EXPLANATORY MODELS IN CROP PHYSIOLOGY

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R. S. Loomis

Department of Agronomy and Range Science, University of California,
Davis, California 95616

R. Rabbinge

Department of Theoretical Production Ecology, The Agricultural University,
Wageningen, The Netherlands

E. Ng

Department of Agronomy and Range Science, University of California,
Davis, California 95616

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"We can claim to understand the plant when we can express it all in a mathematical model."

Folke Skoog, over coffee, 1955

INTRODUCTION

An inherent feature of biological science is the conceptualization of complex systems into organization levels—from lower levels such as molecules, organelles, and cells to higher levels such as communities, populations, and ecosystems. Each of those hierarchic levels possesses a characteristic behavior resulting from integration of sublevel processes under influences from the external environment. Classical plant physiology explores the mechanistic basis for that behavior by reductionist techniques, by seeking to isolate each sublevel process from the influences of higher levels and from competing elements at the same level. Quantitative integration of those mechanisms into an explanation of system behavior, however, remains a task for integrative physiology. In that task, the interactions within and between levels become the foci of research. Particularly concerned with that problem are crop physiologists, whose task is to explain the behavior of vegetation in a variable environment.

Some types of physiological information are readily extrapolated from lower to higher levels; others are not. An understanding of certain qualitative phenomena, such as photoperiodism or the phase changes of lipids with temperature, may be used more or less directly in interpreting and predicting organism behavior. In other cases, the extrapolations may be frustrated by the very complexity of the interactions and their quantitative and temporal natures. As an example, the adequacy of a nutrient uptake system depends on variations in the activity of ion carriers in root membranes, ion availability in the soil, root surface area and distribution, degree of suberization, cortical and xylem transport resistances, ion assimilation capacity, and sink demand. The system is further complicated by its dynamic character —each of those factors is subject to diurnal and seasonal change.

Mathematical modeling is used increasingly as a method for effecting such integrations. That approach has been favored by the absence of other effective methodologies, by the emerging formalism of systems analysis, and by computers. The efforts in animal science are rather advanced. Major areas of work include explanatory models for thermoregulation, blood circulation, morphogenetic control, neurological functioning, and even artificial intelligence. It has even been possible to deal with the biochemical kinetics of ruminant digestion as a basis for organismal growth (5, 98). The basis for such work in many instances has been feedback theory developed in the 1940s (6, 72, 100), enzyme kinetics (42a, 49, 105), and compartmentalization concepts (2, 49).

The plant sciences have lagged well behind except in the physical aspects of the plant environment and community physiology. We find expanding interest in mathematical formulations of specific biological processes, with major attention given to such subjects as leaf growth and phyllotaxy (35, 69, 124, 128), carrier kinetics (20), photosynthesis (15, 17, 48, 119), and catenary diffusion sequences (84). The biomathematical analysis of physiological problems has been given extended treatments by Nobel (84), Riggs (99), and Thornley (117). In contrast, the integrative systems approach has been limited largely to the higher organization levels. That seems to reflect the quantitative concerns of systems ecologists and others, particularly of agronomists, for the behavior of vegetation. The grassland (56, 88) and tundra (12) biome studies, as examples, are impressive for their scope but are short in physiological detail. Workers in those areas have drawn more on the concepts of systems analysis and environmental physics as the starting point for their work. The systems level is also the arena for our own work on physiological models, emphasized in this essay. Our models focus on the organismal and systems levels, but the approach outlined is also applicable to integration at lower levels.

We distinguish two broad categories of crop models: same-level descriptive models and multilevel explanatory models. A wide range of descriptive models exist. Multivariate regression models, for example, are used widely for the important task of yield prediction in variable climates (10, 81, 82, 93, 96, 116). Such models may be static, i.e. involving no concept of time. Variables in that case are integrated seasonal totals of yield, rainfall, and temperature. Sophistication is improved by introducing some concept of time based, for example, on the calculation of developmental rate as a function of temperature during the season (101, 108) and by sharpening the environmental parameters, e.g. use of a soil moisture balance rather than rainfall as an input variable (3, 10).

The explanatory approach emphasized here is considerably more sophisticated. It employs dynamic models of the system hierarchy in an effort to provide prediction and explanation of integrated behavior from more detailed knowledge of the underlying physiological and morphological processes (26, 28). All such knowledge becomes descriptive at the ultimate level of reduction. While crop models do not go that far, they do become descriptive where knowledge is lacking or simplification is required. However, with a hierarchic structure, description at lower levels becomes explanatory of higher levels. A dynamic structure also aids in explanation, and the capability for continuous printout of many variables contrasts to experimental work generally providing observations only for discrete times.

In dynamic models, a system is described by a set of *state variables* (such as the weights of various organs) that are updated at each iteration of the model by *rate variables* (such as the flow of carbon in photosynthesis and

respiration) defining changes in the state variables (Figure 1, left). The rate variables are considered to be constant during the iteration interval (DELT) so that the change in state is DELT X rate. DELT must be small enough that the assumed constancy is reasonably accurate. Models with too large an iteration interval give wrong results and may develop oscillations because of repeated overshoot and undershoot. The calculation of rate variables depends upon information from external *forcing variables* (such as air temperature) and internal *auxiliary variables* (such as the meristematic status of an organ) drawn from the current state of the system (Figure 1, right). A state variable and its determining processes represent a minimum hierarchy that becomes explanatory when the rate processes are calculated by rules based on the biological, chemical, or physical mechanism involved. A feature of most models is the use of balance equations at each level to ensure that conservation of mass and energy is observed. The method is not limited to integration from lower to higher levels, although that is the approach used with crop models. Recognizing that controls operate both upward and downward in biological hierarchies, one might employ simplified-ecosystem or organismal-level models to provide the controlling environment for a detailed organ or tissue model.
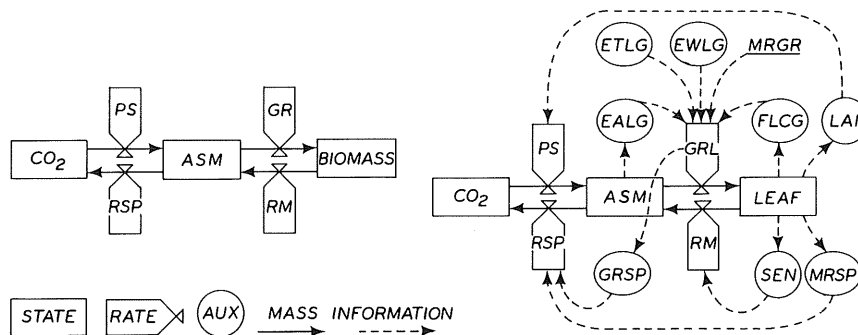

Figure 1 (left) A relational diagram for the transfer of carbon from atmospheric CO_2 to new assimilates (ASM) by photosynthesis (PS) and then by growth (GR) to new BIOMASS. Also shown are the reverse transfers by remobilization (RM) and respiration (RSP). (*right*) The hypothesis is extended with auxiliary variables controlling the growth rate of a leaf (GRL). The effect of assimilate supply on leaf growth rate (EALG) is shown to depend upon the ASM level; effectors for temperature (ETLG) and water status (EWLG) would be calculated in sub-routines. The meristematic fraction of the leaf capable of growth (FLCG) interacts with a maximum relative growth rate parameter (MRGR) to determine potential leaf growth. Other attributes of the leaf feedback to other processes: leaf area index (LAI) to photosynthesis; senescence state (SEN) to remobilization; and leaf weight and development state to maintenance respiration (MRSP). GRSP represents a calculation of the respiration associated with the growth achieved during each iteration of the model.

Although explanatory hierarchic modeling is still in its infancy and has not been subject to extensive development by systems analysts (70), the method holds great potential for plant physiology. Starting in the mid-1960s (11, 22, 114), it has become an active area of research by crop physiologists. For example, Milthorpe & Moorby's *Crop Physiology* (73) derives from their efforts in dynamic modeling, and the Trebon (107) and Long Ashton (62) conference volumes show a heavy modeling content. Much of the current activity is reported at workshops and in limited distribution publications. *Annals of Botany, Agricultural Meteorology, Journal of Theoretical Biology, Crop Science,* and the Dutch *Simulation Monographs* are among the major publications for botanical models. Rather than attempting an exhaustive review, the following essay draws largely from our own work. Our plan is: first, to present a limited background on the state-variable approach to systems analysis; second, to outline some of the special problems and attributes found in crop models at community, organismal, and cellular levels; and then to close with a survey of applications.

THE MODELING PROCESS

Model building should begin with a clear formulation of objectives concerning the use of the completed model. Biological systems are so complex that their models always represent a simplification or abstraction of the real system. That contrasts with some cases in engineering where the realized machine may be only an approximation of the perfection visualized in the model or plan. The objectives provide a basis for decisions about necessary simplifications. A second task, involving identification of the variables and processes that define the system, is aided by relational diagrams for the main variables (such as Figure 1). That task is coupled with the formulation of mathematical expressions for rate variables (i.e. differential equations). The choice and structure of those equations constitute a set of implicit assumptions about the system which should be carefully defined. The same is true in the choice of parameters for the equations. Taken together, the model with its parameterized equations represents a collective hypothesis about the real system. That leads directly to the construction of a computer program to execute the model and then to the critical step of validation (122).

Validation is distinguished from verification, which means testing to see that the computer program in fact operates on input data in the intended way. In addition to an a priori analysis of the model's structure (81a), validation generally involves comparison of model predictions with results from independent experiments relating to both processes (e.g. photosynthesis rate) and system states (e.g. biomass levels) (see Figure 2, p. 347). Some

modelers use such comparisons as a basis for calibrating or "tuning" their models. That usually involves empirical adjustments of parameters to bring model performance into correspondence with standard behavior. Calibration can create a model useful for mimicking reality but is a dangerous practice for explanation. Departures from realism in model behavior usually represent either errors or incompleteness in the implicit assumptions on basic processes which should be given direct attention. de Wit (25) distinguished among real systems as repeatable, recurrent, or unique in terms of validation. Repeatable systems, such as fields of corn or manufactured cars, can easily be done again in independent validation experiments. Peat formation and forest successions, however, although recurrent in time, are too slow to repeat, and validation must be made on submodels or through comparison with a series of real systems in different stages of development. Examples of unique systems are the Mississippi River and biospheric cyling of carbon dioxide. In those cases, experimental perturbations of the real system may be hazardous, impractical, or socially unacceptable. Although validation may be possible from historic knowledge of past great events, it is clear that very strict criteria are needed in such constructions, particularly when they are used in forming public policy.

Validation may be extended through behavioral analyses (response of the model system to some pertubation, e.g. leaf pruning or climate change) and sensitivity analyses (response of the model system to systematic variations in model structure or of one parameter or input variable; Figure 2). They reveal the degree of truthfulness or realism with which the model handles the intended problem. They also tell us about the importance of various components in achieving that truthfulness and thus provide an objective basis for the simplification of complex models.

Those stages in model building are not mutually exclusive, and iteration and feedback among the stages is considerable (4). The process is actually little different from that used in experimental research, with the model hypotheses accepted or rejected through validation tests. Many subjective decisions are involved, and the quality of the model depends greatly on the skill and knowledge of the modeler. Almost invariably, deficiencies are found in the information base that define needs for additional experiments. That in itself has been one of the most rewarding features of modeling.

The choice of an appropriate time interval for iterations of a model is closely linked to objectives and to the levels of the system being modeled. In principle, the iteration interval must be only 0.1 to 0.2 times as long as the time required for a system to recover from a small perturbation. In practice, a sensitivity analysis with shorter intervals is usually necessary to determine the effect on accuracy. Higher levels and/or larger systems usually respond more slowly, and crop growth can be modeled with daily or

weekly advances. But an interval of 1 to 2 hours must be used if sensitivity to diurnal events is required, while stomatal closure and some cellular processes require intervals of minutes or even seconds for accurate simulation.

Those facts cause coupling difficulties of the "stiff-system" sort when very fast subsystems are used to explain the behavior of the slower whole. If computer time is freely available, that problem is overcome by operating with an iteration interval appropriate to the fastest subsystem. Costs can be reduced sharply with special integration routines which allow the use of longer time intervals (43a), but those have yet to be used widely by crop modelers. Crop modelers sometimes use empirical submodels with slower time constants on the basis that less error results from that than from other features of their models. Alternatively, one can avoid the problem by limiting the hierarchic structure to two or three levels and thus restricting the range of time constants within the memory and computational capacities of their computers (and budgets). Either approach tends to compromise our objective of developing explanatory detail. At any level of detail, coupling problems are reduced by the introduction of negative feedback control since slight overshoot in one part of the system in one iteration tends to be corrected by a slight undershoot in the next.

Modeling can be facilitated with special simulation languages designed for use with state-variable models (9, 14, 39, 94). Such languages include integration routines, Gaussian generators, timing and array devices, automatic input/output formating, function generators for interpolation of tabular data, and a selection of more specialized intrinsic functions that can be accessed easily. Such languages are more expensive of computer time but save effort in programming. More important, the simplified programs can serve as a means for communication between modeler and experimenter. Thus far, plant modelers generally have not selected a universal simulation language. That plus the fact that few crop models are directed to the same objective means that very few standard program modules are shared by different modelers.

HIERARCHIC LEVELS IN CROP GROWTH MODELS

The principal focus of the output of crop growth models is community behavior. Such models simulate the production of new photosynthates, the partitioning of that material to growth, respiration and storage, and the related morphogenesis. The greatest attention is given to the state variables that define the environment and the age, weight, and morphology of the main elements of the biomass. That may be done with perhaps 50 to 100 state variables (21, 22, 87, 118). Computer models with 100 state variables

are quite large and carry the danger that the model will be insensitive to incorrect opinions about structure and parameters. But a detailed hierarchic structure may require a very large number of variables, and some crop models concerned with integrative physiology have employed much larger numbers of variables [BACROS (11, 27, 29); SUBGOL (37, 38, 55); PO-TATO: Ng, unpublished].

The level of detail is determined by the aim of the modeling effort and the relative importance of various subprocesses to system behavior. Important processes should be developed with more detail. However, large models such as BACROS and SUBGOL also tend to reflect the present state of knowledge, providing detail on what is known and retreating to simple mimicking efforts on subjects such as morphogenesis where less is known. Models of limited size may be sufficient for many objectives. For that purpose, the highly detailed models can be simplified, following sensitivity analyses. It is also possible in that way to formulate simple algorithms of detailed submodels for use in more comprehensive models (37, 121).

The following sections outline some of the characteristics of model structure found with the various hierarchic levels of crop-growth models. Such models represent limited ecosystems consisting of the producer community and relevant abiotic components.

Community/Ecosystem Level

The milieu for crop growth is determined by environmental processes that function largely at the ecosystem level. The key elements are radiation interception and exchange, evaporation and transpiration, aerodynamic transport, and microclimate profiles as well as water and nutrient supplies. Each of those is some function of the area occupied by the vegetation and can be modeled as a vertical distribution. Environmental physicists have developed highly detailed explanatory models for most of those topics. For example, detailed models are available on infiltration and movement of water in soil (115, 123), including in some cases the influence of an expanding root system (53, 60, 63). Radiation interception by foliage also can be approached with rather sophisticated light distribution models (19, 24, 33, 44, 64, 76, 77, 102), and microweather within the vegetation can be simulated by coupling such models into net radiation budgets (latent and sensible heat exchanges and radiation balance) and eddy transport models (44, 83, 109, 126).

A useful approach for both aerial and soil environments is to subdivide the systems into horizontal layers, considering balances for each property within each layer, and using transport equations to calculate vertical fluxes between layers (Figure 2 shows the results of such calculations for air temperature and humidity). Transport equations (flux = gradient X conduc-

tivity) are used also for nutrient and water fluxes into roots and for water and carbon dioxide exchange by the leaves. Several interesting issues develop here. The conductivity term can be defined explicitly for a small system—in the case of roots, a single cell, or a small root segment—but it takes on a more general, empirical context when applied to a whole root system. But subdivision into smaller parts or layers can introduce a stiff-system problem. Radiation, for example, is absorbed at the surface soil layer and within leaves by very thin strata with a low capacity for heat storage. Those strata change temperature very rapidly in contrast to mixed air and the rest of the soil, which as large systems have much greater heat capacities and change temperature more slowly with time. Goudriaan (44) modeled that with a "bypassing" method in which the fast system is iterated to steady state and then abandoned (assumed to remain in steady state) until a new iteration is made of the higher level.

Organismal/organ-level elements, such as the size and characteristics of the foliage and root systems, enter directly into some of the physical processes. Most crop models have dealt only with random or homogeneous distributions of roots and leaves within each layer, although other distributions may be important in nature. Those other arrangements, e.g. with plants in rows, can become quite complex (16, 42, 44). Microclimate models frequently include biological processes such as stomatal behavior, which
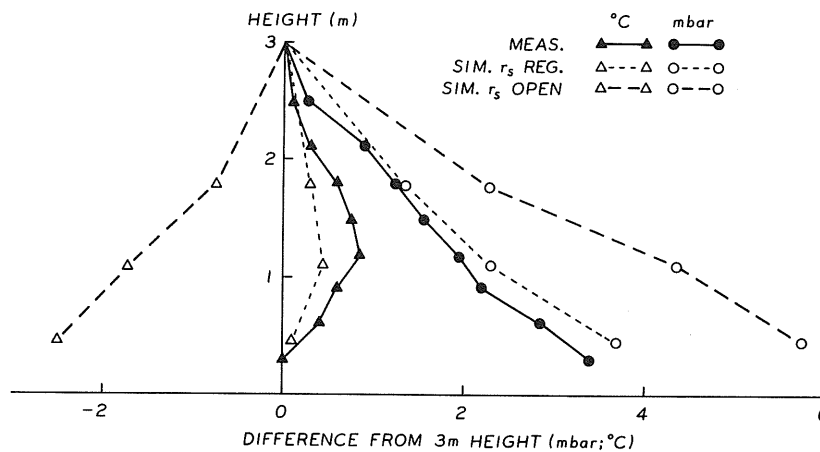

Figure 2   Validation of the BACROS, flux-dependent, microclimate simulator for air temperature and humidity through comparisons with profiles measured within a corn crop at Wageningen, the Netherlands. The profiles indicate the difference in temperature and humidity within the canopy as compared to that observed above the canopy at 3 m. Simulations with and without stomatal regulation represent a sensitivity analysis for the necessity of a submodel on stomatal control [adapted from (29)].

regulates water loss, and "suberization," which modifies root permeability to water and nutrients. The importance of stomatal control is illustrated clearly in Figure 2. Detailed models of stomatal action also have been developed (97, 110), and many ecosystem models include stomatal dependence upon the current levels of CO_2, water, and radiation.

Photosynthesis also is best treated as an ecosystem process because of its close dependence upon foliage display, radiation interception, and eddy transport. The more advanced models include all of those features. Shaw-croft et al (109), for example, started with Duncan's (33) light distribution model for a layered leaf canopy. Ross (102) and Goudriaan (44) also presented highly detailed light models. Coupling light distribution with a leaf photosynthesis model achieves a simulation of canopy production. The simpler approaches employ a measured light-response curve for leaf photosynthesis; for more detail, a leaf model (15, 17, 48, 119) incorporating attributes such as quantum efficiency and a dependence of the saturation rate on temperature and CO_2 internal can be used. CO_2 internal can be simulated with an eddy transport model (to give CO_2 external) and a stomatal model (44).

Ecosystem models of that type offer a high degree of realism and accuracy in simulations of the main processes in crop productivity—photosynthesis, transpiration, and respiration of crop canopies. But it is not yet practical to employ all details available on ecosystem behavior in crop growth models which explore the partitioning of photosynthate during growth and development. The result would be a vast model very taxing to both computers and researchers. Submodels for the ecosystem parts can be simplified in various ways. BACROS retains considerable explanatory detail in the environmental and photosynthesis modules while using only rudimentary plant growth sections. In contrast, SUBGOL and POTATO employ simplified environmental modules while expanding on plant growth and development. In both cases, air and soil temperatures are taken as daylength-dependent, sinusoidal (or other) variations of reported screen temperatures, and evapotranspiration is estimated from a modified Penman equation (75) taking into account dew-point temperature and daily wind run with a submodel to describe (rather than simulate) stomatal conductance. BACROS simulates microweather within the canopy (Figure 2) whereas SUBGOL does not. BACROS approaches photosynthesis with a description of canopy architecture and a simple radiation penetration model coupled with transport equations for estimating the movement of CO_2 into the leaf based on stomatal conductance and the CO_2 gradient between leaf and air. In the Davis models, photosynthesis was reduced to a tabular presentation by running the Duncan photosynthesis simulator for 100 combinations of leaf-area distributions and solar altitude for clear and overcast skies, using a standard

light-response function for leaf photosynthesis (37). The clear and overcast tables are interpolated at each hour according to solar angle and the ratio of potential and current daily total radiation (thus adjusting for cloudiness). Those hourly rates are then reduced by temperature and water-deficit functions, but CO_2 variations are ignored. Both approaches provide fast and reasonably accurate simulations of the photosynthate supply available for plant growth.

Organ/Organismal Level

The simplified vegetation models provide a framework within which the whole-plant level can be developed. An important aspect of that coupling is that a simulation of competitive effects due to varying plant density is achieved. At the plant level we can focus on detailed morphological descriptions of roots, stems, and leaves and their growth and ontogeny. Such models serve as means to explore partitioning and developmental processes and as a basis for integrative explanations of vegetation-level processes. Gutierrez et al (46) and Wang et al (127) incorrectly characterized crop growth models of that type as "single-plant" models (and also their limited-ecosystem model as a "population" model). Rather clearly, vegetation processes are simulated in such models at the ecosystem level, and those processes provide the photosynthate supply, water and nutrient status, and external environment which serve as forcing and auxiliary variables for the plant level. The multilevel model thus becomes reductionist as well as integrative.

Options exist to divide the plant into functional morphological classes (leaves, stems, and roots) and model each class en masse, or to model each individual leaf, internode, tuber, or fibrous root. Even when successive organs are considered separately, that is usually done for a "standard plant" so that the organs of all plants are identical. The en masse method may be used when ecosystem behavior is the principal interest, but the individual organ approach is usually required when integrative physiology is the aim. Some models take an intermediate approach by simulating the bulk behavior of all leaves or roots within specific "age" classes. That facilitates distinction of physiological capabilities (e.g. growth or senesence) according to developmental state and is a common approach for root systems. The age classes can be retained in programming devices known as "pushdown tables," advanced by an aging or developmental-rate submodel.

Modeling the initiation, growth, and development of individual organs in an explanatory way is not always easy or in some cases even possible. Little information exists about the mechanisms controlling the morphogenesis of individual organs. In many cases, the modeling becomes descriptive—for example, by using a temperature-dependent plastochron to control the

initiation of successive leaves. Difficult questions also arise with the morphogenetic rules for integration and coordination of organs into whole plants. The rules center on partitioning (the distribution of new assimilates to growth centers) and physiological age. One approach to partitioning is to set the model "genotype" into descriptive allocation patterns (74, 96, 120) which may be drawn from real plants. But fixed allocations are likely to fail when the simulations are placed in a new environment. A more explanatory approach requires simulating morphological and physiological plasticity in response to density and other features of the environment, using variables that introduce the properties of apical dominance, photosynthate and water supplies, microclimate position, and age.

Photosynthate supply is made a central factor for organismal integration by following the nutritional-control approach of Brouwer and de Wit (11, 27) in which organ growth is dependent upon the concentration of available assimilates. The assimilate pool visualized in Figure 1 includes all readily available carbon fractions. It is fed by rates of photosynthesis and remobilization of materials from senescing organs, and is depleted by rates of growth, respiration, and storage. The growth of one organ then indirectly affects all others by altering that common pool. A division of the general pool into compartments for each growth center according to transport resistance (117) or axial position (52) attempts an explanatory basis compatible with morphological concepts but opens the issue of how to model vascular transport as a variable function of growth and development. Thornley (117) and Goeschl et al (131) have developed very nice models of phloem transport based on the number and dimension of cells but without a good solution to the developmental aspects. We have settled on a empirical "priority" concept in which each class of organs is given a different response function for substrate dependence. Those functions incorporate qualitative properties of transport resistance or position, as deduced from shading and pruning experiments with whole plants (37, 38), and the quantitative nature of substrate dependence of growth when unconstrained by transport (54). That approach gives more explanation to the simulation than descriptive allometry.

Similar pools can be established for water status and nutrient supplies. With water, which affects growth through variations in turgor, we have used a bulked water-status parameter such as plant relative water content (RWC), which is simulated from a balance between water uptake and transpiration.

The interaction of two or more pools, plus other variables relating to age and environment, establishes a dynamic pattern of partitioning that may include a balancing of root and shoot functions (11, 37). The balancing can be done with a model analogy (Figure 3) to real plants in which shoot
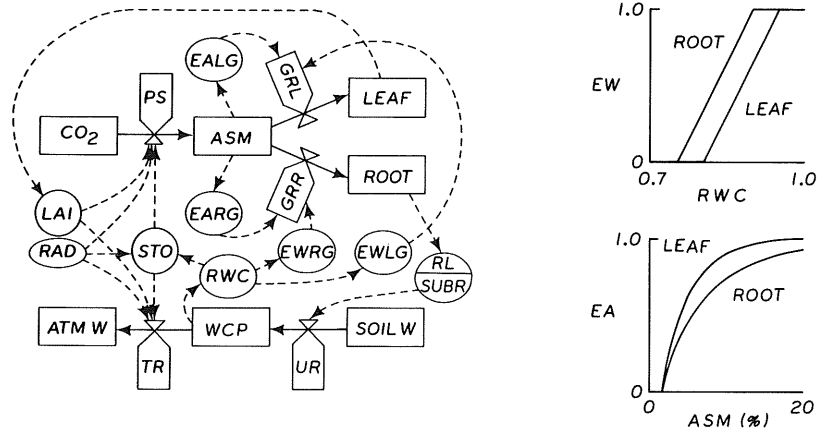
Figure 3 A relational diagram for a hypothesis about the functional balance of root and leaf growth based on carbon and water. The transfer of water from the soil through the plant to the air determines the current water content of the plant (WCP) and its relative water content (RWC). RWC in turn regulates root and leaf growth rates, according to the response functions (EW) shown to the right, and stomates. Also on the right are the response functions for the effects of assimilate supply (EA) on growth rates. Stomatal status (STO) is influenced by current radiation (RAD) and RWC and in turn regulates transpiration (TR) and photosynthesis (PS). The feedback from ROOT weight to water uptake rate (UR) involves root length (RL) and its suberization (SUBR) with age.

Structure similar to this is used in BACROS, SUBGOL, and POTATO.

growth is more affected than root growth by water or nutrient status (root supply functions) and root growth is more affected than shoot growth by assimilate status (a shoot supply function). Such *functional balances* represent hierarchic (across level) feedback loops, and their inclusion provides realistic organismal integration and greatly increases the power of the model. In addition, the door is then open to validation against data from root pruning and defoliation experiments (27, 38).

The state variables of interest in simulating the growth of an organ are its weight at present (W_t) and its rate of growth (GR). A common formulation is:

$$GR = MRGR \cdot F(AGE) \cdot W_t \cdot MIN(EA, EW, ET)$$

where MRGR is the maximum unrestrained relative growth rate (g $g^{-1}t^{-1}$), and F(AGE) is an "age"-dependent fraction of organ weight still capable of growth. MIN(EA, EW, ET) indicates the use of Liebig's law of the minimum to choose among the response functions for the most limiting of the effects of assimilate supply (EA), water status (EW), or temperature (ET) in that iteration. The new weight of the organ at the future time can

be simply W_t + GR $\times$ DELT. Figure 1, right, diagrams that scheme while Figure 4 shows the operation of such effectors during the growing season for sugar beet.

The cleanest conception of a response function is as the relative effect of one factor on the rate of a process with all other factors maintained near optimal levels. Thus, we would have the relative effect of temperature on growth rate, with assimilate, nutrients, and water nonlimiting. Such idealizations are not easy to achieve in experiments but can sometimes be approached with isolated systems (54, 79).

Liebig's law seems to hold in many cases, particularly when short time steps (1 hr) are employed. But in other cases, the effects of several factors may be additive or multiplicative and a multivariate approach [e.g. F(EA, EW, ET)] is required for limiting factor interactions. That is always necessary when growth rates are calculated for long time intervals (1 day). With either method, the modeling becomes descriptive at this level. The response functions and their interactions result from complex cell-level processes that cannot be modeled in detail largely because we do not understand the systems. For example, the basis of the response function for the temperature dependence of growth rate is unknown, and the manner and
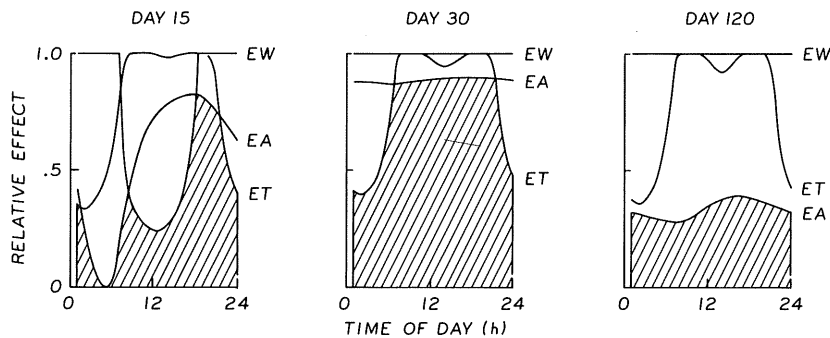

Figure 4 Operation of the Liebig's law analogy in SUBGOL for the effects of water status (EW), assimilate supply (EA), and temperature (ET) on sugar-beet leaf growth rate. The effect factors are derived from response functions such as those shown in Figure 3; a value of 1.0 indicates that the factor is not limiting to growth rate. The diurnal course of the effectors is shown for 15, 30, and 120 days after emergence on May 16, at Davis, California (38 N) with 7 plants m^{-2}; LAI, $m^2 m^{-2}$/total biomass, g m^{-2} were 0.14/33, 1.18/180, and 4.82/2520 respectively at 15, 30, 120 days.

The shaded area shows the course of the most limiting factors. Inadequate root length leads to a water deficit (low EW) on day 15 but is not a factor thereafter in this well watered crop. On day 30, sink capacity is limited by the small size of the storage root and EA is near saturation for leaf growth; low night temperature (ET) is the main limiting factor. But at day 120, the system is source-limited (low EA; the storage root is very large and has a high capacity for growth) and temperature (ET), surprisingly, is not directly limiting to leaf growth rate.

mechanisms of how that may interact with substrate supply and other factors are also unknown.

Similar problems arise with the developmental concepts embodied in F(AGE). We can visualize F(AGE) as dependent upon the fractions of the organ that remain capable of further weight additions through division, expansion, or differentiation. With the sugar beet model, we approached that with descriptive cell division/differentiation generators to gain realistic simulations of the size of successive leaves (see Figure 5 later) (68). With wheat, Morgan (78) employed a simulation of apex size and primordium generation for that purpose. While the meristematic fraction of a particular organ depends to a considerable extent on past growth, other developmental events depend more on age or inductive conditions. Most crop growth models include aging routines in which chronological time is converted to "physiological time," or experience, with a temperature-response function such as has been found for plastochron events (37, 51), or as a "heat sum" (46). Suberization of roots, senescence, and "maturity" can be mimicked in that way while phasic development may require an additional dependence upon photoperiod (61, 117). Processes such as germination can be modeled with "dispersed delay" routines to generate a distribution of developmental states (28, 57, 95). But all of those approaches are only descriptive of developmental rate.

Leaf initiation rate is a key developmental control for organismal integration because that sets the rate of production of new leaves and lateral potential (67). Modeling of lateral branch initiation and growth has not been well developed. Frijters has expressed branching (41) and inflorescence (40) rule information in analytical equations, but the few crop models which deal with branching (78, 129; Ng unpublished with POTATO) have taken a simpler approach. A potential branching rule is set which is then limited at each iteration by assimilate status and physiological age (i.e. old axillary buds, long suppressed by lack of assimilate, lose their potential for growth). Similar aging/stress routines can be invoked for shedding of plant parts such as the flowers and bolls of cotton (32, 129).

The number, dry weight, and physiological age of various organs thus simulated represent a basic morphological description of the plant. It is also important to know something about the size and disposition of those organs. With leaves, for example, disposition in a foliage canopy influences mutual shading, affecting both production rate and leaf senescence. Crop models generally have depended on descriptive translation techniques using morphological response functions for converting a simulated increment of dry weight into an increment of size. With leaves, the key expression is area and can be translated from the weight of a leaf using an area/weight ratio expressed as a function of temperature and radiation environments, age, and

assimilate status by means of the same "effector" approach we showed for the calculation of growth rates. Fortunately, crop ecology provides considerable information on how area/weight ratios vary with internal and external conditions (but not on why). Information is much less satisfactory on the variations in physiological capability during development.

Cell/Tissue Level

The effort given to modeling tissue and lower levels of organization has been much less than we saw at the higher levels. Crop modelers, with their principal focus on community behavior, find that cellular submodels not only tax their competence but also lead to unmanageably large models. More seriously, we have a very poor understanding of how organ behavior is determined by cellular processes. As a result, tissue-level information in organismal models frequently consists of descriptive functions.

Considering the great amount of information which exists on metabolic pathways, the kinetic properties of enzymes, and biomathematics of component elements, the modeling of tissues does not appear difficult. Some progress has been made with integration of differential equations for uncompartmentalized biochemical components of such systems (43, 71). But placing that into a physiological model of a tissue is another matter (2, 49, 85). Morphological and developmental description is just as essential at the cellular level as at the organismal level. We need to work toward an ability to simulate the changes in metabolic ability and compartmentation which occur during development, and an explanatory approach will require a simulation of the controls over cell differentiation (130).

Critical in our current work with a simulator of nitrate metabolism (85) are the size of the cytosol and vacuolar compartments and the membrane transport capacity between them. No explanatory basis exists now for simulating those entities over time, and they must be dealt with descriptively. Indeed, the word vacuole has become rare in indices of plant physiology texts. We also must use descriptive generators to translate experimental data on the kinetics of biochemical processes in vitro (generally per unit tissue fresh weight or per unit protein) into cellular-level physiological process. Despite those problems, the insights gained from the nitrate model are quite intriguing: while the biochemical model explains the dynamics of certain intermediates, organismal properties (supplies of nitrate and carbon, sinks for amino acids) rather than enzyme kinetics provide the principal means of regulation. Except where branched pathways occur, it seems that metabolic systems can be simplified to single operators, or a few sequentially linked operators, each performing a transfer function according to certain rules.

Models dealing with the stoichiometry of biochemical processes have been more successful than kinetic models. The best example is the elegant

respiration model of Penning de Vries and coworkers (91). In that, a simple set of assumptions regarding synthesis via least-cost pathways, degree of respiratory coupling, and "tool" maintenance allows the model to calculate substrate use, O_2 requirement, and CO_2 production for the respiration associated with the biosynthesis of specific end products. The model has been subjected to validation tests (89, 92) with reasonable success, and unknown elements such as tool maintenance (cost of enzyme and mRNA turnover) were subjected to sensitivity analyses (91).

The Penning de Vries model has been used to calculate biological efficiency in the formation of complex organs (7, 111). And it has been simplified for use in crop growth models (29, 55), where it adds a great deal of explanation to the simulations, and season-long consequences of biomass composition can be evaluated. Its success in those instances results from treatment of the new growth en masse, without attention to cellular detail except to specify the biochemical composition of existing and newly formed biomass.

That approach holds that the respiration costs of biosyntheses and growth are independent of temperature and that temperature operates only through an influence on the rates of biosynthesis. The respiratory costs of cell maintenance must be approached more empirically. In Penning de Vries' (90) analysis, the explanatory basis of maintenance respiration lies principally in coupling to lipid and nonenzymic protein turnover and maintence of ion concentrations. Those processes cannot be assessed in detail, but under normal conditions they can be estimated (90) to require 15 to 25 mg glucose g^{-1} (dry weight) day^{-1} for leaf tissue. That amount falls within the range of observed values. The maintenance respiration load is a critical factor to productivity—variations in its rate between 1 and 3% per day lead to large difference in predictions of organ growth (104) and seasonal productivity (55).

SPECIAL ISSUES IN PHYSIOLOGICAL MODELING

We have noted how the concept of physiological age and the relations between structure and function introduce difficulties for modeling crop growth. In those cases, the modeling efforts provide a new viewpoint for experimental studies on uncommon topics in plant physiology. The following sections comment on two other biological issues of similar promise and on the ways in which modelers have coped with them.

Stochastic Versus Deterministic Simulation

Real biological systems display a great deal of variation at all levels of organization. One part of that variation is the result of the plasticity that plants show with variations in environment; another arises from the geno-

typic variability of plant populations. There are good arguments for sto-
chastic treatment of environment and biological response, but the models
we have described are mostly deterministic in that all plants are of a single
genotype and are exposed to a single starting time and a single environment.
The deterministic approach provides a prediction of mean behavior, follow-
ing the law of large numbers. On a small scale (one cell, one plant), however,
there can be large departures from that mean. Methods for introducing
probabilistic elements into initial conditions and rate variables are readily
available in computer languages. Their use can quickly become a meaning-
less exercise, however. A community model of stochastic plants requires
three-dimensional treatment of space with lateral duplication of the organis-
mal model—a prohibitively large problem. More fundamentally, the
"noise" generated by realistic stochastic treatment of 100 variables over
1000 iterations can exceed by many orders of magnitude the variation found
in real systems. The explanation for that difference is that real systems are
strongly constrained by feedback, functional balances, and other homeo-
static mechanisms. Stochastic variations in individual processes are strongly
damped or eliminated in the integrated system. Thus, explanatory models
must also include feedback mechanisms if they are to achieve realism. The
only alternative is to provide arbitrary limits to the course of the simulation,
and that degenerates to description and leads to a loss of predictive value.
One way of studying variation is to introduce distributive (57) or stochastic
generators into only selected processes. A large number of simulations
would then generate a "genetic" or "environmental" population sample.
We have done little of that because of high cost and questions in interpreta-
tion.

Those questions bear closely on the problems associated with the impor-
tant issue of simulations of mixed vegetation (8, 12, 56, 88). That problem
has yet to be studied seriously with detailed plant growth models, but it is
easier in some respects since specific spatial arrays can be established and
a limited number of genetically different organismal models can be linked
laterally. Complementary models of that sort must give attention to the
vertical distribution of leaves and roots so that central issues of interference
among species for radiation, nutrients, and water are simulated properly.

Adaptation

Some crop growth models automatically predict the larger aspects of cli-
mate-induced physiological and morphological change. Since the simula-
tions are dynamic, the current state of the system (number, size, and age
of organs) represents a condition with adaptation to the environmental
history used in the simulation. Also, as noted above, morphological transla-
tions can be made subject to the current environment (e.g. sun vs shade for
leaves) for each increment of growth.

The deterministic aspects of genetic adaptation are handled easily by a change in model structure to a new "genotype." But physiological adaptation involving alterations in physiological capability per unit tissue (in contrast to the weight of tissue capable of a function) must be handled carefully. Some physiological adjustments occur rapidly. Those can be accommodated by broadening the physiological functions so that optimum performance occurs over a broader range of conditions than might be found with short-term observations [e.g. the photosynthesis-temperature relation in BACROS (29)]. Phenomena such as hardening, with their attendant slow changes in anatomy and physiological capability of both existing and new tissues, are more difficult. If a reasonable data base can be found (which unfortunately is generally not the case), the process can be described in a manner analogous to that of physiological age, using an integrator of stress experience. That indicator can then be used in modifying physiological processes and morphological translations to produce a hardened state. Crop modelers have yet to give serious attention to physiological adaptation. Most are still focused on developing realistic simulations of "normal" plants, well watered and well supplied with nutrients, but eventually we must also come to an ability to simulate acclimatory processes (112).

APPLICATIONS

Crop physiologists have long sought some means for applying physiological information to quantitative interpretations of plant growth in agricultural systems. State-variable models with hierarchic structure deal directly with the translation to the field of mechanisms elucidated in the laboratory. Progress toward interpretation of field behavior has been slow, however, largely because of the nature and infancy of the method. The rather special kinds of physiological and morphological information required as input come largely from specialized-organ and organismal-level research in which the information base is weak. Thus, the modeling efforts couple poorly with the current mainstreams of cellular-level research. In our own programs, we find that 50 to 80% of our effort goes into experiments to fill such information gaps. Other problems arise from the interdisciplinary and subjective nature of the work. Good biology is essential, but biologists generally are not very skilled in systems analysis and the best systems analysts may be poor biologists.

Fall-out benefits, however, such as Penning de Vries' respiration studies (90, 91), the erect-leaf hypothesis (31, 33) and the Buringh-van Heemst (13) analysis of world food production have been significant, and the crop models themselves have been highly useful in certain applications. Some of the major areas merit brief review.

Productivity and Bioclimatology

Many crop models have had yield prediction as a principal objective. In some cases that objective has been attained consistently and well, in others, accuracy is poor. The estimates of gross photosynthesis provided by ecosystem-level models, when corrected for respiration, provide good predictions of primary productivity (1, 24). Economic yields can be derived from that using generalized partitioning factors, and our best current estimates of global food production under various agricultural strategies have been obtained in that way (13).

The addition of an organismal level adds additional environmental dependence and accuracy to the prediction. But most dynamic models with organismal level submodels are aimed more at optimal conditions than at usual commercial conditions. As a result, the multivariate regression models reviewed earlier are still the principal means for yield prediction. With proper tuning, such models accommodate better to average field conditions since the historic data include the effects of variations in plant stand, disease and pests, and nutrient and water supply which may be the principal determinants of yield. Such regression models perform best in predicting the mean performance of a population of fields, whereas the dynamic models may work best with the individual field. Among dynamic models, the Gutierrez cotton model, when parameterized for normal production practice, performs well in prediction (46). BACROS and SUBGOL, which give emphasis to the achievement of realism through hierarchic structure rather than to accuracy, have done surprisingly well in prediction for optimum conditions. That success probably derives from accuracy in simulating photosynthetic productivity, which under optimal conditions varies chiefly with radiation (1).

The orientation of existing crop growth models toward optimal conditions limits their use in crop management research. Exceptions occur with varietal-choice and timing aspects of management. With forage crops, for example, management decisions center on timing and intensity of clipping or grazing. The SIMED alfalfa simulator (52) handles the recovery from such defoliation quite well. The consequences of various management strategies can be given in graphical displays useful for extension education and research.

Dynamic models, either complex or simplified, will be particularly useful in climatological assessments. Preliminary results including the prediction that thermoperiodism can result from the integration of growth processes under diurnal regimes are promising (66). Such models can be used in regional climate analyses (66, 113, 121) and as a basis for upgrading the multivariate methods.

Integrative Physiology and Ideotype Evaluation

The integrative physiological aspects of crop models have been directly relevant to some of the major issues in crop physiology. The greatest advantage comes from quantitative integration over time of simple physiological and morphological traits in source-sink relations. Such models constitute organized bodies of knowledge about whole-plant physiology. The simulations provide a way to describe and explain the consequences of increasing or decreasing photosynthate supply and the number of meristematic centers or their capability for growth. Similarly, one can explore the effects of specific weather sequences.

In the thermoperiodism case (66), large diurnal fluctuations in air temperature placed the growing leaves at temperatures unfavorable for growth for many hours each day. Soil temperature fluctuated less and the roots remained at temperatures favorable for growth throughout the day. Larger sugar beet storage roots were obtained in such simulations.

Since the opinions in the models can be viewed as "genetic traits," the models can serve in a similar way for formulating and evaluating genetic combinations (ideotypes) more suitable in crop production than existing strains (30, 65). At present, plant breeders have little basis other than trial and error for combining quantitative physiological and morphological traits into new phenotypes. An integrative tool is needed because yield improvements through plant breeding almost invariably have come through changes in partitioning rather than through improvements in photosynthetic capability (23, 36). In one example, Duncan et al (34) have shown with a simulation model of peanut that dramatic yield increases in cultivars of that species came solely from changes in flowering time and other aspects of partitioning. In other cases, the simulations allow clear identification of features such as crop duration and slow development of leaf area as principal limits to seasonal yield. It seems likely that future improvements in most crops will also come through changes in partitioning rather than in photosynthesis. That certainly is the case with cotton and sugar beet. But many of the simple partitioning traits such as lodging resistance in small grains have been well explored, and progress will rest more on combinations of quantitative traits. The possible combinations of traits can be very large, but by simulation, certain optimal hypotheses can be identified as breeding objectives.

It is surprising how many model predictions for ideotype concepts are counter-intuitive—a low maintenance respiration requirement may translate into a greater respiration loss over a season [because more biomass is accumulated early (55)]—or outside of conventional wisdom. One hypothesis about sugar beet (from shading experiments) was that storage beet

growth was accomplished from surplus assimilate not used by leaves. That opinion yielded a decent sugar beet simulator, and by changing leaf growth potentials (genetic switch), sugar beet, chard, and mangel phenotypes were generated (67, 68). The simulated result was similar (Figure 5), however, when the control was placed on root growth, i.e. chard leaves became large because their roots had a low capacity for growth. That conflict led to experiments with reciprocal grafts between chard and beet that confirmed the concomitant operation of both hypotheses (68). As another example, the models generally predict that source, not sinks, is limiting to production rate in closed stands. That shows clearly in Figure 4 where growth rate at 120 days is surprisingly independent of temperature. Under those conditions, a high capacity for growth as characterized in hybrid vigor is quickly negated by areal restraints (radiation, water and CO_2 flux). High densities of small plants are shown to do as well as low densities of large, heterotic plants.
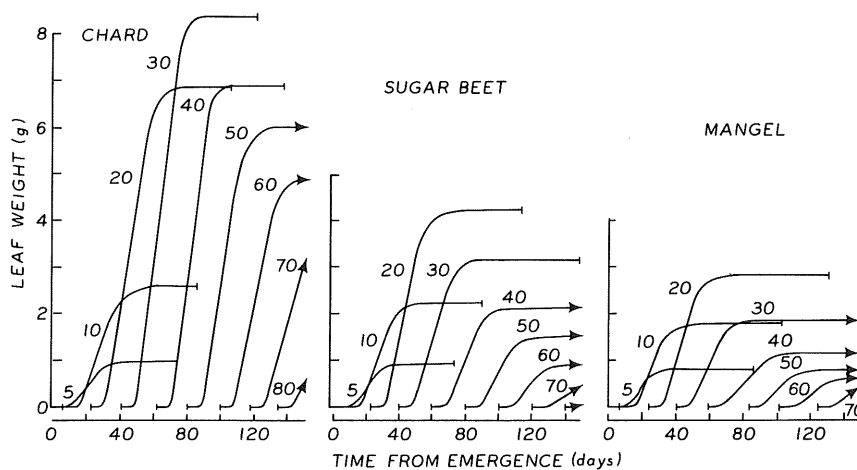

Figure 5   Simulations with SUBGOL of the weights of successively numbered genetically identical sugar-beet leaves. The storage-root submodel was modified to mimic the small roots of chard and the large roots of mangel-wurzeln. Leaves grown in competition with normal sugar beet storage roots are shown in the center, in competition with chard roots to the left, and with mangel-wurzeln roots to the right. Emergence on May 16 with 7 plants m^{-2} at Davis, California (38 N).

The principal features of the juvenile-adult leaf sequence in these varieties is duplicated: small, slow growing leaves early followed by large leaves and then smaller leaves, reflecting the effectors displayed in Figure 4. However, the later leaves are smaller than real leaves, indicating some defect in the model in simulating the plasticity to intra- and interplant competition [adapted from (68)].

Plant-Herbivore Relations

There is an increasing use of crop growth models across trophic levels in which the crop model serves as a dynamic description of the substrate and environment for grazing animals. The emphasis in pest management studies is reflected in Ruesink's review (103). Most entomological models emphasize the description of pest population dynamics, with stochastic submodels to simulate the infection and spread of the insects. The amount and specific sites for insect feeding or disease damage become important. Combined models of that sort have proved to be reliable predictors of pest or disease development and expected injury to the crop, and they are useful in the study of control strategies. Combined models have been developed for many situations with those for cotton (46, 47, 58, 59, 127), alfalfa (45), and apple (95) serving as examples. In some cases, those have led to simplified econometric models for decisions about spraying or praying. There have been similar efforts toward the simulation of plant diseases (125). The combined models also offer a means, little used as yet, for examining biological efficiency (energy and nutrient transfers) in host-parasite couplings.

Similar activity is found with researchers concerned in analyses of the grazing of vegetation by large animals. Much of that work centers on range and pasture management (18, 88, 106) and ruminant nutrition (98), but the issue is met also in studies of natural grazing of tundra (12) and grassland (56, 88). Here again, somewhat simplified vegetation models characterize the supply and nutritional status of feed and the physical environment of the animals. Such models frequently must deal with mixed vegetation, such as the grass-legume combination, and with variations in animal preferences for the various forages.

AN ASSESSMENT: SENSE OR NONSENSE

Several things are now clear about the future of systems analysis in plant physiology. The unbridled enthusiasm that many of us displayed during our early euphoria with the method must now be tempered. A great deal of hard work remains, and "grand" models are not about to substitute for real plants and real experiments. Still, in many ways the modeling is ahead of the information base, and it is likely to remain there as computer capacities increase and costs decline. That is particularly true at the whole-plant level which has not been emphasized in plant physiology research. We can expect the modeling efforts to continue as sources of innovative questions (and sometimes of answers) about those gaps in our knowledge of plant life.

Passioura (86) raised a storm among modelers with a pungent and thoughtful essay on "Sense and Nonsense in Crop Simulation." One of his suggestions was that a little clear thinking about systems problems would contribute more to the advance of our science than complex models. Passioura was not alone among the cautionaries. Crop modeling has shared the criticism directed at other areas of modern ecology as lacking in depth and unifying concepts and subject to excessive jargon. But just as conceptual models such as "carriers" and "genes" and simple analytical models such as Fick's Law and the Michaelis-Menten expression are now integral features of plant physiology, so are hierarchic simulation models. Their *raison d'être* is that the problem is there. No other means exists as powerful for the integrative physiology of plants as adaptive control systems. Quantitative assessments of the importance of various physiological and morphological traits, extrapolations from laboratory to field, conduct of otherwise impossible experiments, and the exploration of integrative controls are all within their domain (4, 80). It was once hoped that phytotrons would fill that role. But phytotrons have not been used effectively for that, and it now seems that modelers will be the principal consumers of phytotron results (37, 50) and that models will be the integrative tool.

We feel also that there is considerable promise for the use of systems analysis for integration at lower levels. The early efforts are promising but nothing in plant physiology yet approaches the detail and sophistication of the models of cellular processes found in animal research. One limitation is the evident lack of a physiological systems view in plant biochemistry for processes other than photosynthesis; modern plant biochemistry texts reflect this in their focus on natural product classes rather than plants. Cell physiologists are well equipped to fill the serious information gap between cell and whole-plant physiology. Progress with tissue-level models would provide considerable help for crop modelers, who have generally proceeded from the top down.

The fact that hierarchic models have been limited more by our knowledge and conceptualizations of the system than by computing facilities, software, and system theory is a natural reflection of the need for at least a few more years of effort in plant physiology research. But the more we learn through reductionist research, the greater the need and opportunity for integrative research. Our conviction is that systems methods will become more and more central to plant physiology.

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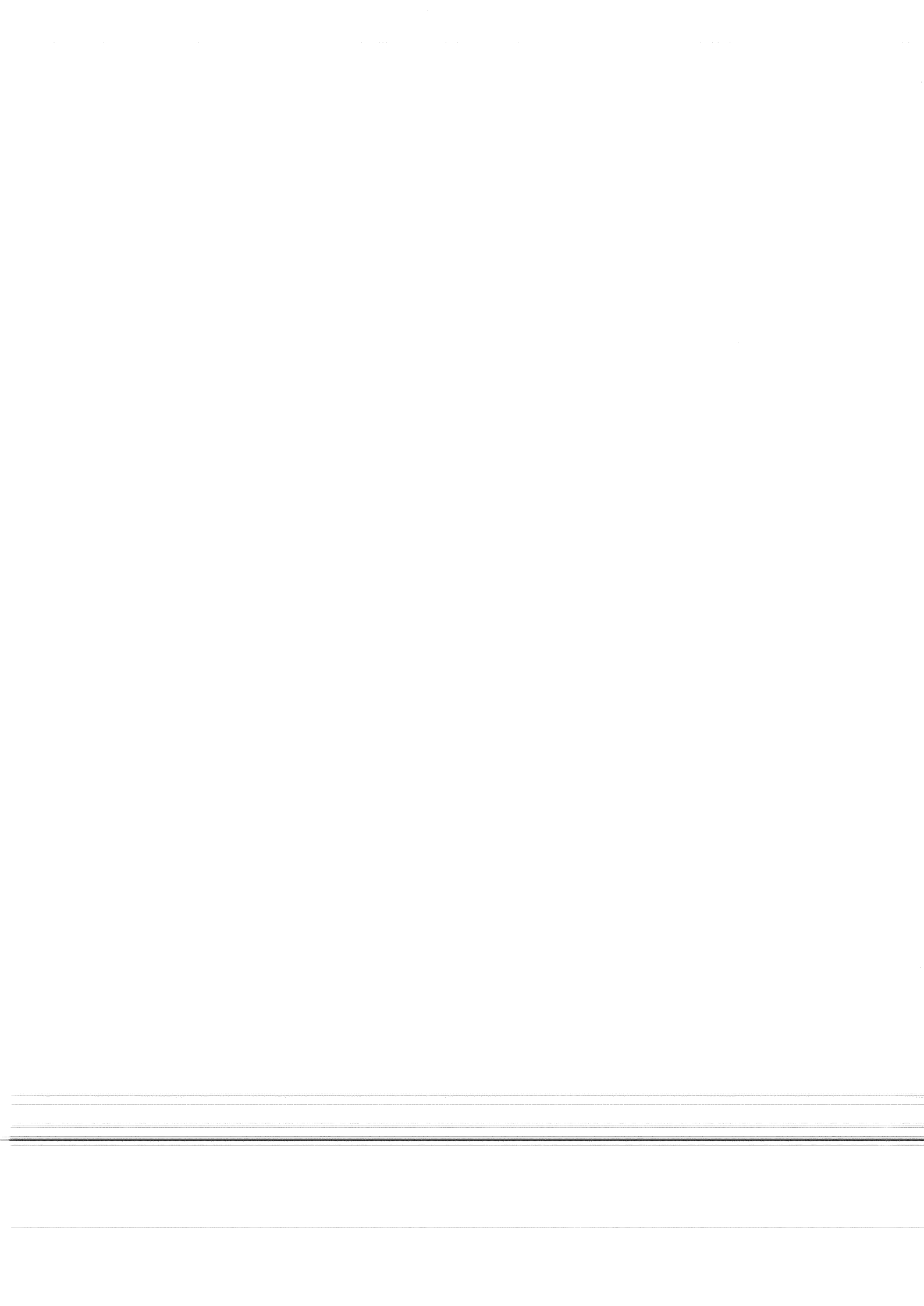52. Holt, D. A., Bula, R. J., Miles, G. E., Schreiber, M. M., Peart, R. M. 1975.

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EXPLANATORY MODELS
IN CROP PHYSIOLOGY

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R. S. Loomis

Department of Agronomy and Range Science, University of California,
Davis, California 95616

R. Rabbinge

Department of Theoretical Production Ecology, The Agricultural University,
Wageningen, The Netherlands

E. Ng

Department of Agronomy and Range Science, University of California,
Davis, California 95616

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The plant sciences have lagged well behind except in the physical aspects of the plant environment and community physiology. We find expanding interest in mathematical formulations of specific biological processes, with major attention given to such subjects as leaf growth and phyllotaxy (35, 69, 124, 128), carrier kinetics (20), photosynthesis (15, 17, 48, 119), and catenary diffusion sequences (84). The biomathematical analysis of physiological problems has been given extended treatments by Nobel (84), Riggs (99), and Thornley (117). In contrast, the integrative systems approach has been limited largely to the higher organization levels. That seems to reflect the quantitative concerns of systems ecologists and others, particularly of agronomists, for the behavior of vegetation. The grassland (56, 88) and tundra (12) biome studies, as examples, are impressive for their scope but are short in physiological detail. Workers in those areas have drawn more on the concepts of systems analysis and environmental physics as the starting point for their work. The systems level is also the arena for our own work on physiological models, emphasized in this essay. Our models focus on the organismal and systems levels, but the approach outlined is also applicable to integration at lower levels.

We distinguish two broad categories of crop models: same-level descriptive models and multilevel explanatory models. A wide range of descriptive models exist. Multivariate regression models, for example, are used widely for the important task of yield prediction in variable climates (10, 81, 82, 93, 96, 116). Such models may be static, i.e. involving no concept of time. Variables in that case are integrated seasonal totals of yield, rainfall, and temperature. Sophistication is improved by introducing some concept of time based, for example, on the calculation of developmental rate as a function of temperature during the season (101, 108) and by sharpening the environmental parameters, e.g. use of a soil moisture balance rather than rainfall as an input variable (3, 10).

The explanatory approach emphasized here is considerably more sophisticated. It employs dynamic models of the system hierarchy in an effort to provide prediction and explanation of integrated behavior from more detailed knowledge of the underlying physiological and morphological processes (26, 28). All such knowledge becomes descriptive at the ultimate level of reduction. While crop models do not go that far, they do become descriptive where knowledge is lacking or simplification is required. However, with a hierarchic structure, description at lower levels becomes explanatory of higher levels. A dynamic structure also aids in explanation, and the capability for continuous printout of many variables contrasts to experimental work generally providing observations only for discrete times.

In dynamic models, a system is described by a set of *state variables* (such as the weights of various organs) that are updated at each iteration of the model by *rate variables* (such as the flow of carbon in photosynthesis and

Although explanatory hierarchic modeling is still in its infancy and has not been subject to extensive development by systems analysts (70), the method holds great potential for plant physiology. Starting in the mid-1960s (11, 22, 114), it has become an active area of research by crop physiologists. For example, Milthorpe & Moorby's *Crop Physiology* (73) derives from their efforts in dynamic modeling, and the Trebon (107) and Long Ashton (62) conference volumes show a heavy modeling content. Much of the current activity is reported at workshops and in limited distribution publications. *Annals of Botany, Agricultural Meteorology, Journal of Theoretical Biology, Crop Science,* and the Dutch *Simulation Monographs* are among the major publications for botanical models. Rather than attempting an exhaustive review, the following essay draws largely from our own work. Our plan is: first, to present a limited background on the state-variable approach to systems analysis; second, to outline some of the special problems and attributes found in crop models at community, organismal, and cellular levels; and then to close with a survey of applications.

THE MODELING PROCESS

Model building should begin with a clear formulation of objectives concerning the use of the completed model. Biological systems are so complex that their models always represent a simplification or abstraction of the real system. That contrasts with some cases in engineering where the realized machine may be only an approximation of the perfection visualized in the model or plan. The objectives provide a basis for decisions about necessary simplifications. A second task, involving identification of the variables and processes that define the system, is aided by relational diagrams for the main variables (such as Figure 1). That task is coupled with the formulation of mathematical expressions for rate variables (i.e. differential equations). The choice and structure of those equations constitute a set of implicit assumptions about the system which should be carefully defined. The same is true in the choice of parameters for the equations. Taken together, the model with its parameterized equations represents a collective hypothesis about the real system. That leads directly to the construction of a computer program to execute the model and then to the critical step of validation (122).

Validation is distinguished from verification, which means testing to see that the computer program in fact operates on input data in the intended way. In addition to an a priori analysis of the model's structure (81a), validation generally involves comparison of model predictions with results from independent experiments relating to both processes (e.g. photosynthesis rate) and system states (e.g. biomass levels) (see Figure 2, p. 347). Some

weekly advances. But an interval of 1 to 2 hours must be used if sensitivity to diurnal events is required, while stomatal closure and some cellular processes require intervals of minutes or even seconds for accurate simulation.

Those facts cause coupling difficulties of the "stiff-system" sort when very fast subsystems are used to explain the behavior of the slower whole. If computer time is freely available, that problem is overcome by operating with an iteration interval appropriate to the fastest subsystem. Costs can be reduced sharply with special integration routines which allow the use of longer time intervals (43a), but those have yet to be used widely by crop modelers. Crop modelers sometimes use empirical submodels with slower time constants on the basis that less error results from that than from other features of their models. Alternatively, one can avoid the problem by limiting the hierarchic structure to two or three levels and thus restricting the range of time constants within the memory and computational capacities of their computers (and budgets). Either approach tends to compromise our objective of developing explanatory detail. At any level of detail, coupling problems are reduced by the introduction of negative feedback control since slight overshoot in one part of the system in one iteration tends to be corrected by a slight undershoot in the next.

Modeling can be facilitated with special simulation languages designed for use with state-variable models (9, 14, 39, 94). Such languages include integration routines, Gaussian generators, timing and array devices, automatic input/output formating, function generators for interpolation of tabular data, and a selection of more specialized intrinsic functions that can be accessed easily. Such languages are more expensive of computer time but save effort in programming. More important, the simplified programs can serve as a means for communication between modeler and experimenter. Thus far, plant modelers generally have not selected a universal simulation language. That plus the fact that few crop models are directed to the same objective means that very few standard program modules are shared by different modelers.

HIERARCHIC LEVELS IN CROP GROWTH MODELS

The principal focus of the output of crop growth models is community behavior. Such models simulate the production of new photosynthates, the partitioning of that material to growth, respiration and storage, and the related morphogenesis. The greatest attention is given to the state variables that define the environment and the age, weight, and morphology of the main elements of the biomass. That may be done with perhaps 50 to 100 state variables (21, 22, 87, 118). Computer models with 100 state variables

tivity) are used also for nutrient and water fluxes into roots and for water and carbon dioxide exchange by the leaves. Several interesting issues develop here. The conductivity term can be defined explicitly for a small system—in the case of roots, a single cell, or a small root segment—but it takes on a more general, empirical context when applied to a whole root system. But subdivision into smaller parts or layers can introduce a stiff-system problem. Radiation, for example, is absorbed at the surface soil layer and within leaves by very thin strata with a low capacity for heat storage. Those strata change temperature very rapidly in contrast to mixed air and the rest of the soil, which as large systems have much greater heat capacities and change temperature more slowly with time. Goudriaan (44) modeled that with a "bypassing" method in which the fast system is iterated to steady state and then abandoned (assumed to remain in steady state) until a new iteration is made of the higher level.

Organismal/organ-level elements, such as the size and characteristics of the foliage and root systems, enter directly into some of the physical processes. Most crop models have dealt only with random or homeogeneous distributions of roots and leaves within each layer, although other distributions may be important in nature. Those other arrangements, e.g. with plants in rows, can become quite complex (16, 42, 44). Microclimate models frequently include biological processes such as stomatal behavior, which
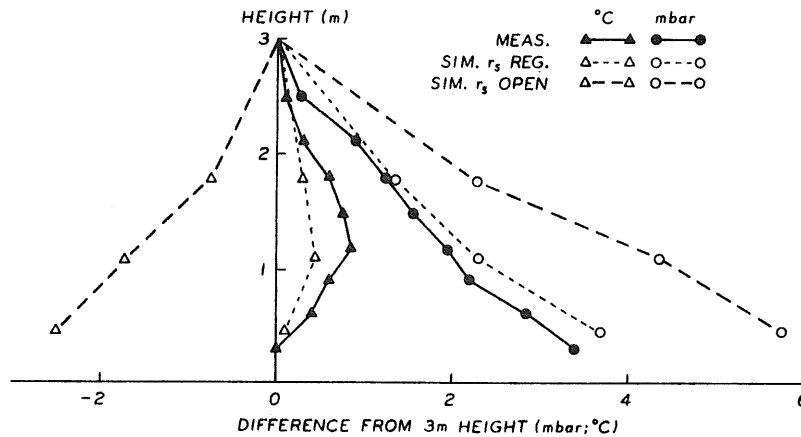

Figure 2 Validation of the BACROS, flux-dependent, microclimate simulator for air temperature and humidity through comparisons with profiles measured within a corn crop at Wageningen, the Netherlands. The profiles indicate the difference in temperature and humidity within the canopy as compared to that observed above the canopy at 3 m. Simulations with and without stomatal regulation represent a sensitivity analysis for the necessity of a submodel on stomatal control [adapted from (29)].

light-response function for leaf photosynthesis (37). The clear and overcast tables are interpolated at each hour according to solar angle and the ratio of potential and current daily total radiation (thus adjusting for cloudiness). Those hourly rates are then reduced by temperature and water-deficit functions, but CO_2 variations are ignored. Both approaches provide fast and reasonably accurate simulations of the photosynthate supply available for plant growth.

Organ/Organismal Level

The simplified vegetation models provide a framework within which the whole-plant level can be developed. An important aspect of that coupling is that a simulation of competitive effects due to varying plant density is achieved. At the plant level we can focus on detailed morphological descriptions of roots, stems, and leaves and their growth and ontogeny. Such models serve as means to explore partitioning and developmental processes and as a basis for integrative explanations of vegetation-level processes. Gutierrez et al (46) and Wang et al (127) incorrectly characterized crop growth models of that type as "single-plant" models (and also their limited-ecosystem model as a "population" model). Rather clearly, vegetation processes are simulated in such models at the ecosystem level, and those processes provide the photosynthate supply, water and nutrient status, and external environment which serve as forcing and auxiliary variables for the plant level. The multilevel model thus becomes reductionist as well as integrative.

Options exist to divide the plant into functional morphological classes (leaves, stems, and roots) and model each class en masse, or to model each individual leaf, internode, tuber, or fibrous root. Even when successive organs are considered separately, that is usually done for a "standard plant" so that the organs of all plants are identical. The en masse method may be used when ecosystem behavior is the principal interest, but the individual organ approach is usually required when integrative physiology is the aim. Some models take an intermediate approach by simulating the bulk behavior of all leaves or roots within specific "age" classes. That facilitates distinction of physiological capabilities (e.g. growth or senesence) according to developmental state and is a common approach for root systems. The age classes can be retained in programming devices known as "pushdown tables," advanced by an aging or developmental-rate submodel.

Modeling the initiation, growth, and development of individual organs in an explanatory way is not always easy or in some cases even possible. Little information exists about the mechanisms controlling the morphogenesis of individual organs. In many cases, the modeling becomes descriptive—for example, by using a temperature-dependent plastochron to control the
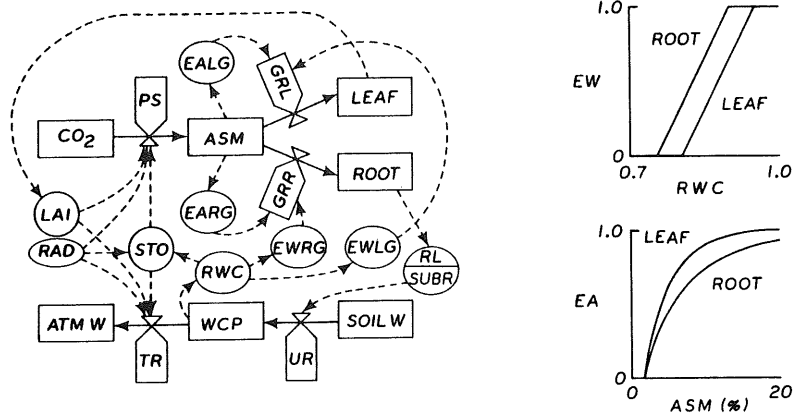
Figure 3   A relational diagram for a hypothesis about the functional balance of root and leaf growth based on carbon and water. The transfer of water from the soil through the plant to the air determines the current water content of the plant (WCP) and its relative water content (RWC). RWC in turn regulates root and leaf growth rates, according to the response functions (EW) shown to the right, and stomates. Also on the right are the response functions for the effects of assimilate supply (EA) on growth rates. Stomatal status (STO) is influenced by current radiation (RAD) and RWC and in turn regulates transpiration (TR) and photosynthesis (PS). The feedback from ROOT weight to water uptake rate (UR) involves root length (RL) and its suberization (SUBR) with age.

Structure similar to this is used in BACROS, SUBGOL, and POTATO.

growth is more affected than root growth by water or nutrient status (root supply functions) and root growth is more affected than shoot growth by assimilate status (a shoot supply function). Such *functional balances* represent hierarchic (across level) feedback loops, and their inclusion provides realistic organismal integration and greatly increases the power of the model. In addition, the door is then open to validation against data from root pruning and defoliation experiments (27, 38).

The state variables of interest in simulating the growth of an organ are its weight at present (W_t) and its rate of growth (GR). A common formulation is:

$$GR = MRGR \cdot F(AGE) \cdot W_t \cdot MIN(EA, EW, ET)$$

where MRGR is the maximum unrestrained relative growth rate (g $g^{-1}t^{-1}$), and F(AGE) is an "age"-dependent fraction of organ weight still capable of growth. MIN(EA, EW, ET) indicates the use of Liebig's law of the minimum to choose among the response functions for the most limiting of the effects of assimilate supply (EA), water status (EW), or temperature (ET) in that iteration. The new weight of the organ at the future time can

mechanisms of how that may interact with substrate supply and other factors are also unknown.

Similar problems arise with the developmental concepts embodied in F(AGE). We can visualize F(AGE) as dependent upon the fractions of the organ that remain capable of further weight additions through division, expansion, or differentiation. With the sugar beet model, we approached that with descriptive cell division/differentiation generators to gain realistic simulations of the size of successive leaves (see Figure 5 later) (68). With wheat, Morgan (78) employed a simulation of apex size and primordium generation for that purpose. While the meristematic fraction of a particular organ depends to a considerable extent on past growth, other developmental events depend more on age or inductive conditions. Most crop growth models include aging routines in which chronological time is converted to "physiological time," or experience, with a temperature-response function such as has been found for plastochron events (37, 51), or as a "heat sum" (46). Suberization of roots, senescence, and "maturity" can be mimicked in that way while phasic development may require an additional dependence upon photoperiod (61, 117). Processes such as germination can be modeled with "dispersed delay" routines to generate a distribution of developmental states (28, 57, 95). But all of those approaches are only descriptive of developmental rate.

Leaf initiation rate is a key developmental control for organismal integration because that sets the rate of production of new leaves and lateral potential (67). Modeling of lateral branch initiation and growth has not been well developed. Frijters has expressed branching (41) and inflorescence (40) rule information in analytical equations, but the few crop models which deal with branching (78, 129; Ng unpublished with POTATO) have taken a simpler approach. A potential branching rule is set which is then limited at each iteration by assimilate status and physiological age (i.e. old axillary buds, long suppressed by lack of assimilate, lose their potential for growth). Similar aging/stress routines can be invoked for shedding of plant parts such as the flowers and bolls of cotton (32, 129).

The number, dry weight, and physiological age of various organs thus simulated represent a basic morphological description of the plant. It is also important to know something about the size and disposition of those organs. With leaves, for example, disposition in a foliage canopy influences mutual shading, affecting both production rate and leaf senescence. Crop models generally have depended on descriptive translation techniques using morphological response functions for converting a simulated increment of dry weight into an increment of size. With leaves, the key expression is area and can be translated from the weight of a leaf using an area/weight ratio expressed as a function of temperature and radiation environments, age, and

respiration model of Penning de Vries and coworkers (91). In that, a simple set of assumptions regarding synthesis via least-cost pathways, degree of respiratory coupling, and "tool" maintenance allows the model to calculate substrate use, O_2 requirement, and CO_2 production for the respiration associated with the biosynthesis of specific end products. The model has been subjected to validation tests (89, 92) with reasonable success, and unknown elements such as tool maintenance (cost of enzyme and mRNA turnover) were subjected to sensitivity analyses (91).

The Penning de Vries model has been used to calculate biological efficiency in the formation of complex organs (7, 111). And it has been simplified for use in crop growth models (29, 55), where it adds a great deal of explanation to the simulations, and season-long consequences of biomass composition can be evaluated. Its success in those instances results from treatment of the new growth en masse, without attention to cellular detail except to specify the biochemical composition of existing and newly formed biomass.

That approach holds that the respiration costs of biosyntheses and growth are independent of temperature and that temperature operates only through an influence on the rates of biosynthesis. The respiratory costs of cell maintenance must be approached more empirically. In Penning de Vries' (90) analysis, the explanatory basis of maintenance respiration lies principally in coupling to lipid and nonenzymic protein turnover and maintence of ion concentrations. Those processes cannot be assessed in detail, but under normal conditions they can be estimated (90) to require 15 to 25 mg glucose g^{-1} (dry weight) day^{-1} for leaf tissue. That amount falls within the range of observed values. The maintenance respiration load is a critical factor to productivity—variations in its rate between 1 and 3% per day lead to large difference in predictions of organ growth (104) and seasonal productivity (55).

SPECIAL ISSUES IN PHYSIOLOGICAL MODELING

We have noted how the concept of physiological age and the relations between structure and function introduce difficulties for modeling crop growth. In those cases, the modeling efforts provide a new viewpoint for experimental studies on uncommon topics in plant physiology. The following sections comment on two other biological issues of similar promise and on the ways in which modelers have coped with them.

Stochastic Versus Deterministic Simulation

Real biological systems display a great deal of variation at all levels of organization. One part of that variation is the result of the plasticity that plants show with variations in environment; another arises from the geno-

The deterministic aspects of genetic adaptation are handled easily by a change in model structure to a new "genotype." But physiological adaptation involving alterations in physiological capability per unit tissue (in contrast to the weight of tissue capable of a function) must be handled carefully. Some physiological adjustments occur rapidly. Those can be accommodated by broadening the physiological functions so that optimum performance occurs over a broader range of conditions than might be found with short-term observations [e.g. the photosynthesis-temperature relation in BACROS (29)]. Phenomena such as hardening, with their attendant slow changes in anatomy and physiological capability of both existing and new tissues, are more difficult. If a reasonable data base can be found (which unfortunately is generally not the case), the process can be described in a manner analogous to that of physiological age, using an integrator of stress experience. That indicator can then be used in modifying physiological processes and morphological translations to produce a hardened state. Crop modelers have yet to give serious attention to physiological adaptation. Most are still focused on developing realistic simulations of "normal" plants, well watered and well supplied with nutrients, but eventually we must also come to an ability to simulate acclimatory processes (112).

APPLICATIONS

Crop physiologists have long sought some means for applying physiological information to quantitative interpretations of plant growth in agricultural systems. State-variable models with hierarchic structure deal directly with the translation to the field of mechanisms elucidated in the laboratory. Progress toward interpretation of field behavior has been slow, however, largely because of the nature and infancy of the method. The rather special kinds of physiological and morphological information required as input come largely from specialized-organ and organismal-level research in which the information base is weak. Thus, the modeling efforts couple poorly with the current mainstreams of cellular-level research. In our own programs, we find that 50 to 80% of our effort goes into experiments to fill such information gaps. Other problems arise from the interdisciplinary and subjective nature of the work. Good biology is essential, but biologists generally are not very skilled in systems analysis and the best systems analysts may be poor biologists.

Fall-out benefits, however, such as Penning de Vries' respiration studies (90, 91), the erect-leaf hypothesis (31, 33) and the Buringh-van Heemst (13) analysis of world food production have been significant, and the crop models themselves have been highly useful in certain applications. Some of the major areas merit brief review.

Integrative Physiology and Ideotype Evaluation

The integrative physiological aspects of crop models have been directly relevant to some of the major issues in crop physiology. The greatest advantage comes from quantitative integration over time of simple physiological and morphological traits in source-sink relations. Such models constitute organized bodies of knowledge about whole-plant physiology. The simulations provide a way to describe and explain the consequences of increasing or decreasing photosynthate supply and the number of meristematic centers or their capability for growth. Similarly, one can explore the effects of specific weather sequences.

In the thermoperiodism case (66), large diurnal fluctuations in air temperature placed the growing leaves at temperatures unfavorable for growth for many hours each day. Soil temperature fluctuated less and the roots remained at temperatures favorable for growth throughout the day. Larger sugar beet storage roots were obtained in such simulations.

Since the opinions in the models can be viewed as "genetic traits," the models can serve in a similar way for formulating and evaluating genetic combinations (ideotypes) more suitable in crop production than existing strains (30, 65). At present, plant breeders have little basis other than trial and error for combining quantitative physiological and morphological traits into new phenotypes. An integrative tool is needed because yield improvements through plant breeding almost invariably have come through changes in partitioning rather than through improvements in photosynthetic capability (23, 36). In one example, Duncan et al (34) have shown with a simulation model of peanut that dramatic yield increases in cultivars of that species came solely from changes in flowering time and other aspects of partitioning. In other cases, the simulations allow clear identification of features such as crop duration and slow development of leaf area as principal limits to seasonal yield. It seems likely that future improvements in most crops will also come through changes in partitioning rather than in photosynthesis. That certainly is the case with cotton and sugar beet. But many of the simple partitioning traits such as lodging resistance in small grains have been well explored, and progress will rest more on combinations of quantitative traits. The possible combinations of traits can be very large, but by simulation, certain optimal hypotheses can be identified as breeding objectives.

It is surprising how many model predictions for ideotype concepts are counter-intuitive—a low maintenance respiration requirement may translate into a greater respiration loss over a season [because more biomass is accumulated early (55)]—or outside of conventional wisdom. One hypothesis about sugar beet (from shading experiments) was that storage beet

Plant-Herbivore Relations

There is an increasing use of crop growth models across trophic levels in which the crop model serves as a dynamic description of the substrate and environment for grazing animals. The emphasis in pest management studies is reflected in Ruesink's review (103). Most entomological models emphasize the description of pest population dynamics, with stochastic submodels to simulate the infection and spread of the insects. The amount and specific sites for insect feeding or disease damage become important. Combined models of that sort have proved to be reliable predictors of pest or disease development and expected injury to the crop, and they are useful in the study of control strategies. Combined models have been developed for many situations with those for cotton (46, 47, 58, 59, 127), alfalfa (45), and apple (95) serving as examples. In some cases, those have led to simplified econometric models for decisions about spraying or praying. There have been similar efforts toward the simulation of plant diseases (125). The combined models also offer a means, little used as yet, for examining biological efficiency (energy and nutrient transfers) in host-parasite couplings.

Similar activity is found with researchers concerned in analyses of the grazing of vegetation by large animals. Much of that work centers on range and pasture management (18, 88, 106) and ruminant nutrition (98), but the issue is met also in studies of natural grazing of tundra (12) and grassland (56, 88). Here again, somewhat simplified vegetation models characterize the supply and nutritional status of feed and the physical environment of the animals. Such models frequently must deal with mixed vegetation, such as the grass-legume combination, and with variations in animal preferences for the various forages.

AN ASSESSMENT: SENSE OR NONSENSE

Several things are now clear about the future of systems analysis in plant physiology. The unbridled enthusiasm that many of us displayed during our early euphoria with the method must now be tempered. A great deal of hard work remains, and "grand" models are not about to substitute for real plants and real experiments. Still, in many ways the modeling is ahead of the information base, and it is likely to remain there as computer capacities increase and costs decline. That is particularly true at the whole-plant level which has not been emphasized in plant physiology research. We can expect the modeling efforts to continue as sources of innovative questions (and sometimes of answers) about those gaps in our knowledge of plant life.

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