,  $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ ], is given by

$$P(g) = \sum q (P_a + R_s) + (1.4R_d) 2^{\frac{(T_d - T_d)}{10}}, \quad (16)$$

where  $\sum_{\text{d}} (P_a + R_s)$  represents the summation over daylight hours of net canopy photosynthesis ( $P_a$ ) and soil microorganism respiration ( $R_s$ ). The term in Eq. (16) involving  $R_d$  (net respiration loss in the dark,  $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ ) describes a daytime 'dark' respiration rate ( $\sum_{\text{d}} R_{\text{d}}$ ,  $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ ;  $R_{\text{d}}$  = hourly daytime respiration) where  $T_{\text{d}}$  is the mean daytime tissue temperature and  $T_{\text{n}}$  is the mean nighttime tissue temperature. Air temperature at the height of maximum foliage density is used to estimate tissue temperature. This representation of respiration is based loosely on work by McCree (1970).

Biscoe, Scott, and Monteith (1975) calculated the flux of  $\text{CO}_2$  above the canopy using the micrometeorological measurements of Biscoe, Clark, et al. (1975). The downward flux of  $\text{CO}_2$  from air to canopy during daylight hours is net daytime photosynthesis or assimilation by photosynthetic tissue in the canopy ( $P_c$ ,  $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) plus soil microbial respiration ( $R_s$ ). The measurements of Biscoe, Clark, et al. (1975) allowed estimation of  $P_c$ , and a constant  $0.11 \text{ g m}^{-2} \text{ h}^{-1}$  was used to approximate  $R_s$ . Biscoe, Gallagher, et al. (1975) modified the calculation of  $P_c$  [their  $P(n)$ ] using a canopy photosynthesis model. Biscoe, Gallagher, et al. (1975) also defined photosynthesis-light relationships for the various photosynthetically active organs of barley during the grain-filling period. Rather than approximate these relationships using rectangular hyperbola, as is frequently done, Biscoe, Gallagher, et al. (1975) followed the example of Peat (1970) and Littleton (1971) and described net photosynthesis ( $P_c$ ,  $\text{g CO}_2 \text{ m}^{-2} \text{ organ area h}^{-1}$ ) by

$$P_c = n - ml^S, \quad (17)$$

where  $S$  is photosynthetically active radiation (PAR,  $\text{W m}^{-2}$ ) and  $n$ ,  $m$ , and  $l$  are parameters. The parameters  $n$  and  $m$  vary with time, and their dependence on time may vary with the organ being considered (see Biscoe, Gallagher, et al. 1975). The irradiance of a particular organ is determined using an adaptation of Monteith's (1965) model of light distribution in a multilayered canopy:

$$S(L) = S(0)(s + (1 - s)t)^L, \quad (18)$$

where  $S(L)$  is irradiance below a total canopy area index ( $L$ ),  $S(0)$  is irradiance at the top of the canopy,  $s$  is the fraction of radiation not intercepted by a foliage layer with unit area index, and  $t$  is the transmission coefficient for solar radiation through leaves. The adaptation involves organ area and height distribution (see Biscoe, Gallagher, et al. 1975). Organ area per unit ground area is used to convert organ photosynthesis to a field area basis.

Assuming that  $S$  is zero, Eq. (17) describes the dark respiration rate of each organ. The sum of  $P_c$  over organ type gives hourly values of daytime net photosynthesis and of nighttime respiration for the whole canopy.

Comparisons of canopy photosynthesis calculated according to the canopy model approach of Biscoe, Gallagher, et al. (1975) and the micrometeorological methods of Biscoe, Clark, et al. (1975) were in general agreement (Biscoe, Gallagher, et al. 1975), suggesting that the canopy model could substitute for the more exacting micrometeorological measurements of  $CO_2$  flux. Dry weight standing crop values measured by growth analysis and calculated from  $CO_2$  flux were relatively similar (Biscoe, Scott, and Monteith 1975);  $CO_2$  flux estimates were generally less than dry matter observations. Comparisons of weekly dry matter growth rates ( $g\ C\ m^{-2}\ week^{-1}$ ) demonstrated general agreement between  $CO_2$  flux estimates and field observations. Agreement in the latter weeks of growth was poor, but Biscoe, Scott, and Monteith (1975) ascribed the discrepancies to inaccuracies in the conventional dry matter sampling. The carbon budget of the barley stand was not determined for periods when barley plants were not growing.

#### 1.1.5 Soybean Models

The model SOYMOD I (Curry, Baker, and Streeter 1975) is an environmentally driven simulator of soybean growth and development. Designed as a preliminary framework or potential submodel for use in a more detailed model, SOYMOD I divides a soybean plant into leaves, stems, roots, and reproductive parts. The model simulates canopy photosynthesis, synthate partitioning, respiration, organ growth,

plant nitrogen, and the distribution of light within the soybean canopy. The distribution of light in a multilayered canopy is modeled after Monteith (1965) and Curry and Chen (1971). Light intensity ( $I$ ,  $\text{cal m}^{-2} \text{h}^{-1}$ ) after  $L$  layers have been penetrated is given by

$$I = I_0(1 - s)[s + (1 - s)a]^L, \quad (19)$$

where  $I_0$  ( $\text{cal m}^{-2} \text{h}^{-1}$ ) is the light intensity at the top of the canopy,  $s$  is the fraction of light passing through a layer without interception,  $a$  is the leaf transmission coefficient, and  $L$  is the number of layers penetrated.

The photosynthetic rate ( $\text{g m}^{-2} \text{h}^{-1}$ ) of an individual leaf (or leaf layer) is expressed by

$$\frac{dP}{dt} = \left[ \frac{A}{C} + \frac{B}{I_0 g(\text{canopy})} \right]^{-1} \times f(T), \quad (20)$$

where

$A$  = a  $\text{CO}_2$  canopy resistance constant

(for soybean,  $A = 67.6 \text{ ppm CO}_2 \text{ m}^2 \text{ h g}^{-1}$ ),

$B$  = a photosynthetic efficiency constant

(for soybean,  $B = 0.0715 \text{ cal g}^{-1}$ ),

$C$  =  $\text{CO}_2$  concentration (ppm),

$I_0$  = incident radiation (400 to 700 nm) above canopy ( $\text{cal m}^{-2} \text{h}^{-1}$ ),

$f(T)$  = a temperature function.

The term  $g(\text{canopy})$  is a function of light attenuation and penetration.

SOYMOD I simulates respiration as the sum of maintenance respiration, growth respiration, and light respiration. Maintenance respiration ( $\text{g g}^{-1} \text{h}^{-1}$ ) is proportional to organ biomass (leaves, stems, roots, and reproductive parts). The constant of proportionality may vary with organ, and maintenance respiration is assumed to respond to temperature according to a  $Q_{10}$  function. Growth respiration

( $\text{g g}^{-1} \text{h}^{-1}$ ) is proportional to the change in organ dry matter, and, again, the coefficient of proportionality may vary with organ. Light respiration is proportional to the photosynthetic rate and varies with temperature. Hence, total plant respiration is expressed as

$$\frac{dR}{dt} = r_p \frac{dP}{dt} f_1(T) + \sum_{i=1}^4 r_{o,i} M_i f_2(T) + r_{b,i} \frac{dM_i}{dt}, \quad (21)$$

where

- $r_p$  = photorespiration coefficient ( $\text{g g}^{-1}$ ), which is a function of light;
- $dP/dt$  = photosynthetic rate ( $\text{g h}^{-1}$ );
- $r_{o,i}$  = maintenance respiration coefficient ( $\text{g g}^{-1} \text{h}^{-1}$ ) for the  $i$ th organ;
- $M_i$  = biomass of the  $i$ th organ (g);
- $r_{b,i}$  = growth respiration coefficient ( $\text{g g}^{-1}$ ) for the  $i$ th organ;
- $dM_i/dt$  = rate of change of biomass in the  $i$ th organ ( $\text{g h}^{-1}$ ).

The terms  $f_1(T)$  and  $f_2(T)$  represent temperature functions (dimensionless). Photosynthate distribution is controlled by fixed organ weight to total weight ratios, temperature, and a variable dry matter to nitrogen ratio which is organ specific [see Curry, Baker, and Streeter (1975) for details].

A comparison of total weight ( $\text{g/m}^2$ ) values over a 2800-h period following emergence showed very close agreement between observations and model predictions. Curry, Baker, and Streeter (1975) did not discuss the reliability of photosynthesis or respiration predictions.

The soybean crop simulation model, GLYCIM (Acock et al. 1983), describes the growth of an average soybean plant in a uniform crop. The plant is divided into a number of organs, including leaves, stems, roots, flowers, and seeds. The model simulates fluxes of carbon, nitrogen, and dry matter for the plant; plant water status is also

modeled. GLYCIM models water, heat, nitrate, and oxygen in the soil below and between plant rows, but it does not model soil carbon dynamics. The model is not a micrometeorological model per se, but canopy structure is involved in the simulation of evapotranspiration and the integration of leaf photosynthesis parameters (Acock et al. 1978).

The model simulates plant growth and development and, consequently, includes a mechanistic submodel of plant carbon dynamics (assimilation, respiration, and partitioning) which is initialized at the cotyledon (early seedling) stage. Canopy gross photosynthesis ( $P_G$ ,  $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ ) is modeled as a hyperbolic function of light and  $\text{CO}_2$  concentration

$$P_G = \frac{[(eI)(aC)539.66]/(273.15 + T)}{(eI) + [(aC)539.66]/(273.15 + T)} \times k \quad , \quad (22)$$

where

- e = canopy light utilization efficiency,
- I = light (PAR) incident on the canopy,
- a = canopy conductance to  $\text{CO}_2$  transfer,
- C = atmospheric  $\text{CO}_2$  concentration,
- T = air temperature at time t (t is measured in tenths of a day from dawn),
- k = proportion of soil covered by crop.

The  $P_G$  rate is reduced by temperature, leaf nitrogen, and leaf senescence limitations [see Acock et al. (1983) for details].

Light respiration ( $R_L$ ) is a function of  $P_G$ , leaf age or leaf nitrogen,  $\text{CO}_2$  concentration, and temperature, or

$$R_L = \{[P_G \min(A,N)151890.0]/C\}0.00012\exp(0.0295T) \quad , \quad (23)$$

where  $\min(A,N)$  represents the effect of either the age of the youngest leaf (A) or leaf nitrogen (N), whichever is most limiting, and the other terms are as in Eq. (22). Maintenance respiration ( $R_M$ ) is

calculated after Penning de Vries (1975), with the assumption that only leaf tissue experiences significant maintenance respiration. Maintenance respiration is given by

$$R_M = \frac{[(11.733L_W) + (366.67L_W N D.05)]/86400.0}{(SP100.0)[0.25\exp(0.0693T)]}, \quad (24)$$

where  $L_W$  is leaf weight (g/plant),  $N$  is the nitrogen supply:demand ratio for vegetative parts,  $S$  is row spacing (in centimeters),  $P$  is plant population per meter of row, and  $T$  is air temperature at time  $t$ . Notably, GLYCIM does not associate respiration with the growth of the various plant parts.

Net photosynthesis is gross photosynthesis minus light respiration and maintenance respiration. Net photosynthesis is in turn reduced by a stomatal closure factor if the plant is in water stress. Fixed carbon is either stored in the shoot carbon pool or allocated to organ growth. Translocation out of the leaf is controlled by a source-storage relationship. Net photosynthesis of the lower leaves is calculated using the same equations used for upper canopy leaves but with the additional consideration of self-support. If, over a 24-h period, the lower leaves are not self-supporting (i.e., respiration exceeds photosynthesis), they are dropped from the plant.

The report by Acock et al. (1983) describing GLYCIM does not provide comparisons of simulated and observed photosynthesis or respiration. Comparisons of observed and simulated plant height, leaf area, and numbers of various organs for 120 d following the cotyledon stage were reasonable. Predictions of dry weight were less comparable, but simulated growth trends resembled the observed patterns.

#### 1.1.6 Cotton Models

A systems-oriented cotton crop model, COTCROP, has been described by Jones, Brown, and Hesketh (1980). COTCROP, which models crop growth for plants on one square meter of ground area, was preceded and influenced by models of single plants designed to predict the numbers

of fruit produced (Duncan 1972; Hesketh, Baker, and Duncan, 1972; Stapleton et al. 1973; McKinion et al. 1975; McKinion, Jones, and Hesketh 1974; Jones et al. 1974). More recent refinements have been implemented in the model GOSSYM (Baker, Lambert, and McKinion 1983). The structure of COTCROP is a set of simple first-order-difference equations with a time step of one day. The model simulates plant growth, flowering, boll development, photosynthesis, carbohydrate balance, nitrogen balance, and soil water and nitrogen balance. Many of these processes are driven by environmental variables, which include solar radiation, rainfall, pan evaporation, and temperature. For example, photosynthesis is a function of solar radiation and soil water potential. Phenology is also used in the model to drive growth dynamics.

The model assumes a plant of six parts (main stem leaves, fruiting branch leaves, main stems, fruiting branches, fruits, and roots), a carbohydrate pool, and a nitrogen pool. The photosynthesis submodel (taken from SIMCOT II, McKinion et al. 1975) calculates gross photosynthesis ( $P_R$ ,  $\text{g CH}_2\text{O m}^{-2} \text{d}^{-1}$ ) by

$$P_R = 0.23903 + 0.137379(\text{RAD}) - [(5.4136 \times 10^{-5})\text{RAD}^2] - 0.68R_w, \quad (25)$$

where RAD is radiation ( $\text{W m}^{-2} \text{d}^{-1}$ ),  $R_w$  is the reduced photosynthetic potential due to water deficits, and 0.68 is the conversion factor from  $\text{CO}_2$  to  $\text{CH}_2\text{O}$ . Photosynthesis provides carbohydrates for the pool and the model utilizes and distributes this supply according to respiration and growth-demand priorities. Maintenance respiration is a fixed proportion of total plant weight; growth respiration is a fixed proportion of the potential organ growth rates summed over all organs. The synthate remaining in the carbohydrate pool after respiration demands are met is allocated to organ growth. Synthate distribution is also affected by nitrogen, carbohydrate, and water availability. COTCROP simulates crop growth from crop emergence to harvest.

COTCROP was developed for application to problems of cotton crop management; hence, validation studies were directed toward predictions

such as numbers of fruit per square meter and yield (bales acre<sup>-1</sup>). Simulated results for such variables agreed very nicely with field observations. However, Jones, Brown, and Hesketh (1980) did not discuss how well COTCROP simulated CO<sub>2</sub> exchange rates or total dry weight.

An entirely different sort of model, but one of potential usefulness in predicting cotton crop carbon flux [and in fact used in COTCROP by Jones, Brown, and Hesketh 1980], was developed by Hesketh, Baker, and Duncan (1971) and Baker, Hesketh, and Duncan (1972). The respiratory rates (mg CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) and dry weight of cotton squares, bolls, and leaves were measured under growth chamber conditions. From these data, regression equations relating dry weight and respiration rates were developed. Then, utilizing a theory of growth and maintenance respiration, Hesketh, Baker, and Duncan (1971) derived three equations that together could be used as a model of plant growth, given a model of gross photosynthate per day per plant to serve as a forcing function. Baker, Hesketh, and Duncan (1972) developed a means of estimating gross photosynthesis from measurements of apparent photosynthesis and day and night respiration. This photosynthetic input was used with their model of respiration to derive a simple model of change in cotton dry weight per unit ground area over time. The authors did not indicate how well their formulation simulated observed cotton growth, although a simulated diurnal pattern of photosynthesis was presented.

Gutierrez et al. (1975, 1984) have developed a mechanistic simulation model of cotton crop growth and development which integrates the physiology of photosynthesis (McKinion, Jones, and Hesketh 1974; McKinion et al. 1975; also see discussion of COTCROP above) and population biology. Gutierrez et al. (1984) reported that comparisons of observations and simulation results were very favorable. Certainly, simulations of seasonal dry matter standing crop and fruit number fit comparable observation data from Brazil very well. The reliability of photosynthesis and respiration simulations was not discussed, although the authors suggested implicitly that photosynthesis and respiration routines were acceptable.

### 1.1.7 Potato Model

Ng and Loomis (1984) have described a crop growth model for potato. Developed as a tool for studying integrative physiology, POTATO simulates plant water balance, photosynthesis, respiration, vegetative growth, and organ initiation. POTATO divides the plant into a reserve assimilate pool and six organs: mainstem internodes, mainstem leaves, branch stem internodes, branch stem leaves, tubers, and fibrous roots. Growth rates are modeled for each organ. Plant growth and development are influenced by environmental driving variables which include air temperature, dew point, wind, and solar radiation. Soil moisture and nutrients are assumed to be above limiting levels. Input data are daily values, but a subroutine calculates hourly values for the environmental variables. POTATO operates on hourly time steps and can simulate both diurnal and seasonal dynamics.

Gross photosynthesis ( $\text{g CH}_2\text{O m}^{-2} \text{h}^{-1}$ ) is modeled after Duncan et al. (1967; see Sect. 1.1.3). Modified net photosynthesis light-response curves from Ku, Edwards, and Tanner (1977) are used in the Duncan model. The Duncan photosynthesis program, which includes a canopy effect on light distribution, is used to construct pairs of tables for hourly potential gross photosynthesis: one pair for clear skies and one pair for overcast skies. Each pair of tables includes a table for normal potential gross photosynthesis and a table for sink-affected photosynthesis. The photosynthetic maximum of the light-response curve for sink-affected photosynthesis is twice that for normal photosynthesis. POTATO uses feedback from tuber growth to regulate the contributions of normal and sink-affected rates (see Ng and Loomis 1984).

The photosynthetic rate with daily radiation ( $P_g$ ) is a combination of the overcast and clear sky potential rates in proportion to the fractions of sky which are clear and overcast, or,

$$P_g = [(f_c P_c) + (f_o P_o)] E_a \min(E_t, E_w) \quad , \quad (26)$$

where  $f_c$  is the fraction of clear sky,  $f_o$  is the fraction of overcast sky,  $P_c$  is the potential rate ( $\text{g CH}_2\text{O m}^{-2} \text{h}^{-1}$ ) for clear sky, and  $P_o$  is the potential rate ( $\text{g CH}_2\text{O m}^{-2} \text{h}^{-1}$ ) for overcast sky. The term  $E_a$  [dimensionless (0, 1)] represents the effect of leaf age on photosynthesis. The effect of air temperature on gross photosynthesis is represented by  $E_t$  [dimensionless (0, 1)]. The temperature response function is an optimum temperature (near 25°C) curve. The term  $E_w$  is the effect of plant water content on photosynthesis. A decline in relative plant water content below 0.9 quickly becomes limiting. The  $\min(E_t, E_w)$  formulation in Eq. (26) indicates that only the most limiting effect of either temperature or plant water content influences gross photosynthesis.

Respiration ( $\text{g CH}_2\text{O m}^{-2} \text{h}^{-1}$ ) is the sum of growth respiration and maintenance respiration. Growth respiration ( $\text{g CH}_2\text{O plant}^{-1} \text{h}^{-1}$ ) is calculated as the sum of the products of the growth rates ( $\text{g CH}_2\text{O plant}^{-1} \text{h}^{-1}$ ) of each organ and an organ-specific growth respiration coefficient. The maintenance respiration rate is more complicated. A maintenance respiration rate is calculated for each organ. The equation for mainstem (and branch) leaves, for example, is

$$R_m = [W_l - (f_r W_l)] R_{25} E_T E_a E_m, \quad (27)$$

where

- $R_m$  = rate of maintenance respiration, totaled for all mainstem leaves ( $\text{g CH}_2\text{O plant}^{-1} \text{h}^{-1}$ ),
- $W_l$  = total dry weight of mainstem leaves ( $\text{g plant}^{-1}$ ),
- $f_r$  = fraction of total plant dry weight which is reserve assimilate,
- $R_{25}$  = base maintenance respiration coefficient at 25°C ( $\text{g CH}_2\text{O g}^{-1} \text{h}^{-1}$ ),
- $E_T$  = the effect of air temperature [dimensionless (0, 3)],
- $E_a$  = the effect of leaf age [dimensionless, (0, 1)],
- $E_m$  = The effect of past metabolic activity [dimensionless (0, 1)], related to photosynthesis.

Maintenance respiration for internodes and fibrous roots is calculated using similar equations, except that age and metabolic activity effects are not involved. Tuber maintenance respiration ( $\text{g CH}_2\text{O tuber}^{-1} \text{h}^{-1}$ ) is proportional to tuber weight. The coefficient of proportionality is affected by soil temperature according to the temperature relationship describing  $E_T$  in Eq. (27). Tuber maintenance respiration per plant is the summation of the per tuber rate over the number of tubers per plant. Total plant maintenance respiration is the sum of the rates for each organ, and maintenance respiration per square meter is obtained using an estimate of plant density.

Simulation of vegetative growth and organ initiation are major components of POTATO. Briefly, organ growth rate is given by a maximum relative growth rate that is reduced by temperature-dependent age and the most limiting influence of assimilate status, temperature, and plant water status. Organ initiation is dealt with similarly. Details can be found in Ng and Loomis (1984).

Ng and Loomis (1984) described in some detail the performance of POTATO. Simulated and observed dry weight agreed satisfactorily. Total dry weight and tuber dry weight were consistently, but only slightly, overestimated throughout a 90-d period following emergence. An observed decrease in leaf dry weight at about day 50 was simulated, but the model overestimated the magnitude of the downturn. Ng and Loomis (1984) described the seasonal course of simulated photosynthesis and respiration, but field observations for comparison were apparently not available.

#### 1.1.8 Tobacco Model

Wann, Raper, and Lucas (1978) have described a model of dry matter accumulation for tobacco. The model simulates growth in response to variations in temperature and PAR. The plant is conceptualized as a system of three organ classes (leaves, stems, and roots), each compartmentalized into a soluble carbohydrate pool, young growing tissue, mature tissue, growth respiration, and nongrowth respiration.

Photosynthesis, a function of light (PAR) and temperature, fixes photosynthate (heat energy equivalents) in the leaf carbohydrate pool. Gross photosynthesis ( $f_p$ ,  $J\ cm^{-2}\ d^{-1}$ ) is described by a Michaelis-Menten function:

$$f_p = B_0 aIL / (B + aI) \quad , \quad (28)$$

where  $B_0$  is the maximum light-saturated photosynthetic rate per unit leaf area ( $J\ cm^{-2}\ d^{-1}$ ) at a given  $CO_2$  concentration and temperature,  $aI$  is absorbed PAR ( $J\ cm^{-2}\ d^{-1}$ ),  $L$  is total leaf area ( $cm^2$ ), and  $B$  is a constant equal to the value of  $aI$  where  $f_p = B_0 L / 2$ . Temperature affects the maximum photosynthetic rate according to the relationship

$$B_0 = B_1 \exp(-B_2/T) \quad , \quad (29)$$

where  $B_1$  ( $J\ cm^{-2}\ d^{-1}$ ) and  $B_2$  (degrees K) are constants and  $T$  is the absolute temperature (degrees K). Water and mineral nutrients are assumed to be above growth-limiting levels. The model then simulates the translocation of heat energy (bound in the photosynthate) to stem and root and the dispersal of heat in respiration from the reserve pools of leaves, stems, and roots. The rate of energy flow (i.e., respiration) associated with the maintenance of a particular organ  $i$  is given by a proportion,  $p_i$ , of the energy stored in the young and mature tissues of that organ. This proportion, the respiration rate per unit of energy content, is a function of temperature ( $T$ ), or

$$p_i = a[\exp(-b/T)] \quad , \quad (30)$$

where  $a$  ( $d^{-1}$ ) and  $b$  (degrees K) are constants. Growth respiration is a function of energy content, carbohydrate pool concentration, and temperature. A fixed proportion of the energy utilized for growth is lost in growth respiration:

$$f(i_0, i_2) = (1 - c_i) f_i \quad , \quad (31)$$

where  $f(i_0, i_2)$  represents the rate of energy flow by growth respiration ( $J d^{-1}$ ) for the  $i$ th organ;  $c_i$  is a constant  $[(0, 1)]$ , and  $f_i$  ( $J d^{-1}$ ) is the rate of energy utilized in the growth of organ  $i$ . This growth rate is described by a Michaelis-Menten relationship:

$$f_i = l_{i0} X_{i1} C_i / (g_i + C_i) \quad , \quad (32)$$

where  $X_{i1}$  ( $J$ ) is the energy content of young tissue in the  $i$ th organ,  $C_i$  ( $J J^{-1}$ ) is the carbohydrate pool concentration of that organ, and  $g_i$  is a Michaelis-Menten constant. The term  $l_{i0}$  is the maximum possible growth rate per unit energy content of plant material and is dependent upon temperature according to a complex optimum temperature function [see Wann, Raper, and Lucas (1978) for details].

Translocation is a function of source and sink strengths (i.e., energy content and concentration in pool and organ tissue). The model also describes aging as the energy content and temperature-regulated flow of energy from young tissue to mature tissue. Conversion from energy units to gram dry weight ( $1 J = 6 \times 10^{-5} g dw$ ) permits prediction of dry matter growth on a plant-weight or plant-part-weight basis.

Simulated dry weights were in good agreement with measured weights from a greenhouse growth experiment conducted over a 30-d period following the transplanting of tobacco seedlings (Wann, Raper, and Lucas 1978). Parameters for the model were derived from phytotron experiments, and the model gave reasonable predictions when driven by greenhouse environmental conditions. However, the authors noted that the model had not been tested against field conditions. Presumably such a test would include simulation over an entire growing season.

#### 1.1.9 Sorghum Models

Arkin, Vanderlip, and Ritchie (1976) have described a model of growth and development for an average grain sorghum plant in a field stand. The mechanistic simulation model includes submodels of light

interception, photosynthesis, respiration, and water use. Plant dry matter (grams per plant) and leaf area (square centimeters) are modeled, but individual plant organs are not considered.

Potential photosynthesis ( $P$ ,  $\text{mg CO}_2 \text{ dm}^{-2} \text{ land area h}^{-1}$ ) is calculated as a function of intercepted light:

$$P = 31.35I^{1/2} - 13.32 \quad , \quad (33)$$

where  $I$  is the light (PAR) intercepted by the plant ( $\text{mE m}^{-2} \text{ h}^{-1}$ ). Light interception is modeled hourly following Beers' law, in which irradiance decreases exponentially with increasing total leaf area (see Saeki 1960). The photosynthetic rate calculated by Eq. (33) is reduced by two efficiency parameters (dimensionless, values between zero and one): one a function of mean ambient temperature, the other a function of available soil water. The temperature parameter decreases to zero as temperatures fall below  $25^\circ\text{C}$  or rise above  $40^\circ\text{C}$ . An extractable soil water (Ritchie 1972) content of less than 20% is assumed to be limiting.

Net photosynthesis is the gross rate, dependent on light, temperature, and soil water, minus night respiration. Night respiration is modeled after McCree (1974) such that

$$N = 0.14D + (c_T W) \quad , \quad (34)$$

where  $N$  is total night respiration ( $\text{g CO}_2 \text{ plant}^{-1}$ );  $D$  is daytime photosynthesis ( $\text{g CO}_2 \text{ plant}^{-1}$ );  $W$  is the  $\text{CO}_2$  equivalent of plant dry weight ( $\text{g CO}_2 \text{ plant}^{-1}$ ), and  $c_T$  is a temperature-dependent coefficient given by a weighted second order polynomial in  $T$ . This formulation includes growth respiration (the dependence on daytime photosynthesis) and maintenance respiration (the dependence on plant weight).

The model's cumulative dry matter predictions agreed well with observations made over a 105-d postemergence period. Results of simulation experiments involving altered environmental variables also compared well with field observations. Comparisons for photosynthesis and respiration were not discussed.

Shih, Gascho, and Rahi (1981) have described a model of sorghum aboveground biomass, but their model does not include an explicit consideration of photosynthesis or respiration. The empirical model predicts biomass from leaf area index and dry biomass accumulation (DAR) per unit leaf area. The DAR is an empirically derived function of time.

#### 1.1.10 Sugar Beet Models

Patefield and Austin (1971) presented a model of sugar beet growth in environments where nutrients and water are not limiting. The model simulates changes in dry weight per unit area. Plants are subdivided into two tissue types, leaf laminae and other tissue; these are referred to as 'leaves' and 'roots' respectively. Photosynthetic rates are modeled as functions of light intensity and temperature at the scale of a single leaf. Patefield and Austin (1971) followed Monteith (1965) in defining light interception in a canopy of several discrete layers with leaves distributed uniformly in a horizontal plane. The leaves are classified as sunlit, once-shaded, twice-shaded, or fully shaded. These designations correspond to the number of leaf layers light passes through before reaching a particular leaf surface. Sunlit leaves are the first (outer) layer and fully shaded leaves are in the fourth and deepest layer.

The single-leaf photosynthesis equation used by Monteith (1965) was modified by Patefield and Austin to account for leaf respiration and a constant photochemical efficiency at low light intensity. The modified equation is

$$p(I) = \begin{cases} [(a + (b/(I - (br))))^{-1}] & \text{for } I \geq I_c \\ (I/b) - r & \text{for } I < I_c \end{cases}, \quad (35)$$

where  $p(I)$  is the rate of net photosynthesis ( $\text{g m}^{-2}$  leaf area  $\text{h}^{-1}$ ) at light intensity  $I$  ( $\text{cal cm}^{-2} \text{h}^{-1}$ ),  $I_c$  is the light compensation point, and  $r$  is the respiration rate ( $\text{g m}^{-2} \text{h}^{-1}$ ).

The coefficient  $a$  ( $\text{m}^2 \text{h g}^{-1}$ ) is temperature dependent

$$1/a = 1/a_{15} + (T_c) \quad (36)$$

where  $a_{15}$  is the value of  $a$  at  $15^\circ\text{C}$ ;  $T$  is temperature ( $^\circ\text{C}$ ), and  $c$  is a constant ( $\text{g m}^{-2} \text{h}^{-1} \text{C}^{-1}$ ). The coefficient  $b$  ( $\text{cal g}^{-1}$ ) is independent of temperature. The rate of respiration,  $r$ , is discussed below. Leaf photosynthetic rates decrease with shading as intercepted radiation decreases from  $(1 - s)I$  at the sunlit level to  $[(1 - s)t]I$  for once-shaded leaves,  $[(1 - s)t^2]I$  for twice-shaded leaves, and 0.0 for fully shaded leaves [ $s$  and  $t$  are Monteith's (1965) light transmission coefficients]. Net photosynthesis is negative and equal to the corresponding daytime respiration rate (see below) for twice-shaded or fully shaded leaves. Canopy photosynthesis is the sum of the products of leaf area and photosynthetic rate for each of the leaf categories. Daily photosynthesis is the integral of this canopy rate over daylight hours.

Leaf respiration rates are calculated using one of two alternative methods. In the first, a basal, temperature-dependent rate is calculated as follows:

$$r(T) = r_{15}(1 + Tm) \quad . \quad (37)$$

where  $r(T)$  is the respiration rate ( $\text{g m}^{-2} \text{h}^{-1}$ ) of leaves or roots at temperature  $T$  ( $^\circ\text{C}$ ),  $r_{15}$  is the appropriate respiration rate at  $15^\circ\text{C}$ , and  $m$  is a constant fractional change with temperature. The respiration rates at  $15^\circ\text{C}$  ( $r_{15} = r_m$  and  $r_r$  for leaves and roots respectively) are decreasing linear functions of corrected organ biomass. This biomass dependence is included to account for the influence of growth respiration (see Patefield and Austin 1971). The alternative method calculates respiration as a constant proportion of gross photosynthesis, yielding growth respiration, plus a temperature-dependent rate of maintenance respiration. This temperature-dependent rate is calculated using Eq. (37).

Photosynthate is allocated to leaves and roots according to an allometric relationship between leaf weight and total weight. The photosynthetic production of a given day, allowing for respiration losses, is allocated such that the net increments in leaf and root

weight are consistent with that day's allometric ratio. This ratio is a function of total simulated weight for the previous day (Patefield and Austin 1971). The weight of either leaves or roots on a given day is calculated as the previous day's weight plus the growth increment (i.e., allocated photosynthate), times one minus the respiratory losses.

Simulated leaf and root weights agreed reasonably well with observed weights over a period of from 10 d to 110 d after sowing. Simulations in which respiration was calculated as a fixed proportion of photosynthesis (25%) fit observations slightly better. Also, leaf weight was more accurately predicted than root weight, particularly from 50 d after sowing. Observed weights were derived from potted seedlings grown in the open under closely managed conditions. It is not clear how well model predictions would fit observations from actual field conditions.

A model of seasonal dry weight growth for sugar beet was developed by Fick (1971); Fick, Williams, and Loomis (1973); and Fick, Williams, and Loomis (1975). The model, SUBGRO, is based on a hypothesis of hierarchical priorities for photosynthate partitioning. Photosynthesis, as a function of light, is modeled using the crop canopy model of Duncan et al. (1967; also see Sect. 1.1.3). Respiration is calculated as 25% of apparent photosynthesis at 25°C, adjusting for temperature effect (Thomas and Hill 1949; Nevins and Loomis 1970). Because SUBGRO concentrates on dry matter distribution, photosynthesis and respiration are treated rather simply.

In SUBGRO, various sinks are assigned priorities for the use of synthate or reserves. The model then establishes the use rates for these sinks. Sink priorities are based on physiological demand and proximity to the source of supply; the rankings are then converted to a quantitative scale of threshold concentrations. Details of this process can be found in Fick (1971) and Fick, Williams, and Loomis (1973). Rates of transfer of reserves are calculated from sink-specific maximum growth rates which are adjusted downward to account for limiting factors. Relative water content of the leaves and synthate reserve concentration are limiting factors. The model assumes

that external water supply and nutrients are not limiting. Only the most limiting factor is used to reduce the maximum growth rate. Fick (1971) provides details and derivations of the partitioning functions.

Initially, simulations underestimated field observations of the dry weights of various sinks. However, an adjustment in the calculation of leaf area from dry weight of tops to account for small top weights (Fick, Williams, and Loomis 1973) resulted in "excellent agreement" (Fick, Williams, and Loomis 1973, p. 415) with field results. Simulations and observations were compared over a 120-d period from 20 to 140 days after emergence. Although total storage root weight was accurately predicted, sucrose concentration was not. Simulation experiments predicting the effect of pruning on top:fibrous root ratios also resulted in patterns similar to observations.

#### 1.1.11 A Comment on the Diversity of the Crop Models

The crop models described above span a wide variety of assumptions, structures, and mathematical formulations. Some models are quite complex and involved (e.g., the SPAM cornfield model, Sect. 1.1.3); others are much simpler (e.g., the wheat model of Rickman, Ramig, and Allmaras 1975, Sect. 1.1.1), and still others strike some middle ground (e.g., the SOYMOD I soybean model, Sect. 1.1.5). The various models do exhibit some similarities. For example, the multilayered canopy and light interception approach of Monteith (1965) occurs in many models, with and without modifications. Respiration is frequently divided into growth and maintenance respiration, with  $Q_{10}$  temperature responses also involved. Nevertheless, the diversity of approaches and formulations is as striking, if not more so, than their shared, basic similarities.

Some of these differences might be ascribed to differences in the crops involved. However, most of the variation is more appropriately attributed to differences in objectives. Despite passing through our filter of models of crop growth involving photosynthesis and respiration, there still exist notable differences in the many aspects of crop growth which the models address or attempt to incorporate. Some focus on canopy architecture and microclimate

[e.g., the wheat and corn models of Sects. 1.1.1 and 1.1.2, and the Biscoe, Scott, and Monteith (1975) barley model, Sect. 1.1.4]. Kallis and Tooming (1974, Sect. 1.1.4), among others, wished to address the effects of photosynthesis and respiration on crop yield. Other models serve as syntheses and explorations of whole-plant physiology [e.g., the GLYCIM model, Sect. 1.1.5; COTCROP, Sect. 1.1.6; and the Ng and Loomis (1984) potato model, Sect. 1.1.7]. A result of these differences in objectives is that frequently models may lack various components of more general interest (e.g., the lack of respiration terms in the wheat models of Sect. 1.1.1), or they may become very involved, either in their treatment of microclimate or their treatment of physiology.

These observations are not intended as criticisms of the models themselves; there is much to be said for models that address specific objectives. However, our comments do illustrate some of the complications involved in incorporating existing crop models into models of seasonal CO<sub>2</sub> flux for regions dominated by agroecosystems. A new, or amalgamated, model may be necessary to meet the goals of the DOE Carbon Dioxide Research Division. Such a model should be applicable, with only parameter changes, to the majority of the principal agricultural crops. Consequently, it should be designed to have, as biomass compartments and fluxes, only those functional characteristics common to all plants and appropriate to the needs of modeling crop-level CO<sub>2</sub> fluxes. The model described in the next section is a step in the direction of dealing with some of these problems.

## 1.2 CANOPY: A General Crop Canopy-Photosynthesis Model

A variety of crop types might be involved in a regional consideration of agroecosystem carbon fluxes. Rather than implement a separate crop growth model for each crop, the needs of such a project might be more readily met by a general crop model. A single model capable of simulating carbon fluxes for a diversity of crop systems could represent considerable savings over implementing of multiple models. A multilayered canopy leaf energy budget-photosynthesis

model, CANOPY, has been developed by Terjung, Louie, and O'Rourke (1976); Terjung and O'Rourke (1980); and Band et al. (1981), illustrates the direction the development of a general crop model might take.

CANOPY is, as the name suggests, a model of canopy microclimate and photosynthesis. The model assumes a canopy with a leaf area index of 4.0 (typical of many field crops; see Band et al. 1981) and eight layers of horizontally arranged leaves. The short-wave radiation components of Monteith (1969) are modeled: direct radiation, diffuse reflected radiation, and diffuse sky radiation. The turbulent exchange coefficients (vertical exchange coefficients between canopy layers) for air temperature, vapor pressure, and wind velocity are assumed to be infinitely large (Sinclair, Murphy, and Knoerr 1976; see Sect. 1.1.3). Hence, only radiation varies in its distribution throughout the canopy. Further, CANOPY assumes optimal water and nutrient supplies, the result being that photosynthesis is driven only by climate (irradiance, relative humidity, wind speed, air temperature, and cloud cover).

The model emphasizes the simulation of leaf temperatures. A complex leaf energy budget is modeled using the methods of Gates and Papian (1971). (See also Terjung and O'Rourke 1980.) Leaf net photosynthesis for each layer is predicted after the leaf energy budget of each layer is determined. Net photosynthesis ( $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ ) is modeled as a forcing of the leaf energy budget according to a photosynthesis response 'curve.' This response 'curve' is defined by the response of net photosynthesis to absorbed solar radiation ( $\text{langley min}^{-1}$ ) and leaf temperature [ $^{\circ}\text{C}$ ]; Terjung, Louie, and O'Rourke 1976; Band et al. 1981]. The response 'curve' is actually a set of temperature-response curves, each curve of the set being designated by an irradiance level. The generality of CANOPY is incorporated into these net photosynthesis response curves. CANOPY includes three photosynthesis submodels, each with its own response curve set. The Model 1 curves are used to predict net photosynthesis for C4 crops (e.g., maize, sorghum, sugar cane), and Model 2 is used for C3 crops (i.e., the majority of agricultural crops: wheat, rice, soybeans, barley, oats, rye, potatoes, etc.). The third model represents

shade-tolerant C3 species (e.g., many woody species); consequently, the model can easily be applied to a variety of agricultural crops, provided that the assumption of a general C3 and C4 characterization of photosynthetic physiology is acceptable.

The computer model that describes CANOPY requires daily values for the environmental driving variables as input. These input data are converted to hourly and quarter-hourly data, and the model computes the leaf energy budgets at 15 min intervals. The model performs the proper integrations and generates daily net canopy photosynthetic rates ( $\text{mg CO}_2 \text{ dm}^{-2} \text{ d}^{-1}$ ). Given the appropriate seasonal input data, CANOPY can predict net photosynthesis over an entire growing season. The model does not predict respiration or crop growth.

Band et al. (1981) have applied CANOPY over a range of climatically diverse agricultural regions in California. Net photosynthesis was modeled over a 4-month growing season. The authors concluded that CANOPY was useful in defining areas of high- and low-potential photosynthetic activity, and the model predicted unique responses by each of the photosynthetic systems (Models 1, 2, and 3) to the seasonal forcing of California's diverse climate. There were no comparisons of field observations and simulation results.

CANOPY's generality is an important characteristic, but the model is not adequate to serve as the general crop growth model for relating global agriculture to atmospheric  $\text{CO}_2$ . Application of CANOPY to the problem of cropland-atmosphere  $\text{CO}_2$  exchange is hindered by the absence from the model of any consideration of respiration or crop growth. Additionally, the complex leaf energy budget submodel may be more detailed than is necessary for many applications. CANOPY is not the general crop model needed. However, the introduction of CANOPY's photosynthetic response curve strategy to a true crop growth model of the type reviewed in Sect. 1.1 might prove useful. Development of such a model should be a priority in biosphere-atmosphere  $\text{CO}_2$  research.

## 2. SEASONAL RELEASE OF CARBON DIOXIDE VIA DECOMPOSITION

The decomposition of standing dead, litter, and soil organic matter in agroecosystems releases  $\text{CO}_2$  to the atmosphere. This

release can be an important component of the seasonal exchange between cropland and atmosphere, particularly during the nongrowing season. However, we know of no models that were developed to deal explicitly with seasonal decomposition in agricultural systems. Parton et al. (1983) and Parton, Persson, and Anderson (1983) have developed a model (SOM) to simulate the long-term effects of cultivation on soil organic matter levels and crop yield. However, the temporal resolution of SOM is too coarse (one-year time steps) to deal with seasonal  $\text{CO}_2$  evolution. We are also unaware of any crop models which include decomposition processes. The crop growth models of Sect. 1.1 are limited to live plant carbon dynamics during the growing season. The barley carbon budget of Biscoe, Scott, and Monteith [(1975); see also Sect. 1.1.4] includes a soil microorganism respiration term; however, this flux is assumed to be constant and is estimated based on the mean difference between observed soil  $\text{CO}_2$  evolution and calculated (modeled) root respiration. This general deficiency might be partly alleviated by using decomposition models developed either for general purposes or for use in natural ecosystem models. The dynamics of decomposition in agroecosystems may differ from those in natural ecosystems, but the processes are probably sufficiently similar so that decomposition models developed for other purposes could be adapted (Coleman, Cole, and Elliott 1984). We will not review these decomposition models here. King and DeAngelis (1985) provide a brief review of compartment modeling of organic matter decomposition and review the treatment of decomposition in seasonal ecosystem-oriented models. General decomposition models can be found in Bunnell et al. (1977), Smith (1979, 1982), and McGill et al. (1981). The PHOENIX model of McGill et al. (1981) has apparently been used to explore some of the effects of management perturbations in grassland systems (Coleman, Cole, and Elliott 1984). The explicit modeling of seasonal decomposition in an agricultural crop system would be a welcome contribution to understanding the ecology of agroecosystems, and it is essential for estimating  $\text{CO}_2$  fluxes. The release of  $\text{CO}_2$  via decomposition must be simulated in any general crop land model developed for use in investigations of the exchange of  $\text{CO}_2$  between the atmosphere and regions dominated by agroecosystems.

### 3. EMPIRICAL DATA SOURCES FOR SEASONAL CARBON DIOXIDE FLUX

We have surveyed some of the relevant literature to compile empirical data on seasonal CO<sub>2</sub> fluxes from a variety of agroecosystems. These fluxes include those involving live plants and those from decomposing soil organic matter. The survey is not exhaustive, but it represents the type and resolution of data available and provides an introduction to the literature. The cited literature will often refer to additional sources of data. We have not included discussions of reports of data from laboratories (e.g., Crapo and Bowmer 1973; Silvius, Johnson, and Petus 1977), growth chambers (e.g., Snyder and Carlson 1978), or greenhouses (e.g., Mauney, Fry, and Guinn 1978). These types of data sets may prove useful in the development of seasonal CO<sub>2</sub> flux models for agricultural regions, but we decided to restrict this initial survey to field situations. We also have not included field data for isolated plant parts, such as inflorescences (e.g., Tieszen and Imbramba 1978) or fruiting bodies.

In the synopses which follow we give the geographic site of the data source (generally the nearest city); the literature citation; and, briefly, the type of data (e.g., photosynthesis, growth rate, or CO<sub>2</sub> concentration). The actual data are not presented here, although the approximate highs and lows of the seasonal fluxes are usually noted. Other data, such as seasonal temperature and solar radiation, are mentioned if available. Unless otherwise indicated, the unit-area terms appearing in the flux data refer to ground area. Leaf area is indicated by "LA." We have retained the original units used by the various data sources, in part to illustrate the variety of perspectives and spatio-temporal resolutions involved. To facilitate comparisons of the data, Table 3.1 provides a list of conversion factors needed to convert many of the data in the synopses to a common basis. However, conversions from flux per unit leaf area to flux per unit ground area are not possible without information on leaf area (e.g., leaf area index).

Table 3.1. Factors for converting the units included in the synopses of Sect. 3.0 to a common basis

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Phytomass

$$1 \text{ g dry matter m}^{-2} = 10 \text{ kg dry matter ha}^{-1}$$

$$1 \text{ g dry matter m}^{-2} = 0.01 \text{ t dry matter ha}^{-1}$$

$$1 \text{ g organic dry matter} = 0.45 \text{ g C} = 1.5 \text{ g CO}_2$$

$$1 \text{ g CO}_2 = 0.65 \text{ g organic dry matter} = 0.30 \text{ g C}$$

Gas exchange

$$1 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} = 0.044 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$$

$$1 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1} = 22.7 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$$

$$1 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1} = 0.028 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$$

$$1 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1} = 0.63 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$$

$$1 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1} = 0.278 \text{ mg m}^{-2} \text{ s}^{-1}$$

CO<sub>2</sub> concentration

$$1 \text{ } \mu\text{L CO}_2 \text{ L}^{-1} = 1 \text{ ppm}$$

$$1 \text{ mg CO}_2 \text{ L}^{-1} = 508.8 \text{ } \mu\text{L L}^{-1}$$

$$1\% \text{ CO}_2 \text{ by volume} = 10,000 \text{ } \mu\text{L L}^{-1}$$


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## 3.1 Wheat Field

Authors: Connor and Cartledge (1971)  
 Site: Archerfield, Queensland, Australia  
 Type of data: Periodic measurements of daily photosynthesis  
 for two varieties of wheat (July-November 1969)  
 Seasonal high: Olympic --- 24 October -  $341.5 \text{ mg CO}_2 \text{ dm}^{-2} \text{ d}^{-1}$   
 Chile 1B --- 21 October -  $374.7 \text{ mg CO}_2 \text{ dm}^{-2} \text{ d}^{-1}$   
 Seasonal low: Olympic --- 12 September -  $39.2 \text{ mg CO}_2 \text{ dm}^{-2} \text{ d}^{-1}$   
 Chile 1B --- 4 August -  $65.4 \text{ mg CO}_2 \text{ dm}^{-2} \text{ d}^{-1}$   
 Other data: Seasonal leaf area index and solar radiation

Authors: Fischer et al. (1981)  
 Site: Ciudad Obregon, Mexico  
 Type of data: Weekly measurements of leaf photosynthesis from  
 20 January to 30 April 1975  
 Seasonal high: late February ---  $21 \text{ mg CO}_2 \text{ dm}^{-2} \text{ LA h}^{-1}$   
 Seasonal low: late April ---  $7 \text{ mg CO}_2 \text{ dm}^{-2} \text{ LA h}^{-1}$   
 Other data: Seasonal leaf conductance, leaf permeability,  
 green area index, and total dry weight

Authors: Gent and Kiyomoto (1985)  
 Site: Mt. Carmel, Connecticut  
 Type of data: Seasonal variation of canopy net carbon dioxide  
 exchange (NCE), daily integrated NCE (DNCE),  
 dark respiration (Rd), and dry weight of shoots  
 and heads from 20 March to 30 June 1983 for two  
 wheat varieties (Honor and Houser)

Seasonal high: 1982  
     NCE --- mid-June -  $1.97 \text{ mg CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$   
     Rd --- mid-June -  $0.617 \text{ mg CO}_2 \text{ kg}^{-1} \text{ s}^{-1}$   
 1983  
     NCE --- late May -  $1.8 \text{ mg CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$   
     DNCE --- mid-May -  $51 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$   
     Rd --- mid-June -  $-0.28 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$

- Seasonal low: 1982  
 NCE -- mid-August -  $0.90 \text{ mg CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$   
 Rd -- mid-August -  $0.114 \text{ mg CO}_2 \text{ kg}^{-1} \text{ s}^{-1}$
- 1983  
 NCE -- late June -  $0 \text{ mg CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$   
 DNCE -- late June -  $0 \text{ mg CO}_2 \text{ m}^{-2} \text{ d}^{-1}$   
 Rd -- late June -  $0 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
- Note: Values above are for the Honor variety; there was little difference between varieties in seasonal highs and lows. Dark respiration values were reported on a per unit weight basis for 1982 and a per unit area basis for 1983.
- Authors: Havelka, Wittenbach, and Boyle (1984)  
 Site: Newark, Delaware  
 Type of data: Weekly measurements of flag leaf apparent photosynthesis under control  $\text{CO}_2$  concentration ( $340 \text{ } \mu\text{L/L}$ ) and at high  $\text{CO}_2$  levels ( $1200 \text{ } \mu\text{L/L}$ ) for a 8 week period surrounding anthesis (17 May)
- Seasonal high: Control  $\text{CO}_2$   
 1 week before anthesis -  $19 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$   
 High  $\text{CO}_2$   
 1 week after anthesis -  $27 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$
- Seasonal low: Control  $\text{CO}_2$   
 5 weeks after anthesis -  $0 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$   
 High  $\text{CO}_2$   
 5 weeks after anthesis -  $1 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$
- Other data: Changes in specific leaf weight, chlorophyll,
- Authors: Johnson, Witters, and Ciha (1981)  
 Site: Lind, Washington  
 Type of data: Periodic measurements of apparent photosynthesis for approximately 30 d before and after anthesis (approx. 30 May 1977)

Seasonal high: Mornings  
 19 d before anthesis -  $5 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$   
 Afternoons  
 5 d after anthesis -  $4 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$

Seasonal low: Mornings  
 22 d after anthesis -  $0.5 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$   
 Afternoons  
 21 d after anthesis -  $0.0 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$

Other data: Time course of leaf-area index (LAI), tiller density,  
 and evapotranspiration

Authors: McCraig and Clark (1982)  
 Site: Swift Current, Saskatchewan, Canada  
 Type of data: Weekly measurements of standing crop of plant  
 tissues for a 65 d period beginning 25 d  
 after planting on 5 May 1978 and 14 May 1979

Seasonal high: 1978  
 Stem  
 73-80 d after seeding -  $4200 \text{ to } 4600 \text{ kg ha}^{-1}$   
 Green leaf  
 59 days after seeding -  $1500 \text{ to } 2000 \text{ kg ha}^{-1}$

1979  
 Stem  
 73-80 d after seeding -  $2600 \text{ to } 3500 \text{ kg ha}^{-1}$   
 Green leaf  
 51 d after seeding -  $1100 \text{ to } 1950 \text{ kg ha}^{-1}$

Note: Seasonal values varied with variety of wheat

Authors: Morgan and Willis (1983)  
 Site: Fort Collins, Colorado  
 Type of data: Diurnal patterns of apparent canopy  
 photosynthesis over growing season by irrigation  
 treatment

- Seasonal high: Weekly irrigation  
 18 June -  $8 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$   
 Biweekly irrigation  
 18 June -  $5.5 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$
- Seasonal low: Weekly irrigation  
 6 July -  $2.0 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$   
 Biweekly irrigation  
 9 July -  $0.5 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$
- Note: Values given are maximum values recorded on indicated dates
- Other data: Seasonal diurnal patterns for solar radiation, canopy temperature, evapotranspiration, flag leaf water potential, and stomatal resistance
- Author: Osman (1971)
- Site: Sutton Bonington, Loughborough, England
- Type of data: Weekly measurements of gross photosynthesis (Pg) and dark respiration (Rd) over two growing seasons (1966, planted 10 March 1966; and 1967: planted 31 October 1966)
- Seasonal high: 1966  
 Pg -- 9-10th week -  $224 \text{ g CH}_2\text{O m}^{-2} \text{ week}^{-1}$   
 Rd -- 12-15th week -  $88 \text{ g CH}_2\text{O m}^{-2} \text{ week}^{-1}$   
 1967  
 Pg -- 18-19th week -  $277 \text{ g CH}_2\text{O m}^{-2} \text{ week}^{-1}$   
 Rd -- 17-18th week -  $183 \text{ g CH}_2\text{O m}^{-2} \text{ week}^{-1}$
- Seasonal low: 1966  
 Pg -- 17-18th week -  $32 \text{ g CH}_2\text{O m}^{-2} \text{ week}^{-1}$   
 Rd -- 17-18th week -  $16 \text{ g CH}_2\text{O m}^{-2} \text{ week}^{-1}$   
 1967  
 Pg -- 21-22nd week -  $156 \text{ g CH}_2\text{O m}^{-2} \text{ week}^{-1}$   
 Rd -- 21-22nd week -  $83 \text{ g CH}_2\text{O m}^{-2} \text{ week}^{-1}$
- Other data: Measurements of photosynthesis and respiration on a  $\text{mm CO}_2 \text{ cm}^{-2} \text{ LA h}^{-1}$  basis; leaf resistance parameterization

Authors: Pearman and Garratt (1973)  
 Site: Rutherglen, Victoria, Australia  
 Type of data: Diurnal patterns of CO<sub>2</sub> gradient (CO<sub>2</sub> at 2 m - CO<sub>2</sub> at 1 m) for July, September, and November 1971  
 Seasonal high: Noon -- September - +2 ppm CO<sub>2</sub>  
                   Midnight -- July - (-4) ppm CO<sub>2</sub>  
 Seasonal low: Noon -- June - +0.5 ppm CO<sub>2</sub>  
                   Midnight -- September - (-13) ppm CO<sub>2</sub>

### 3.2 Rice Paddy

Authors: Kamiyama and Horie (1975)  
 Sites: Sendai and Konosu, Japan  
 Type of data: Weekly measurements of net assimilation rate (NAR) and relative growth rate (RGR) over growing season (June-November) for 1967-1970  
 Seasonal high: Sendai  
                   NAR --- early June 1967  
                                   0.26 g dw dm<sup>-2</sup> LA d<sup>-1</sup>  
                   RGR --- late July 1967 - 25% d<sup>-1</sup>  
                   Konosu  
                   NAR --- late August 1967  
                                   0.2 g dw dm<sup>-2</sup> LA d<sup>-1</sup>  
                   RGR --- early August 1970 - 25% d<sup>-1</sup>  
 Seasonal low: Sendai  
                   NAR --- November 1968  
                                   0.02 g dw dm<sup>-2</sup> LA d<sup>-1</sup>  
                   RGR --- November 1968 - 1% d<sup>-1</sup>  
                   Konosu  
                   NAR --- late September 1970  
                                   0.05 g dw dm<sup>-2</sup> LA d<sup>-1</sup>  
                   RGR --- early October 1967 - 5% d<sup>-1</sup>  
 Note: Values presented here are absolute highs and lows; seasonal values varied from year to year

- Other data: Seasonal temperature over growing season; seasonal trends of NAR (60-d moving average at several sites; correlations between NAR and solar radiation
- Author: Kanda (1975)
- Site: Akita, Japan
- Type of data: Time course of net assimilation rate (NAR), crop growth rate (CGR), and leaf area index over 13 week growth period (average for 5 years)
- Seasonal high: NAR -- 6 weeks before heading  
 $9 \text{ g dw dm}^{-2} \text{ LA d}^{-1}$   
 CGR -- 1.5 weeks before heading  
 $15 \text{ g m}^{-2} \text{ d}^{-1}$
- Seasonal low: NAR -- 4.5 weeks after heading  
 $2.5 \text{ g dw dm}^{-2} \text{ LA d}^{-1}$   
 CGR -- 7 weeks before heading  
 $4 \text{ g m}^{-2} \text{ d}^{-1}$
- Authors: Lafitte and Travis (1984)
- Site: Davis, California
- Type of data: 'Weekly' measurements of photosynthesis for six rice genotypes for a period from 9 to 21 weeks after planting on 5 May 1981
- Seasonal high: 13 weeks -  $0.54\text{--}0.75 \text{ mg CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$
- Seasonal low: 21 weeks -  $0.1\text{--}0.14 \text{ mg CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$
- Note: Seasonal values varied with variety of rice
- Other data: Time course of sugar and starch;  $\text{CO}_2$  uptake per unit leaf weight and unit leaf protein at two weeks before and after heading

Author: Uchijima (1975)  
 Sites: Akita, Konosu, and Chikugo, Japan  
 Type of data: Seasonal course of standing crop (SC), crop growth rate (CGR), and leaf area index over growing season (May-October)  
 Seasonal high: Akita  
                   CGR -- July -  $25 \text{ g m}^{-2} \text{ d}^{-1}$   
                   SC -- September -  $1250 \text{ g m}^{-2}$   
                   Konosu  
                   CGR -- August -  $19 \text{ g m}^{-2} \text{ d}^{-1}$   
                   SC -- October -  $1400 \text{ g m}^{-2}$   
                   Chikugo  
                   CGR -- July-August -  $22 \text{ g m}^{-2} \text{ d}^{-1}$   
                   SC -- September-October -  $1600 \text{ g m}^{-2}$   
 Other data: Seasonal temperature and solar radiation

### 3.3 Corn Field

Author: Allen (1971)  
 Site: Ithaca, New York  
 Type of data: Seasonal course of daytime average, nighttime minimum, and nighttime maximum  $\text{CO}_2$  concentration (July-December 1962 and January-June 1964)  
 Seasonal high: Daytime average -- late winter - 339 ppm  $\text{CO}_2$   
 Seasonal low: Daytime average -- late summer - 291 ppm  $\text{CO}_2$   
 Other data: Nocturnal  $\text{CO}_2$  concentration as a function of a temperature-wind speed parameter

Author: Duncan et al. (1967)  
 Site: Davis, California  
 Type of data: Biweekly measurements of dry matter production from 30 d after planting to maturity, at three densities

- Seasonal high: 7,000 plants/acre -- 10 August -  $31 \text{ g m}^{-2} \text{ d}^{-1}$   
 20,000 plants/acre -- 31 July -  $32 \text{ g m}^{-2} \text{ d}^{-1}$   
 56,000 plants/acre -- 18 July -  $39 \text{ g m}^{-2} \text{ d}^{-1}$
- Seasonal low: 7,000 plants/acre -- 5 July -  $5 \text{ g m}^{-2} \text{ d}^{-1}$   
 20,000 plants/acre -- 5 July -  $14 \text{ g m}^{-2} \text{ d}^{-1}$   
 56,000 plants/acre -- 25 August -  $20 \text{ g m}^{-2} \text{ d}^{-1}$
- Authors: Kamiyama and Horie (1975)
- Site: Morioka, Japan
- Type of data: Weekly measurements of net assimilation rate (NAR) and relative growth rate (RGR) over growing seasons for 1967 to 1970
- Seasonal high: NAR -- mid-July 1967 -  $0.23 \text{ g dw dm}^{-2} \text{ LA d}^{-1}$   
 RGR -- late August 1970 -  $28\% \text{ d}^{-1}$
- Seasonal low: NAR -- early October 1968 -  $0.03 \text{ g dw dm}^{-2} \text{ LA d}^{-1}$   
 RGR -- early October 1968 -  $4\% \text{ d}^{-1}$
- Note: Values reported here are absolute highs and lows; seasonal values varied from year to year
- Other data: Seasonal temperature over growing season
- Author: Kanada (1975)
- Site: Sapporo, Japan
- Type of data: Time course of net assimilation rate (NAR), crop growth rate (CGR), and leaf area index over 12-week growth period (average for 5 years)
- Seasonal high: NAR -- 4.5 weeks before silking  
 $9 \text{ g dw dm}^{-2} \text{ LA d}^{-1}$   
 CGR -- 1.5 weeks before silking  
 $20 \text{ g m}^{-2} \text{ d}^{-1}$
- Seasonal low: NAR -- 4.5 weeks after silking  
 $4 \text{ g dw dm}^{-2} \text{ LA d}^{-1}$   
 CGR -- 4.5 weeks after silking  
 $5 \text{ g m}^{-2} \text{ d}^{-1}$

- Author: Snyder (1974)  
 Site: East Lansing, Michigan  
 Type of data: Net assimilation rate (NAR) and relative growth rate (RGR) for 113 d after emergence (planted on 18 May)  
 Seasonal high: NAR --- 0-15 d - 5.25 mg dw cm<sup>-2</sup> LA d<sup>-1</sup>  
                   RGR -- 0-15 d - 19.5%  
 Seasonal low:  NAR -- 71-92 d - 0.78 mg dw cm<sup>-2</sup> LA d<sup>-1</sup>  
                   RGR -- 71-92 d - 1.4%  
 Other data:  Seasonal radiation, daylight hours, and temperature; seasonal leaf area, total and root biomass on a leaf area and per plant basis
- Author: Uchijima (1970)  
 Site: Tokyo, Japan  
 Type of data: Ten-day interval measurements of net CO<sub>2</sub> fixation (Pn), downward flux (Ph), and soil flux (Ps) during the growing season of 1966  
 Seasonal high: Pn -- 20 August - -8.90 mg CO<sub>2</sub> cm<sup>-2</sup> d<sup>-1</sup>  
                   Ph -- 20 August - -7.07 mg CO<sub>2</sub> cm<sup>-2</sup> d<sup>-1</sup>  
                   Ps -- 20 August - 1.83 mg CO<sub>2</sub> cm<sup>-2</sup> d<sup>-1</sup>  
 Seasonal low:  Pn -- 26 July - -4.98 mg CO<sub>2</sub> cm<sup>-2</sup> d<sup>-1</sup>  
                   Ph -- 26 July - -4.13 mg CO<sub>2</sub> cm<sup>-2</sup> d<sup>-1</sup>  
                   Ps -- 9 August - 0.82 mg CO<sub>2</sub> cm<sup>-2</sup> d<sup>-1</sup>  
 Note: Daily values are for daylight hours only  
 Other data: Diurnal pattern of CO<sub>2</sub> concentration above and within corn canopy for 1966 growing season (diurnal extremes of 245 ppm CO<sub>2</sub> at midday and 350 ppm CO<sub>2</sub> at 1900 h on 8 August); 'seasonal' short-wave radiation above crop

- Author: Uchijima (1975)  
 Sites: Sapporo, Morioka, and Tanashi, Japan  
 Type of data: Seasonal course of crop growth rate (CGR), standing crop (SC), and leaf area index over growing season (June-September)  
 Seasonal high: Sapporo  
     CGR -- August -  $21 \text{ g m}^{-2} \text{ d}^{-1}$   
     SC -- October -  $1700 \text{ g m}^{-2}$   
     Morioka  
         CGR -- August -  $31 \text{ g m}^{-2} \text{ d}^{-1}$   
         SC -- September -  $1200 \text{ g m}^{-2}$   
     Tanashi  
         CGR -- July-August -  $35 \text{ g m}^{-2} \text{ d}^{-1}$   
         SC -- August -  $1400 \text{ g m}^{-2}$
- Authors: Vietor, Ariyanayagam, and Musgrave (1974)  
 Site: Ellis Hollow, New York  
 Type of data: Apparent photosynthetic rates measured at various developmental stages after emergence (in May) for a variety of leaf positions and strains  
 Seasonal high: 77 d after emergence -  $65.5 \text{ mg CO}_2 \text{ dm}^{-2} \text{ LA h}^{-1}$   
 Seasonal low: 117 d after emergence -  $33.7 \text{ mg CO}_2 \text{ dm}^{-2} \text{ LA h}^{-1}$   
 Note: Values reported here are plant means  
 Other data: Canopy photosynthetic rate as a function of irradiance, plant age, and strain
- Authors: De Wit, Brouwer, and Penning de Vries (1970), and de Wit et al. (1978)  
 Sites: Ames, Iowa; Davis, California; Flevoland and Wageningen, The Netherlands  
 Type of data: Standing crop of corn shoots over growing season (May-October)

Seasonal high: Davis  
 20 October - 12,752-20,619 kg shoot ha<sup>-1</sup>  
 Ames  
 17 September - 13,258-22,813 kg shoot ha<sup>-1</sup>  
 Flevoland  
 11-13 September - 12,012-17,095 kg shoot ha<sup>-1</sup>  
 Wageningen  
 21 September - 20,910-21,630 kg shoot ha<sup>-1</sup>

Note: Standing crop varied with planting density at Ames and Davis, with year at Flevoland, and with variety at Wageningen

Other data: Seasonal leaf area index (de Wit et al. 1978); environmental effects on gas exchange

### 3.4 Barley Field

Authors: Biscoe, Scott, and Monteith (1975)  
 Site: Nottingham, England  
 Type of data: Weekly measurements of CO<sub>2</sub> uptake, net CO<sub>2</sub> fixation, gross photosynthesis, dark respiration, and light respiration (10 May to 26 July 1972); weekly measurements of total crop respiration, fixed carbon, and standing crop (10 May to 26 July 1972); weekly measurements of standing crop by tissue type (24 April to 26 July); weekly measurements of root weight and root respiration; weekly measurements of CO<sub>2</sub> release from the soil (17 May to 19 July 1972), and soil microorganism respiration (10 May to 26 July 1972)

Seasonal high: Standing crop  
 July - 1605 g C m<sup>-2</sup>  
 Net photosynthesis  
 31 May to 7 June - 202 g CO<sub>2</sub> m<sup>-2</sup> week<sup>-1</sup>  
 Total respiration  
 12-19 July - 200 g CO<sub>2</sub> m<sup>-2</sup> week<sup>-1</sup>

- Seasonal low: Standing crop  
 10-17 May - 341 g C m<sup>-2</sup>  
 Net photosynthesis  
 19-26 July - 26 g CO<sub>2</sub> m<sup>-2</sup> week<sup>-1</sup>  
 Total Respiration  
 24-31 May - 100 g CO<sub>2</sub> m<sup>-2</sup> week<sup>-1</sup>
- Other data: Weekly solar radiation and temperature  
 hourly rates of net CO<sub>2</sub> fixation  
 (14-21 June 1972); CO<sub>2</sub> fixation as a function of  
 solar radiation
- Authors: Biscoe, Gallagher, et al. (1975b)  
 Site: Nottingham, England  
 Type of data: Two-day interval measurements of green area  
 index (20 June to  
 20 July), dry weight (21 June  
 to 2 August), and diurnal variation in photosynthesis,  
 by plant part (30 June and 14 July).
- Authors: Fukai, Koh, and Kumura (1976)  
 Site: Tokyo, Japan  
 Type of data: Seasonal net photosynthesis (Pn), dark  
 respiration (Rd) during the night, standing crop  
 (SC), and crop growth rate (December-May 1968-69,  
 1969-70)
- Seasonal high: Pn -- 4 May 1970 - 35.5 g dw m<sup>-2</sup> d<sup>-1</sup>  
 Rd -- 23 April 1970 - 5.97 g dw m<sup>-2</sup> d<sup>-1</sup>  
 SC -- 10 June 1970 - 1100 g m<sup>-2</sup>
- Seasonal low: Pn -- 5 December 1969 - 0.75 g dw m<sup>-2</sup> d<sup>-1</sup>  
 Rd -- 9 February 1969 - 0.18 g dw m<sup>-2</sup> d<sup>-1</sup>  
 SC -- November - 0.0 g m<sup>-2</sup>
- Other data: Seasonal leaf area index, organ weight as a percentage  
 of total dry weight, solar radiation,  
 temperature; seasonal changes in the relationship  
 between net photosynthesis and solar energy

Authors: Monteith, Szeic, and Yabuki (1964)  
 Site: Harpenden, Hertfordshire, England  
 Type of data: Weekly measurements of dry weight assimilation  
 (June-July 1963); 15-d interval measurements of  
 average CO<sub>2</sub> flux from cropped and fallow soil  
 (June-August 1963)  
 Seasonal high: Assimilation  
                   mid-June - 34 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>  
                   Soil flux  
                   Cropped -- early July - 10.5 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>  
                   Fallow -- late July - 9.5 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>  
 Seasonal low: Assimilation  
                   Early June - 7 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>  
                   Soil flux  
                   Cropped -- late August - 4.5 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>  
                   Fallow -- late August - 5.5 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>  
 Other data: Soil CO<sub>2</sub> flux related to soil temperature and  
 soil moisture

### 3.5 Soybean Field

Authors: Boon-Long, Egli, and Leggett (1983)  
 Site: Lexington, Kentucky  
 Type of data: Periodic measurements of photosynthesis of last  
 fully expanded leaves over a 55 d reproductive  
 period after planting on 31 May 1978 and 30 May  
 1979  
 Seasonal high: 1978  
                   75 d after planting - 25 mg CO<sub>2</sub> dm<sup>-2</sup> LA h<sup>-1</sup>  
                   1979  
                   88 d after planting - 48-50 mg CO<sub>2</sub> dm<sup>-2</sup> LA h<sup>-1</sup>

- Seasonal low: 1978  
 111 d after planting -  $0.7 \text{ mg CO}_2 \text{ dm}^{-2} \text{ LA h}^{-1}$   
 1979  
 103-109 d after planting -  $0 \text{ mg CO}_2 \text{ dm}^{-2} \text{ LA h}^{-1}$
- Other data: Seasonal leaf nitrogen and protein; relationship  
 between  $\text{CO}_2$  uptake and soluble protein
- Authors: Curry, Baker, and Streeter (1975)  
 Site: Wooster, Ohio  
 Type of data: Periodic measurements of standing crop over a  
 117 d period following emergence in June 1972  
 Seasonal high: 100-117 d -  $900 \text{ g m}^{-2}$
- Authors: Ford, Shibles, and Green (1983)  
 Site: Ames, Iowa  
 Type of data: Biweekly measurements of standing crop from  
 31 July to 9 September for 1979 and 1980  
 Seasonal high: 1979 --  $0.89\text{--}0.91 \text{ kg m}^{-2}$   
 1980 --  $1.09\text{--}1.19 \text{ kg m}^{-2}$   
 Note: Values varied with varieties differing in the  
 rate of photosynthesis
- Authors: Havelka et al. (1984) and Ackerson, Havelka, and  
 Boyle (1984)  
 Site: Newark, Delaware  
 Type of data: Periodic measurements of photosynthesis at  
 control ( $321 \text{ uL CO}_2 \text{ L}^{-1}$ ) and enriched  
 ( $1232 \text{ uL CO}_2 \text{ L}^{-1}$ )  $\text{CO}_2$  levels over an 80-d period,  
 beginning 40 d after planting in mid-June 1982  
 Seasonal high: Control  $\text{CO}_2$   
 60 d after planting -  $1 \text{ mg CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$   
 High  $\text{CO}_2$   
 62 d after planting -  $1.4 \text{ mg CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$

- Seasonal low: Control CO<sub>2</sub>  
 115 d after planting - 0.2 mg CO<sub>2</sub> m<sup>-2</sup> LA s<sup>-1</sup>  
 High CO<sub>2</sub>  
 115 d after planting - 0.25 mg CO<sub>2</sub> m<sup>-2</sup> LA s<sup>-1</sup>
- Other data: Seasonal trends in leaf conductance, chlorophyll, protein, protease, abscisic acid, carbohydrates, and dry weight
- Authors: Ingram et al. (1981)  
 Site: Quincy, Florida  
 Type of data: Weekly measurements of net photosynthesis (Pn), dark respiration (Rd), and soil CO<sub>2</sub> efflux (SCER) for August-October 1979.
- Seasonal high: Pn -- early September - 60 mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup>  
 Rd -- early September - 11 mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup>  
 SCER -- late August - 8 mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup>
- Seasonal low: Pn -- late October - 5 mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup>  
 Rd -- late October - 2 mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup>  
 SCER -- mid-October - 2 mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup>
- Other data: Effects of protection from defoliating insects; seasonal leaf area index, leaf weight, specific leaf weight, and midday light interception; canopy photosynthesis light response curves over time
- Authors: Kamiyama and Horie (1975)  
 Site: Kumamoto, Japan  
 Type of data: Weekly estimates of net assimilation rate (NAR) and relative growth rate (RGR) over growing seasons (May-October) of 1967 to 1970
- Seasonal high: NAR -- late May and early August 1967  
 0.18 g dw dm<sup>-2</sup> LA d<sup>-1</sup>  
 RGR -- mid-August 1969 - 22% d<sup>-1</sup>

Seasonal low: NAR -- late June 1970 -  $0.04 \text{ g dw dm}^{-2} \text{ LA d}^{-1}$   
 RGR -- late October 1967 -  $8\% \text{ d}^{-1}$

Note: Values reported here are absolute highs and lows;  
 seasonal values varied from year to year

Other data: Seasonal temperature over growing season

Author: Kanada (1975)  
 Site: Tanashi, Japan  
 Type of data: Time course of net assimilation rate (NAR),  
 crop growth rate (CGR), and leaf area index over  
 12 week growth period (average for 5 years)

Seasonal high: NAR  
 1.5 weeks before top-most leaf expansion  
 $6 \text{ g dw dm}^{-2} \text{ LA d}^{-1}$   
 CGR  
 1.5 weeks after top-most leaf expansion  
 $10 \text{ g m}^{-2} \text{ d}^{-1}$

Seasonal low: NAR  
 4.5 weeks after top-most leaf expansion  
 $1 \text{ g dw dm}^{-2} \text{ LA d}^{-1}$   
 CGR  
 4.5 weeks before top-most leaf expansion  
 $2 \text{ g m}^{-2} \text{ d}^{-1}$

Authors: Secor, Shibles, and Stewart (1983)  
 Site: Ames, Iowa  
 Type of data: Periodic measurements of apparent  
 photosynthesis (AP) and dark respiration  
 (Rd) for leaflets at nodes 12 and 15  
 over a 50 d period after planting on  
 25 May 1979

## Seasonal high: Node 12

AP -- 87 d after planting  
 $1.9 \mu\text{mol CO}_2 \text{ cm}^{-2} \text{ LA s}^{-1}$

Rd -- 85 d after planting  
 $0.26 \mu\text{mol CO}_2 \text{ cm}^{-2} \text{ LA s}^{-1}$

## Node 15

AP -- 84 d after planting  
 $2.6 \mu\text{mol CO}_2 \text{ cm}^{-2} \text{ LA s}^{-1}$

Rd -- 84 d after planting  
 $0.36 \mu\text{mol CO}_2 \text{ cm}^{-2} \text{ LA s}^{-1}$

## Seasonal low: Node 12

AP -- 109 d after planting  
 $0.2 \mu\text{mol CO}_2 \text{ cm}^{-2} \text{ LA s}^{-1}$

Rd -- 107 d after planting  
 $0.1 \mu\text{mol CO}_2 \text{ cm}^{-2} \text{ LA s}^{-1}$

## Node 15

AP -- 107 d after planting  
 $0.4 \mu\text{mol CO}_2 \text{ cm}^{-2} \text{ LA s}^{-1}$

Rd -- 106 d after planting  
 $0.18 \mu\text{mol CO}_2 \text{ cm}^{-2} \text{ LA s}^{-1}$

Other data: Seasonal changes in leaflet area, specific leaf weight, pod dry weight, diffusive resistance, chlorophyll, protein, and RuBPCase

Authors: Seddigh and Jolliff (1984)

Site: Corvallis, Oregon

Type of data: Diurnal patterns of  $\text{CO}_2$  exchange on three sampling dates during the summers of 1981 and 1982 and the effect of night temperature on those patterns (controls are reported here)

Seasonal high: 1981 -- 30 July -  $17.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$   
 1982 -- 29 July -  $21.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$

Seasonal low: 1981 -- 27 August -  $11.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$   
 1982 -- 27 August -  $9.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ LA s}^{-1}$

- Note: Values are means for hourly values and replications
- Other data: Stomatal conductance and transpiration for the same sampling dates
- Author: Uchijima (1975)
- Sites: Tokachi, Tanashi, and Kumamoto, Japan
- Type of data: Seasonal course of standing crop (SC), crop growth rate (CGR), and leaf area index over the growing season (May-October)
- Seasonal high: Tokachi  
                   CGR -- August -  $15 \text{ g m}^{-2} \text{ d}^{-1}$   
                   SC -- October -  $750 \text{ g m}^{-2}$
- Tanashi  
                   CGR -- August -  $17 \text{ g m}^{-2} \text{ d}^{-1}$   
                   SC -- September -  $750 \text{ g m}^{-2}$
- Kumamoto  
                   CGR -- June-July -  $12 \text{ g m}^{-2} \text{ d}^{-1}$   
                   SC -- August -  $800 \text{ g m}^{-2}$
- Other data: Seasonal temperature and solar radiation
- Authors: Wittenbach et al. (1980)
- Site: Newark, Delaware
- Type of data: Weekly measurements of leaf photosynthesis for 10 weeks after flowering during the 1st week in August 1978
- Seasonal high: Week 1 -  $35 \text{ mg CO}_2 \text{ dm}^{-2} \text{ LA h}^{-1}$
- Seasonal low: Week 10 -  $0 \text{ mg CO}_2 \text{ dm}^{-2} \text{ LA h}^{-1}$
- Other data: Seasonal specific leaf weight, leaf starch, leaf chlorophyll, leaf protein, and leaf resistance

### 3.6 Cotton Field

- Authors: Gutierrez et al. (1984)
- Site: Londrina, Parana, Brazil

Type of data: Measurements of dry matter standing crop for cotton foliage, stem and root, and fruit from November 1982 to March 1983

Seasonal high: Foliage  
 January - 75 g/(4 plants)  
 Stem and root  
 January-February - 180 g/(4 plants)  
 Fruit  
 March - 200 g/(4plants)

Other data: Seasonal solar radiation, temperature, and degree-days over growing season

Authors: Hesketh, Baker, and Duncan (1971)

Site: Mississippi State, Mississippi

Type of data: Daily measurements of cotton square, boll, and leaf respiration over a 50-d period

Seasonal high: Square -- 8 d - 13.5 mg CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>  
 Boll -- 5 d - 9.0 mg CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>  
 Leaf -- 10 d - 12.0 mg CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>

Seasonal low: Square -- 20 d - 7.5 mg CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>  
 Boll --- 40 d - 1.5 mg CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>  
 Leaf --- 30 d - 2.5 mg CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>

Other data: Leaf, square, and boll weight over study period

Authors: Ibrahim and Buxton (1981)

Site: Tucson, Arizona

Type of data: Periodic measurements of plant weight from 42-60 d after planting on 3 May 1975 and 14-56 d after planting on 2 May 1976

Seasonal high: 1975 -- 60 d after planting - 32 g plant<sup>-1</sup>  
 1976 -- 56 d after planting - 32 g plant<sup>-1</sup>

Other data: Time course of leaf area, stem weight, and leaf weight

Authors: McKinion, Hesketh, and Baker (1974)  
 Site: Mississippi State, Mississippi  
 Type of data: Plant weight over a 140 d period following emergence  
 Seasonal high: 140 d after emergence -  $90 \text{ g CH}_2\text{O plant}^{-1}$

Authors: Pegelow et al. (1977)  
 Site: Tuscon, Arizona  
 Type of data: Seasonal (July-August) measurements of aboveground biomass  
 Seasonal high: 26 July -  $1683 \text{ g m}^{-2}$

### 3.7 Oat Field

Author: Lundegardh (1927)  
 Site: Stockholm, Sweden  
 Type of data: Measurements of soil respiration and  $\text{CO}_2$  concentration 4 m above and 15 cm below the soil surface over the period 19 June to 13 September 1923  
 Seasonal high: Soil respiration  
                   13 September -  $0.540 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$   
                    $\text{CO}_2$  concentration  
                   Aboveground --- 4 September -  $0.625 \text{ mg CO}_2 \text{ L}^{-1}$   
                   Belowground --- 13 September - 1.26 vol %  
 Seasonal low: Soil respiration  
                   24 July -  $0.370 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$   
                    $\text{CO}_2$  concentration  
                   Aboveground -- 24 July -  $0.522 \text{ mg CO}_2 \text{ L}^{-1}$   
                   Belowground -- 29 June - 0.39 vol %  
 Other data: Time course of temperature and rainfall for the sampling period

Authors: McCraig and Clarke (1982)  
 Site: Swift Current, Saskatchewan, Canada  
 Seasonal high: Weekly measurements of plant tissue dry weights  
 for a 60 d period beginning 25 d after  
 seeding on 5 May 1978 and 14 May 1979  
 Seasonal high: 1978  
                   Green leaf -- 65 d after seeding  
   2000-2100 kg ha<sup>-1</sup>  
 Seasonal high: Stem           -- 65 d after seeding  
   4500-5000 kg ha<sup>-1</sup>  
                   1979  
                   Green leaf -- 52 d after seeding  
   1600 kg ha<sup>-1</sup>  
                   Stem           -- 65 d after seeding  
   2400-3000 kg ha<sup>-1</sup>  
 Note: Values varied with variety of oats

### 3.8 Potato Field

Authors: Moorby and Milthorpe (1975)  
 Site: Midlands, England and M. I. A. , Australia  
 Type of data: Seasonal course of tuber standing crop  
 Seasonal high: Australia -- December - 55 t ha<sup>-1</sup>  
   May - 42 t ha<sup>-1</sup>  
                   England -- September - 60 t ha<sup>-1</sup>  
 Other data: Seasonal leaf area index, daily solar  
 radiation, and temperature

Authors: Ng and Loomis (1984)  
 Sites: Aberdeen and Kimberly, Idaho  
 Type of data: 10-d interval measurements of leaf, stem,  
 tuber, and total dry weight over a  
 100-d period following emergence on 9 June at  
 Aberdeen and 24-28 May at Kimberly

Seasonal high: Aberdeen

Total weight -- day 85 - 65 g plant<sup>-1</sup>

Tuber weight -- day 85 - 50 g plant<sup>-1</sup>

Leaf weight -- day 60 - 12.5 g plant<sup>-1</sup>

Kimberly

Total weight -- day 95 - 60 g plant<sup>-1</sup>

Tuber weight -- day 95 - 50 g plant<sup>-1</sup>

Leaf weight -- day 60 - 9 g plant<sup>-1</sup>

Other data: Seasonal leaf area index

### 3.9 Sugar Beet Field

Authors: Brown and Rosenberg (1971)

Site: Scottsbluff, Nebraska

Type of data: Daily measurements of CO<sub>2</sub> flux over a sugar beet field from 11 August to 10 September 1966

Seasonal high: 14 August - 400 x 10<sup>-5</sup> g CO<sub>2</sub> cm<sup>-2</sup>

Seasonal low: 1 September - 168 x 10<sup>-5</sup> g CO<sub>2</sub> cm<sup>-2</sup>

Authors: Fick, Williams, and Loomis (1973)

Site: Davis, California

Type of data: Periodic measurements of standing crop of tops and storage roots for a 140-d period following emergence on 5 June 1967

Seasonal high: Storage roots

140 d after emergence - 650 g m<sup>-2</sup>

Tops

140 d after emergence - 1800 g m<sup>-2</sup>

Other data: Top: fibrous root dry weight ratio for 44 d following emergence

Author: Kanada (1975)

Site: Sapporo, Japan

Type of data: Time course of net assimilation rate (NAR), crop growth rate (CGR), and leaf area index over a 15-week growth period (average for 5 years)

Seasonal high: NAR -- 6 weeks after sowing  
 $6 \text{ g dw dm}^{-2} \text{ LA d}^{-1}$   
 CGR -- 9 weeks after sowing  
 $20 \text{ g m}^{-2} \text{ d}^{-1}$

Seasonal low: NAR -- 18-21 weeks after sowing  
 $1.5 \text{ g dw dm}^{-2} \text{ LA d}^{-1}$   
 CGR -- 21 weeks after sowing  
 $5 \text{ g m}^{-2} \text{ d}^{-1}$

Author: Lundegardh (1927)  
 Site: Stockholm, Sweden  
 Type of data: Measurements of soil respiration and  $\text{CO}_2$   
 concentration 4.5 m and 0.25 m above soil surface  
 for the period 23 June to 1 October 1925

Seasonal high: Soil respiration  
 13-15 July -  $0.256 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$   
 $\text{CO}_2$  concentration  
 4.5 m -- 11-13 August -  $0.776 \text{ mg CO}_2 \text{ L}^{-1}$   
 0.25 m -- 11-13 August -  $0.7640 \text{ mg CO}_2 \text{ L}^{-1}$

Seasonal low: Soil respiration  
 26-27 August -  $0.148 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$   
 $\text{CO}_2$  concentration  
 4.5 m -- 26-27 August -  $0.559 \text{ mg CO}_2 \text{ L}^{-1}$   
 .25 m -- 11-13 August -  $0.5764 \text{ mg CO}_2 \text{ L}^{-1}$

Other data: Seasonal rainfall and air temperature

Author: Marshall (1974)  
 Site: E. Lothiam, Scotland  
 Type of data: Weekly estimates of total dry weight (SC), leaf  
 area index, relative growth rate, net  
 assimilation rate (NAR), and crop growth rate over  
 growing season

Seasonal high: NAR -- late June -  $80 \text{ g m}^{-2} \text{ week}^{-1}$   
 SC -- September -  $1000 \text{ g m}^{-2}$

Seasonal low: NAR -- September -  $10 \text{ g m}^{-2} \text{ week}^{-1}$   
 SC -- June -  $0.03 \text{ g m}^{-2}$

Other data: Similar seasonal data for turnip: biweekly  
 rainfall, potential evapotranspiration,  
 temperature, vapor pressure deficit, soil water,  
 and windspeed

Authors: Patefield and Austin (1971)  
 Site: Wellesbourne, U.K.  
 Type of data: 10-d interval estimates of leaf and root  
 standing crop for 110 d after sowing on  
 11 June 1969

Seasonal high: Leaf -- 100-110 d -  $300 \text{ g m}^{-2}$   
 Root -- 90-100 d -  $1000 \text{ g m}^{-2}$

Author: Snyder (1974)  
 Site: East Lansing, Michigan  
 Type of data: Net assimilation rate (NAR) and relative growth  
 rate (RGR) for 113 d following emergence  
 (planted on 18 May)

Seasonal high: NAR -- 30-50 d -  $1.55 \text{ mg dw cm}^{-2} \text{ LA d}^{-1}$   
 RGR -- 30-50 d - 27.4%

Seasonal low: NAR -- 92-113 d -  $0.54 \text{ mg dw cm}^{-2} \text{ LA d}^{-1}$   
 RGR -- 71-113 d - 1.4%

Other data: Seasonal radiation, daylight hours, temperature,  
 leaf area, total and root biomass on a per plant  
 and per leaf area basis

### 3.10 Sorghum Field

Authors: Arkin, Vanderlip, and Ritchie (1976)  
 Site: Manhattan, Kansas  
 Type of data: 3-d interval estimates of standing crop over a  
 120-d period following emergence in 1965 and  
 1966

Seasonal high: 1965 -- 100-105 d - 150 g plant<sup>-1</sup>  
 1966 -- 100 d - 130 g plant<sup>-1</sup>

Other data: Seasonal temperature

Authors: Garrity, Sullivan, and Watts (1984)

Site: Tryon, Nebraska

Type of data: Periodic measurements of apparent canopy photosynthesis over the period July to September 1978 for unstressed and water-stressed conditions

Seasonal high: Unstressed  
 Late July - 1.025 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>  
 Water stressed  
 Late July - 0.95 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>

Seasonal low: Unstressed  
 Late August - 0.55 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>  
 Water stressed  
 late August - 0.30 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>

Other data: Seasonal soil water, leaf water potential, stomatal resistance, leaf area index, and evapotranspiration

### 3.11 Alfalfa Field

Authors: Baldocchi, Verma, and Rosenberg (1981)

Site: Mead, Nebraska

Type of data: Seasonal canopy CO<sub>2</sub> flux and concentration for June to September 1978

Seasonal high: CO<sub>2</sub> concentration  
 Mid-June - 320 ppm  
 CO<sub>2</sub> flux  
 Mid-June - 3.6 x 10<sup>-6</sup> kg m<sup>-2</sup> s<sup>-1</sup>

- Seasonal low: CO<sub>2</sub> concentration  
Late July - 290 ppm
- CO<sub>2</sub> flux  
Early August -  $0.7 \times 10^{-6} \text{ kg m}^{-2} \text{ s}^{-1}$
- Other data: Leaf area index and dry matter changes after cutting; diurnal patterns of CO<sub>2</sub> flux, sensible and latent heat fluxes, and net radiation on selected dates during the growing season
- Authors: Delaney, Dobrenz, and Poole (1974)
- Site: Tuscon, Arizona
- Type of data: Monthly measurements of apparent photosynthesis (AP) measured at low and high light intensity, and dark respiration (Rd) (June-October)
- Seasonal high: AP  
Low light -- June -  $13.25 \text{ mg CO}_2 \text{ dm}^{-2} \text{ LA h}^{-1}$   
High light -- June -  $28.5 \text{ mg CO}_2 \text{ dm}^{-2} \text{ LA h}^{-1}$   
Rd -- October --  $5 \text{ mg CO}_2 \text{ dm}^{-2} \text{ LA h}^{-1}$
- Seasonal low: AP  
Low light -- late July -  $9.0 \text{ mg CO}_2 \text{ dm}^{-2} \text{ LA h}^{-1}$   
High light -- early July -  $18 \text{ mg CO}_2 \text{ dm}^{-2} \text{ LA h}^{-1}$   
Rd -- August -  $2.1 \text{ mg CO}_2 \text{ dm}^{-2} \text{ LA h}^{-1}$
- Other data: Seasonal temperature, specific leaf weight, and leaf area index

### 3.12 Miscellaneous Fields

- Authors: Bull and Glaszion (1975)
- Sites: Sugar cane fields in Australia, Guyana, Hawaii, and South Africa
- Type of data: Seasonal course of total dry matter (TDM) and crop growth rate (CGR) for 24 months following planting

Seasonal high: Australia

TDM -- 12 months after planting -  $50 \text{ t ha}^{-1}$

CGR -- 4 months after planting -  $24 \text{ g m}^{-2} \text{ d}^{-1}$

Guyana

TDM -- 20 months after planting -  $40 \text{ t ha}^{-1}$

CGR -- 7 months after planting -  $26 \text{ g m}^{-2} \text{ d}^{-1}$

Hawaii

TDM -- 21 months after planting -  $75 \text{ t ha}^{-1}$

CGR -- 7 months after planting -  $27 \text{ g m}^{-2} \text{ d}^{-1}$

South Africa

CGR -- 5 months after planting -  $18 \text{ g m}^{-2} \text{ d}^{-1}$

Authors: Jones et al. (1982)

Site: Peanut field in Gainesville, Florida

Type of data: Weekly measurements of  $\text{CO}_2$  exchange rate for 10 weeks after planting, 22-23 May 1979

Seasonal high: 11 weeks after planting -  $46 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$

Seasonal low: 19 weeks after planting -  $18 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$

Other data: Seasonal changes in leaf area index, specific leaf weight, fraction of light interception, and photosynthetic efficiency

Authors: Monteith, Szeic, and Yabuki (1964)

Site: Kale field in Harpenden, Hertfordshire, England

Type of data: Weekly measurements of dry weight assimilation (August-September 1963); 15-d interval average  $\text{CO}_2$  flux from cropped (May-September 1961 and June-September 1963) and fallow (June-September 1963) soil

Seasonal high: Assimilation

Mid-August -  $30 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$

Soil flux

Cropped -- late June 1961 -  $11 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$

late September 1963 -  $9 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$

Seasonal high: Fallow -- late September 1961 -  $9 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$   
 Seasonal low: Assimilation  
                   Mid-September -  $2 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$   
 Soil flux  
                   Cropped -- May 1961 -  $5 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$   
                   Fallow -- August 1963 -  $6 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$

Authors: Monteith, Szeic, and Yabuki (1964)  
 Site: Bean field in Harpenden, Hertfordshire, England  
 Type of data: Weekly measurements of dry weight assimilation  
 (June-July 1961); 15-d interval average  $\text{CO}_2$   
 flux from soil between rows of beans  
 (May-September 1961)

Seasonal high: Assimilation  
                   Mid-June -  $29 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$   
 Soil flux  
                   Early August -  $8 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$   
 Seasonal low: Assimilation  
                   Late July -  $10 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$   
 Soil flux  
                   May and late August -  $6.5 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$

Authors: Monteith, Szeic, and Yabuki (1964)  
 Site: Grass field in Harpenden, Hertfordshire, England  
 Type of data: Weekly measurements of dry weight assimilation  
 before and after cutting on 31 May 1961  
 (April-August 1961); 15-d interval average  
 $\text{CO}_2$  flux from cropped and fallow soil  
 (April-August 1961)

Seasonal high: Assimilation  
                   Mid-April -  $50 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$   
 Soil flux  
                   Cropped -- late August -  $12 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$   
                   Fallow -- late June -  $6.5 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$

Seasonal low: Assimilation  
 Mid-August -  $11 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$   
 Soil flux  
 Cropped -- early July -  $7.5 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$   
 Fallow -- early July -  $5.5 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$

Authors: Monteith, Szeic, and Yabuki (1964)  
 Site: Bare soil in Harpenden, Hertfordshire, England  
 Type of data: 15-d interval average  $\text{CO}_2$  flux from bare soil  
 (October 1960 to September 1961)  
 Seasonal high: June -  $6.7 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$   
 Seasonal low: November -  $1.5 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$   
 Other data:  $\text{CO}_2$  flux from bare soil as a function of mean  
 soil temperature

Author: Smart (1974)  
 Site: Grapevine canopies in Griffith, N.S.W., Australia  
 Type of data: Hourly, daily, and monthly measurements of  
 photosynthesis at irregular intervals  
 Seasonal high: 7 February 1969 -  $1.812 \times 10^{-6} \text{ kg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$   
 Seasonal low: 17 December 1968 -  $0.892 \times 10^{-6} \text{ kg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$   
 Other data: Leaf area index and light parameters

### 3.13 General Agricultural Region

Author: Enoch (1977)  
 Site: Coastal Plain, vicinity of Tel-Aviv, Israel  
 Type of data: Monthly measurements of diurnal mean  $\text{CO}_2$   
 concentration (October 1973 to September 1974)  
 Seasonal high: October - 365 vpm  
 Seasonal low: July - 335 vpm  
 Other data: Diurnal patterns of  $\text{CO}_2$  concentration

Authors: Verma and Rosenberg (1976)  
 Site: Vicinity of Mead, Nebraska  
 Type of data: Measurements of CO<sub>2</sub> concentration (24-h average) and CO<sub>2</sub> flux (net daily) during the periods September 1972 to January 1973 and June to December 1973  
 Seasonal high: Concentration -- October - 340 ppm  
                   Flux -- July - 19 g m<sup>-2</sup> d<sup>-1</sup>  
 Seasonal low: Concentration -- August - 328 ppm  
                   Flux -- October - 3 g m<sup>-2</sup> d<sup>-1</sup>  
 Note: Seasonal values are based on regression curves  
 Other data: Seasonal solar radiation, wind speed, air temperature; diurnal patterns of CO<sub>2</sub> flux and concentration

#### 4. CONCLUDING REMARKS

The ten crops for which available models are described are far from an exhaustive coverage of the world's important crops. Important crops that are not covered here include oats, sugar cane, manioc, tomatoes, and sunflower. However, the crops included constitute the bulk of terrestrial human food sources. Wheat alone accounts for 20% of the world's calorie consumption; potatoes account for over half of the annual tonnage of all starchy roots and tubers, and soybeans are by far the major pulse crop.

The models reviewed here also represent seven of the world's ten largest crops (with respect to area planted in 1982-1983); only oats (7), peanuts (8), and rye (9) are excluded (U.S. Department of Agriculture 1983). Further, the models represent croplands that involve at least 63% of the world's surface area covered by intensively farmed arable land, rice paddies, and other irrigated land (at least 74% if the last category is excluded, see Hummel and Reck 1979). If only those lands covered by large contiguous fields are considered, the proportion of the world's agricultural land area represented by crops

for which models are reviewed here is probably even greater. Therefore, the systems included should account for the bulk of the agricultural effects on the seasonal pattern of terrestrial CO<sub>2</sub> fluxes.

The objectives of agricultural modeling projects differ for the most part from those of projects dealing with natural, unmanaged ecosystems. Processes which the conventional ecosystem modeler might consider critical to a complete representation of a natural system may appear unimportant or immaterial to the crop modeler; the converse is also true. A notable example of the former case is the virtual absence of any consideration of litter and soil organic matter decomposition in the agricultural models. Natural ecosystem models frequently involve some representation of decomposition (see King and DeAngelis 1985); our review here indicates that agroecosystem models rarely do. Certainly not all ecosystem models deal with decomposition; in this respect, agroecosystem crop models resemble the production models of natural systems. However, the absence of decomposition processes may limit the application of existing agroecosystem models to the problem of modeling seasonal CO<sub>2</sub> dynamics on a regional scale. The crop models only operate over the growing season, sometimes for only a portion of that, while CO<sub>2</sub> fluxes from the terrestrial biosphere to the atmosphere during the nongrowing season, as a result of decomposition, are presumably an important part of the seasonal behavior of the global carbon cycle. Even during the growing season, evolution of CO<sub>2</sub> during decomposition affects the net biosphere-atmosphere fluxes. Consequently, existing crop models are not directly applicable to the objective of a regionally aggregated global carbon model.

There is nothing that inherently precludes consideration of decomposition in agricultural models. In fact, it is somewhat surprising that modelers of soil organic matter have not made more intensive use of agricultural systems. An exploration of seasonal decomposition in agroecosystems is called for. With this information a more complete model of agroecosystems, at least with respect to seasonal CO<sub>2</sub> dynamics, will be possible. In the absence of this

development, it should be relatively easy to adapt the decomposition routines from conventional ecosystem models for use in conjunction with existing crop models. The adapted models will have to incorporate the effects of such things as tillage, fertilization, and irrigation. Many of the crop models deal admirably with the processes of seasonal  $\text{CO}_2$  assimilation, live plant respiration, and carbon storage. An integrated coupling of crop model and decomposition model would go a long way toward fostering the application of agroecosystem models to the study of the global carbon cycle.

On a global, annual, or long-term scale, the impact of agroecosystems on the global carbon cycle is probably significant. On a regional and seasonal scale, these systems are likely to be even more influential. Consequently, a thorough understanding of the global carbon cycle will require consideration of agroecosystem influences. Furthermore, interests in the role land-use changes play in the increase in atmospheric  $\text{CO}_2$  and the resulting impact on agricultural productivity argues for considering the influence agroecosystems have on the global carbon cycle. This consideration will perforce involve modeling. The development of regionally aggregated multidimensional global carbon models is relatively recent. Too great a preoccupation with agroecosystems at this stage may hinder rather than promote progress. However, an expanded exploration and modeling of seasonal carbon dynamics in agroecosystems will benefit both the growing appreciation for agroecosystems as ecological systems in themselves (see Lowrance, Stinner, and House 1984) and will benefit our understanding of their role in global biogeochemical cycles.

## REFERENCES

- Ackerson, R. C., U. D. Havelka, and M. G. Boyle. 1984. CO<sub>2</sub>-enrichment effects on soybean physiology. II. Effects of stage-specific CO<sub>2</sub> exposure. *Crop Sci.* 24:1150-1154.
- Acock, B., D. A. Charles-Edwards, D. J. Fitter, D. W. Hand, L. J. Ludwig, J. Warren Wilson, and A. C. Withers. 1978. The contribution of leaves from different levels of a tomato crop to canopy net photosynthesis: An experimental examination of two canopy models. *J. Exp. Bot.* 29:815-827.
- Acock, B., V. R. Reddy, F. D. Whisler, D. N. Baker, J. M. McKinion, H. F. Hodges, and K. J. Boote. 1983. The soybean crop simulator GLYCIM: Model documentation 1982. Response of Vegetation to Carbon Dioxide O02. U.S. Department of Energy and the U.S. Department of Agriculture, Washington, D.C.
- Allen, L. H., Jr. 1971. Variations in carbon dioxide concentration over an agricultural field. *Agric. Meteorol.* 8:5-24.
- Allen, L. H., Jr. 1973. Crop micrometeorology: A. wide-row light penetration. B. carbon dioxide enrichment and diffusion. Ph.D. dissertation. Cornell University, Ithaca, N.Y.
- Allen, L. H., Jr., S. E. Jensen, and E. R. Lemon. 1971. Plant response to carbon dioxide enrichment under field conditions: A simulation. *Science* 173:256-258.
- Anderson, M. C. 1966. Stand structure and light penetration. II. A theoretical analysis. *J. Appl. Ecol.* 3:41-54.
- Angus, J. 1970. Foliage structure, light utilization, and crop growth in cereals. Ph.D. thesis, University of Melbourne, Australia.
- Angus, J. F., and J. H. Wilson. 1976. Photosynthesis of barley and wheat leaves in relation to canopy models. *Photosynthetica* 10:367-377.
- Arkin, G. F., R. L. Vanderlip, and J. T. Ritchie. 1976. A dynamic grain sorghum growth model. *Trans. ASAE* 19:622-626,630.
- Baker, C. H., and R. D. Horrocks. 1976. CORNMOD, a dynamic simulator of corn production. *Agricultural Systems* 1:57-77.

- Baker, D. N., J. D. Hesketh, and W. G. Duncan. 1972. Simulation of growth and yield in cotton: I. Gross photosynthesis, respiration, and growth. *Crop Sci.* 12:431-435.
- Baker, D. N., J. R. Lambert, and J. M. McKinion. 1983. GOSSYM: A simulator of cotton crop and yield. Tech. Bull. 1089. South Carolina Agric. Exp. Stn.
- Baldocchi, D. D., S. B. Verma, and N. J. Rosenberg. 1981. Seasonal and diurnal variations in CO<sub>2</sub> flux and CO<sub>2</sub>-water flux ratio of alfalfa. *Agric. Meteorol.* 23:231-244.
- Band, L. E., O. B. Elfes, J. T. Hayes, L. O. Mearns, P. A. O'Rourke, B. J. Stevenson, W. H. Terjung, and P. E. Todhunter. 1981. Applications of a photosynthesis model to an agricultural region of varied climates: California. *Agric. Meteorol.* 24:201-217.
- Biscoe, P. V., R. K. Scott, and J. L. Monteith. 1975. Barley and its environment. III. Carbon budget of the stand. *J. Appl. Ecol.* 12:269-293.
- Biscoe, P. V., J. A. Clark, K. Gregson, M. McGowan, J. L. Monteith, and R. K. Scott. 1975. Barley and its environment. I. Theory and practice. *J. Appl. Ecol.* 12:227-257.
- Biscoe, P. V., J. N. Gallagher, E. J. Littleton, J. L. Monteith, and R. K. Scott. 1975. Barley and its environment. IV. Sources of assimilate for the grain. *J. Appl. Ecol.* 12:295-318.
- Bolin, B. 1977. Changes of land biota and their importance for the carbon cycle. *Science* 196:613-615.
- Boon-Long, P., D. B. Eghi, and J. E. Leggett. 1983. Leaf nitrogen and photosynthesis during reproductive growth in soybeans. *Crop Sci.* 23:617-620.
- Brouwer, R., and S. T. de Wit. 1969. A simulation model of plant growth with special attention to root growth and its consequences. pp. 224-244. IN W. J. Whittington (ed.), *Root Growth*. Butterworth, London.
- Brown, K. W., and N. J. Rosenberg. 1971. Energy and CO<sub>2</sub> balance of an irrigated sugar beet (*Beta vulgaris*) field in the Great Plains. *Agron. J.* 63:207-213.

- Bull, T. A., and K. T. Glaszion. 1975. Sugarcane. pp. 51-72. IN L. T. Evans (ed.), Crop Physiology. Cambridge University Press, London.
- Bunnell, F. L., D. E. N. Tait, P. W. Flanagan, and K. Van Cleve. 1977. Microbial respiration and substrate weight loss - I. A general model of the influences of abiotic variables. Soil Biol. Biochem. 9:33-40.
- Chartier, P. 1970. A model of CO<sub>2</sub> assimilation in the leaf. pp. 307-315. IN I. Setlik (ed.), Prediction and Measurement of Photosynthetic Productivity. Pudoc, Wageningen, The Netherlands.
- Coleman, D. C., C. V. Cole, and E. T. Elliott. 1984. Decomposition, organic matter turnover, and nutrient dynamics in agroecosystems. pp. 83-104. IN R. Lowrance, B. R. Stinner, and G. J. House (eds.), Agricultural Ecosystems: Unifying Concepts. John Wiley and Sons, New York.
- Connor, D. J., and O. Cartledge. 1970. Observed and calculated photosynthetic rates of Chloris gayana communities. J. Appl. Ecol. 7:353-362.
- Connor, D. J., and O. Cartledge. 1971. Structure and photosynthesis of wheat communities. J. Appl. Ecol. 8:469-475.
- Crapo, N. L., and R. G. Bowmer. 1973. Respiratory rates in roots of detopped and intact corn. Oikos 24:465-468.
- Curry, R. B., C. H. Baker, and J. G. Streeter. 1975. SOYMOD I: A dynamic simulator of soybean growth and development. Trans. ASAE 18:963-968,974.
- Curry, R. B., and L. H. Chen. 1971. Dynamic simulation of plant growth - Part II. Incorporation of actual daily weather and partitioning of net photosynthate. Trans. ASAE 14:1170-1174.
- Dahlman, R. C. 1984. Carbon Cycle Research Plan. DOE/ER-0188. United States Department of Energy, National Technical Information Service, Springfield, Va.
- Delaney, R. H., A. K. Dobrenz, and H. T. Poole. 1974. Seasonal variation in photosynthesis, respiration, and growth components of nondormant alfalfa (Medicago sativa L.). Crop Sci. 14:58-61.

- Duncan, W. G. 1972. SIMCOT: A simulator of cotton growth and yield. pp. 115-118. IN C. E. Murphy, Jr., J. D. Hesketh, and B. R. Strain (eds.), Modeling the Growth of Trees. EDFB-IBP-72-11. Oak Ridge National Laboratory, Oak Ridge, Tenn.
- Duncan, W. G., R. S. Loomis, W. A. Williams, and R. Hanau. 1967. A model for simulating photosynthesis in plant communities. *Hilgardia* 38:181-205.
- Emanuel, W. R., G. G. Killough, W. M. Post, and H. H. Shugart, Jr. 1984a. Modeling terrestrial ecosystems in the global carbon cycle with shifts in carbon storage capacity by land use change. *Ecology* 65:970-983.
- Emanuel, W. R., G. G. Killough, W. M. Post, and M. P. Stevenson. 1984b. Computer implementation of a globally averaged model of the world carbon cycle. TR010. DOE/NBB-0062. Department of Energy, National Technical Information Service, Springfield, Va.
- Enoch, H. Z. 1977. Diurnal and seasonal variations in carbon dioxide concentration of the lower atmosphere in the coastal plain of Israel. *Agric. Meteorol.* 18:375-385.
- Fick, G. W. 1971. Analysis and simulation of the growth of sugar beet (*Beta vulgaris* L.). Ph.D. thesis, University of California, Davis.
- Fick, G. W., W. A. Williams, and R. S. Loomis. 1973. Computer simulation of dry matter distribution during sugar beet growth. *Crop Sci.* 13:413-417.
- Fick, G. W., R. S. Loomis, and W. A. Williams. 1975. Sugar beet. pp. 259-295. IN L. T. Evans (ed.), *Crop Physiology*, Cambridge University Press, London.
- Fischer, R. A., F. Bidinger, J. R. Syme, and P. C. Wall. 1981. Leaf photosynthesis, leaf permeability, crop growth, and yield of short spring wheat genotypes under irrigation. *Crop Sci.* 21:367-373.
- Ford, D. M., R. Shibles, and D. E. Green. 1983. Growth and yield of soybean lines selected for divergent leaf photosynthetic activity. *Crop Sci.* 23:517-520.
- Fukai, S., S. Koh, and A. Kumura. 1976. Dry matter production and photosynthesis of *Hordeum vulgare* L. in the field. *J. Appl. Ecol.* 13:877-887.

- Garrity, D. P., C. Y. Sullivan, and D. G. Watts. 1984. Changes in grain sorghum stomatal and photosynthetic response to moisture stress across growth stages. *Crop Sci.* 24:441-446.
- Gates, D. M., and I. E. Papias. 1971. *Atlas of Energy Budgets of Plant Leaves.* Academic Press, New York.
- Gent, M. P., and R. K. Kiyomoto. 1985. Comparison of canopy and flag leaf net carbon dioxide exchange of 1920 and 1977 New York winter wheats. *Crop Sci.* 25:81-86.
- Goudriaan, J., and P. Ketner. 1984. A simulation study for the global carbon cycle, including man's impact on the biosphere. *Clim. Change* 6:167-192.
- Gutierrez, A. P., L. A. Falcon, W. Loew, P. A. Liepzig, and R. Van den Bosch. 1975. An analysis of cotton production in California: A model for acala cotton and the effects of defoliators on its yield. *Environ. Entomol.* 4:125-136.
- Gutierrez, A. P., M. A. Pizzamiglio, W. J. Dos Santos, R. Tennyson, and A. M. Villacorta. 1984. A general distributed delay time varying life table plant population model: Cotton (*Gossypium hirsutum* L.) growth and development as an example. *Ecol. Modelling* 26:231-249.
- Havelka, U. D., R. C. Ackerson, M. G. Boyle, and V. A. Wittenbach. 1984. CO<sub>2</sub>-enrichment effects on soybean physiology. I. Effects of long-term CO<sub>2</sub> exposure. *Crop Sci.* 24:1146-1149.
- Havelka, U. D., V. A. Wittenbach, and M. G. Boyle. 1984. CO<sub>2</sub>-enrichment effects on wheat yield and physiology. *Crop Sci.* 24:1163-1168.
- Hesketh, J. D., D. N. Baker, and W. G. Duncan. 1971. Simulation of growth and yield in cotton: Respiration and carbon balance. *Crop Sci.* 11:394-398.
- Hesketh, J. D., D. N. Baker, and W. G. Duncan. 1972. Simulation of growth and yield in cotton: II. Environmental control of morphogenesis. *Crop Sci.* 12:436-439.
- Houghton, R. A., J. E. Hobbie, J. M. Melillo, B. Moore, B. J. Peterson, G. R. Shaver, and G. M. Woodwell. 1983. Changes in the carbon content of terrestrial biota and soils between 1860 and 1980: A net release of CO<sub>2</sub> to the atmosphere. *Ecol. Monogr.* 53:235-262.

- House, G. J., B. R. Stinner, D. A. Crossley, Jr., and E. P. Odum. 1984. Nitrogen cycling in conventional and no-tillage agro-ecosystems: Analysis of pathways and processes. *J. Appl. Ecol.* 21:991-1012.
- Hummel, J. R., and R. A. Reck. 1979. A global surface albedo model. *J. Appl. Meteorol.* 18:239-253.
- Ibrahim, M. E., and D. R. Buxton. 1981. Early vegetative growth of cotton as influenced by leaf type. *Crop Sci.* 21:639-643.
- Ingram, K. T., D. C. Herzog, K. J. Boote, J. W. Jones, and D. C. Barfield. 1981. Effects of defoliating pests on soybean canopy CO<sub>2</sub> exchange and reproductive growth. *Crop Sci.* 21:961-968.
- Iwaki, H. 1975. Computer simulation of vegetative growth of rice plants. pp. 105-121. IN Y. Murata (ed.), *Crop Productivity and Solar Energy Utilization in Various Climates in Japan*. JIBP Synthesis Vol. 11. JCIBP, University of Tokyo Press, Tokyo.
- Johnson, R. C., R. E. Witters, and A. J. Ciha. 1981. Apparent photosynthesis, evapotranspiration, and light penetration in two contrasting hard red winter wheat canopies. *Agron. J.* 73:419-422.
- Jones, J. W., C. S. Barfield, K. J. Boote, G. H. Smerage, and J. Mongold. 1982. Photosynthetic recovery of peanuts to defoliation at various growth stages. *Crop Sci.* 22:744-746.
- Jones, J. W., J. D. Hesketh, E. J. Kamprath, and H. D. Bowen. 1974. Development of a nitrogen balance for cotton growth models: A first approximation. *Crop Sci.* 14:541-546.
- Jones, J. W., L. G. Brown, and J. D. Hesketh. 1980. COTCROP: A computer model for cotton growth and yield. pp. 209-241. IN J. D. Hesketh and J. W. Jones (eds.), *Predicting Photosynthesis for Ecosystem Models*. CRC Press, Boca Raton, Fla.
- Kallis, A., and H. Tooming. 1974. Estimation of the influence of leaf photosynthetic parameters, specific leaf weight, and growth functions on yield. *Photosynthetica* 8:91-103.

- Kamiyama, K., and M. Horie. 1975. Relative growth rate, net assimilation rate, and climate. pp. 21-36. IN Y. Murata (ed.), Crop Productivity and Solar Energy Utilization in Various Climates in Japan. JIBP Synthesis Vol. 11. JCIBP, University of Tokyo Press, Tokyo.
- Kanada, M. 1975. Maximal growth rate and climate. pp. 67-71. IN Y. Murata (ed.), Crop Productivity and Solar Energy Utilization in Various Climates in Japan. JIBP Synthesis Vol. 11. JCIBP, University of Tokyo Press, Tokyo.
- Keeling, C. D. 1983. The global carbon cycle: What we know and could know from atmospheric, biospheric, and oceanic observations. pp. II.3-II.62. IN Proceedings: Carbon Dioxide, Science and Consensus. CONF-820970. U.S. Department of Energy National Technical Information Service, Springfield, Va.
- Keulen, H. van. 1976. A calculation method for potential rice production. Contr. Centr. Res. Inst. Agric. Bogor, No. 21.
- King, A. W., and D. L. DeAngelis. 1985. Information for seasonal models of carbon fluxes in terrestrial biomes. ORNL/TM-9404. Oak Ridge National Laboratory, Oak Ridge, Tenn.
- King, A. W., and D. L. DeAngelis. 1986. Site-specific models of seasonal carbon fluxes in terrestrial biomes. ORNL/TM-9749. Oak Ridge National Laboratory, Oak Ridge, Tenn.
- Kohlmaier, G. H., H. Brohl, U. Fischbach, G. Kratz, and E. O. Sire. 1983. The role of the biosphere in the carbon cycle and biota models. pp. 93-144. IN W. Bach et al. (eds.), Carbon Dioxide: Current Views and Developments in Energy/Climate Research. D. Reidel Publishing Co., Dordrecht, The Netherlands.
- Ku, S. B., G. E. Edwards, and C. B. Tanner. 1977. Effect of light, carbon dioxide, and temperature on photosynthesis, oxygen inhibition of photosynthesis, and transpiration in Solanum tuberosum. Plant Physiol. 59:868-872.
- Kuroiwa, S. 1968. Theoretical evaluation of dry-matter production of a crop canopy under insolation and temperature-climate. pp. 331-332. IN Agroclimatological Methods. Proc. Reading Symp., UNESCO, Paris.

- Lafitte, H. R., and R. L. Travis. 1984. Photosynthesis and assimilate partitioning in closely related lines of rice exhibiting different sink:source relationships. *Crop Sci.* 24:447-452.
- Lemon, E. R., D. W. Stewart, and R. W. Shawcroft. 1971. The sun's work in a cornfield. *Science* 174:371-378.
- Lemon, E. R., D. W. Stewart, R. W. Shawcroft, and S. E. Jensen. 1973. Experiments in predicting evapotranspiration by simulation with a soil-plant-atmosphere model (SPAM). pp. 57-76. IN R. R. Bruce (ed.), *Field Soil Water Regime*. Soil Sci. Soc. Amer. Spec. Pub., Madison, Wis.
- Littleton, E. J. 1971. The gas exchange of barley leaves and ears. Ph.D. thesis, University of Nottingham, United Kingdom.
- Loomis, R. S., and P. A. Gerakis. 1975. Productivity of agricultural systems. pp. 145-172. IN J. P. Cooper (ed.), *Photosynthesis and Productivity in Different Environments*. Cambridge University Press, London.
- Lowrance, R., B. R. Stinner, and G. J. House (eds.). 1984. *Agricultural Ecosystems: Unifying Concepts*. John Wiley and Sons, New York.
- Lundegardh, H. 1927. Carbon dioxide evolution of soil and crop growth. *Soil Sci.* 23:417-452.
- Lupton, F. G. H. 1969. Estimation of yield of wheat from measurements of photosynthesis and translocation in the field. *Ann. Appl. Biol.* 64:363-374.
- Lupton, F. G. H. 1972. Further experiments on photosynthesis and translocation in wheat. *Ann. Appl. Biol.* 71:69-79.
- Marshall, J. K. 1974. Effects of shelter on the growth of turnips and sugar beet. *J. Appl. Ecol.* 11:327-345.
- Mauney, J. R., K. E. Fry, and G. Guinn. 1978. Relationship of photosynthetic rate to growth and fruiting of cotton, soybean, sorghum, and sunflower. *Crop Sci.* 18:259-263.
- McCraig, T. N., and J. M. Clarke. 1982. Seasonal changes in nonstructural carbohydrate levels of wheat and oats grown in a semi-arid environment. *Crop Sci.* 22:963-970.

- McCree, K. J. 1970. An equation for the rate of respiration of white clover plants grown under controlled conditions. pp. 221-230. IN I. Setlik (ed.), Prediction and Measurement of Photosynthetic Productivity. Pudoc, Wageningen, The Netherlands.
- McCree, K. J. 1974. Equations for the rate of dark respiration of white clover and grain sorghum, as functions of dry weight, photosynthetic rate, and temperature. Crop Sci. 14:509-514.
- McGill, W. B., H. W. Hunt, R. G. Woodmansee, and J. O. Reuss. 1981. PHOENIX: A model of the dynamics of carbon and nitrogen in grassland soils. pp. 49-115. IN F. E. Clark and T. Rosswall (eds.), Terrestrial Nitrogen Cycles. Ecol. Bull. Vol. 33, Stockholm.
- McKinion, J. M., J. W. Jones, and J. D. Hesketh. 1974. Analysis of SIMCOT: Photosynthesis and growth. Proc. Beltwide Cotton Production Research Conf., National Cotton Council, Memphis, Tenn.
- McKinion, J. M., J. D. Hesketh, and D. N. Baker. 1974. Analysis of the exponential growth equation. Crop Sci. 14:549-551.
- McKinion, J. M., D. N. Baker, J. D. Hesketh, and J. W. Jones. 1975. SIMCOT II: A simulation of cotton growth and yield. pp. 27-82. IN Computer Simulation of a Cotton Production System - Users' Manual, U.S. Department of Agriculture ARS-S-52.
- Mitchell, R. 1984. The ecological basis for comparative primary production. pp. 13-53. IN R. Lowrance, B. R. Stinner, and G. J. House (eds.), Agricultural Ecosystems: Unifying Concepts. John Wiley and Sons, New York.
- Monteith, J. L. 1965. Light distribution and photosynthesis in field crops. Ann. Bot. 29:17-37.
- Monteith, J. L. 1969. Light interception and radiative exchange in crop stands. pp. 89-111. IN J. D. Eastin, F. A. Haskins, C. V. Sullivan, and C. H. M. Van Bavel (eds.), Physiological Aspects of Crop Yield. American Society of Agronomy, Madison, Wis.
- Monteith, J. L., G. Szeic, and K. Yabuki. 1964. Crop photosynthesis and the flux of carbon dioxide below the canopy. J. Appl. Ecol. 1:321-337.

- Moorby, J., and F. L. Milthorpe. 1975. Potato. pp. 225-257. IN L. T. Evans (ed.), Crop Physiology. Cambridge University Press, London.
- Morgan, J. A., and W. O. Willis. 1983. Gas exchange and water relations of 'olaf' spring wheat. Crop Sci. 23:541-546.
- Nevins, D. J., and R. S. Loomis. 1970. A method for determining net photosynthesis and transpiration by plant leaves. Crop Sci. 10:3-6.
- Ng, N., and R. S. Loomis. 1984. Simulation of Growth and Yield of the Potato Crop. Simulation Monographs, Pudoc, Wageningen, The Netherlands.
- Odum, E. P. 1971. Fundamentals of Ecology. 3rd ed. W. B. Saunders Company, Philadelphia.
- Osman, A. M. 1971. Dry matter production of a wheat crop in relation to light interception and photosynthetic capacity of leaves. Ann. Bot. 35:1017-1035.
- Parton, W. J., D. W. Anderson, C. V. Cole, and J. W. B. Stewart. 1983. Soil organic matter formation model. IN R. Lowrance, R. Todd, L. Asmussen, and R. Leonard (eds.), Nutrient Cycling in Agricultural Ecosystems. University of Georgia College of Agriculture Special Publication No. 23. Athens, Ga.
- Parton, W. J., J. Persson, and D. W. Anderson. 1983. Simulation of organic matter changes in Swedish soils. pp. 511-516. IN W. K. Lauenroth, G. V. Skogerbre, and M. Flug (eds.), Analysis of Ecological Systems: State-of-the-Art in Ecological Modeling. Elsevier Scientific Publishing Co., Amsterdam.
- Patefield, W. M., and R. B. Austin. 1971. A model for the simulation of the growth of Beta vulgaris L. Ann. Bot. 35:1227-1250.
- Pearman, G. I., and J. R. Garratt. 1973. Carbon dioxide measurements above a wheat crop. I. Observations of vertical gradients and concentrations. Agric. Meteorol. 12:13-25.
- Peat, W. E. 1970. Relationships between photosynthesis and light intensity in the tomato. Ann. Bot. 34:319-328.
- Pegelow, E. J., Jr., D. R. Buxton, R. E. Briggs, H. Muramoto, and W. G. Geusler. 1977. Canopy photosynthesis and transpiration of cotton as affected by leaf type. Crop Sci. 17:1-4.

- Penning de Vries, F. W. T. 1975. The cost of maintenance processes in plant cells. *Ann. Bot.* 39:77-92.
- Rickman, R. W., R. E. Ramig, and R. R. Allamaras. 1975. Modelling dry matter accumulation in dryland winter wheat. *Agron. J.* 67:283-289.
- Ritchie, J. T. 1972. Model for predicting evaporation from a row crop with incomplete cover. *Water Resources Res.* 8:1204-1213.
- Saeki, T. 1960. Interrelationships between leaf amount, light distribution, and total photosynthesis in a plant community. *Bot. Mag.* 73:404-408.
- Secor, J., R. Shibles, and C. R. Stewart. 1983. Metabolic changes in senescing soybean leaves of similar plant ontogeny. *Crop Sci.* 23:107-110.
- Seddigh, M., and G. D. Jolliff. 1984. Physiological responses of field-grown soybean leaves to increased reproductive load induced by elevated night temperatures. *Crop Sci.* 24:952-957.
- Shawcroft, R. W. 1970. Water relations and stomatal responses in a corn field. Ph.D. dissertation, Cornell University, Ithaca, N.Y.
- Shawcroft, R. W. 1971. The energy budget at the earth's surface: Water relations and stomatal response in a corn field. U.S. Army ECOM Technical Report 2-68-1-7. U.S. Army Electronics Command, Fort Huachuca, Ariz.
- Shawcroft, R. W., and E. R. Lemon. 1972. Estimation of internal crop water status from meteorological and plant parameters. pp. 449-459. IN *Plant Response to Climatic Factors*. Proc. Uppsala Symp. (Ecology and Conservation-5). UNESCO, Paris.
- Shih, S. F., G. J. Gascho, and G. S. Rahi. 1981. Modeling biomass production of sweet sorghum. *Agron. J.* 73:1027-1032.
- Silvius, J. E., R. R. Johnson, and D. B. Petus. 1977. Effect of water stress on carbon assimilation and distribution in soybean plants at different stages of development. *Crop Sci.* 17:713-716.
- Sinclair, T. R. 1971. An evaluation of leaf angle effect on maize photosynthesis and productivity. Ph.D. dissertation, Cornell University, Ithaca, N.Y.
- Sinclair, T. R. 1972. A leaf photosynthesis model for use in general growth models. Eastern Deciduous Forest Biome Memo Report No. 72-14. Oak Ridge National Laboratory, Oak Ridge, Tenn.

- Sinclair, T. R., C. E. Murphy, Jr., and K. R. Knoerr. 1976. Development and evaluation of simplified models for simulating canopy photosynthesis and transpiration. *J. Appl. Ecol.* 13:813-830.
- Sinclair, T. R., L. H. Allen, Jr., and D. W. Stewart. 1971. A simulation model for crop-environmental interactions and its use in improving crop productivity. pp. 784-794. IN Proceedings 1971 Summer Computer Simulations Council, Inc., La Jolla, Ca.
- Smart, R. E. 1974. Photosynthesis by grapevine canopies. *J. Appl. Ecol.* 11:997-1006.
- Smith, O. L. 1979. An analytical model of the decomposition of soil organic matter. *Soil Biol. Biochem.* 11:585-606.
- Smith, O. L. 1982. *Soil Microbiology: A Model of Decomposition and Nutrient Cycling.* CRC Press, Inc., Boca Raton, Fla.
- Snyder, F. W. 1974. Comparative leaf area and dry matter accumulation by maize and sugar beet. *Crop Sci.* 14:529-533.
- Snyder, F. W., and G. E. Carlson. 1978. Photosynthate partitioning in sugar beet. *Crop Sci.* 18:657-661.
- Stapleton, H. N., D. R. Buxton, F. L. Watson, D. J. Nolting, and D. N. Baker. 1973. COTTON: A computer simulation of cotton growth. Tech. Bull. 206. Agricultural Experimental Station, University of Arizona.
- Stapper, M., and G. F. Arkin. 1980. A dynamic growth and development model for maize (Zea mays L.). Research Center Program and Model Documentation No. 80-2, Blackland Research Center, Texas A & M University.
- Stewart, D. W. 1970. A simulation of net photosynthesis of field corn. Ph.D. dissertation, Cornell University, Ithaca, N.Y.
- Stewart, D. W., and E. R. Lemon. 1969. The energy budget at the earth's surface: A simulation of photosynthesis of field corn. U.S. Army ECOM Tech. Rep. 2-68 I-6, U.S. Army Electronics Command, Ft. Huachuca, Ariz.
- Terjung, W. H., and P. A. O'Rourke. 1980. An economical canopy model for use in urban climatology. *Int. J. Biometeorol.* 24:281-291.

- Terjung, W. H., S. S. -F. Louie, and P. A. O'Rourke. 1976. Toward an energy budget model of photosynthesis predicting world productivity. *Vegetatio* 32:31-53.
- Thomas, M. D., and G. R. Hill. 1949. Photosynthesis under field conditions. pp. 19-52. IN J. Frank and W. E. Loomis (eds.), *Photosynthesis in Plants*. Iowa State College Press, Ames.
- Tieszen, L. L., and S. K. Imbramba. 1978. Gas exchange of finger millet inflorescences. *Crop Sci.* 18:495-498.
- Tooming, H. 1967. Mathematical model of plant photosynthesis considering adaptation. *Photosynthetica* 1:233-240.
- Tooming, K. H., and Y. U. Ross. 1965. Oglablenie integral'noi radiatsii razlichnymi posevami kukuruzy. (Extinction of radiation in various maize crops.). pp. 65-72. IN *Voprosy Radiatsionnogo Rezhima Rastitel'nogo Pokrova*. Akad. Nauk. Est. SSR, Inst. Fiz. Astron., Tartu.
- Uchijima, Z. 1970. Carbon dioxide environment and flux within a corn crop canopy. pp. 179-196. IN I. Setlik (ed.), *Prediction and Measurement of Photosynthetic Productivity*. Pudoc, Wageningen, The Netherlands.
- Uchijima, Z. 1975. Dry matter production of crops in relation to climatic conditions. pp. 86-104. IN Y. Murata (ed.), *Crop Productivity and Solar Energy in Various Climates in Japan*. JIBP Synthesis Vol. 11. JCIBP, University of Tokyo Press, Tokyo.
- U.S. Department of Agriculture. 1983. *Agricultural Statistics 1983*. U.S. Government Printing Office, Washington, D.C.
- Van Dyne, G. M., and Z. Abramsky. 1975. Agricultural systems models and modeling: An overview. pp. 23-106. IN G. E. Dalton (ed.), *Study of Agricultural Systems*. Applied Science Publishers Ltd., London.
- Verma, S. B., and N. J. Rosenberg. 1976. Carbon dioxide concentration and flux in a large agricultural region of the Great Plains of North America. *J. Geophysical Research* 81:399-405.
- Vietor, D. M., R. P. Ariyanayagam, and R. B. Musgrave. 1974. Photosynthetic selection of Zea mays L. I. Plant age and leaf position effects and a relationship between leaf and canopy rates. *Crop Sci.* 14:567-573.

- Waggoner, P. E. 1969. Environmental manipulation for higher yields. pp. 343-373. II J. D. Eastin, F. A. Haskins, C. Y. Sullivan, and C. H. M. Van Bavel (eds.), *Physiological Aspects of Crop Yield*. American Society of Agronomy, Madison, Wis.
- Wann, M., C. D. Raper, Jr., and H. L. Lucas, Jr. 1978. A dynamic model for plant growth: A simulation of dry matter accumulation for tobacco. *Photosynthetica* 12:121-136.
- Warren Wilson, J. 1965. Stand structure and light penetration. I. Analysis by point quadrats. *J. Appl. Ecol.* 2:383-390.
- Warren Wilson, J. 1967. Stand structure and light penetration. III. Sunlit foliage area. *J. Appl. Ecol.* 4:159-165.
- Williams, W. A., R. S. Loomis, and C. R. Lepley. 1965. Vegetative growth of corn as affected by population density. I. Productivity in relation to interception of solar radiation. *Crop Sci.* 5:211-215.
- de Wit, C. T. 1959. Potential photosynthesis of crop surfaces. *Neth. Jour. Agri. Sci.* 7:141-149.
- de Wit, C. T. 1965. Photosynthesis of leaf canopies. *Agr. Res. Rep.* 663. Pudoc, Wageningen, The Netherlands.
- de Wit, C. T., R. Brouwer, and F. W. T. Penning de Vries. 1970. The simulation of photosynthetic systems. pp. 47-70. IN I. Setlik (ed.), *Prediction and Measurement of Photosynthetic Productivity*. Pudoc, Wageningen, The Netherlands.
- de Wit, C. T., J. Goudriaan, H. H. van Laar, F. W. T. Penning de Vries, R. Rabbinge, H. van Keulen, W. Louwerse, L. Sibma, and C. de Jonge. 1978. *Simulation of Assimilation, Respiration, and Transpiration of Crops*. Simulation Monographs, Pudoc, Wageningen, The Netherlands.
- Wittenbach, V. A., R. C. Ackerson, R. T. Giaquinta, and R. R. Hebert. 1980. Changes in photosynthesis, ribulose biophosphate carboxylase, proteolytic activity, and ultrastructure of soybean leaves during senescence. *Crop Sci.* 20:225-231.

- Woodmansee, R. G. 1984. Comparative nutrient cycles of natural and agricultural ecosystems: A step toward principles. pp. 145-156. IN R. Lowrance, B. R. Stinner, and G. J. House (eds.), Agricultural Ecosystems: Unifying Concepts. John Wiley and Sons, New York.
- Wright, A. D., and M. E. Keener. 1982. A test of a maize growth and development model, CORNF. Agricultural Systems 9:181-197.

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