

The next generation models for crops and agro-ecosystems

ZHU XinGuang^{1,2*}, ZHANG GuiLian¹, THOLEN Danny¹, WANG Yu¹,
XIN ChangPeng¹ & SONG QingFeng¹

¹*Plant Systems Biology Group, CAS-MPG Partner Institute and Key Laboratory
for Computational Biology, Shanghai Institutes for Biological Sciences,
Chinese Academy of Sciences, Shanghai 200031, China;*

²*Institute of Plant Physiology and Ecology, Shanghai Institute for Biological Sciences,
Chinese Academy of Sciences, Shanghai 200032, China*

Received May 10, 2010; accepted December 31, 2010

Abstract Growth in population, decrease in arable land area, and change in climate are endangering our food security. Precision agriculture has the potential to increase crop productivity through tailored agricultural practices for different growing areas. Many models of crops and agro-ecosystems capable of predicting interaction between plants and environments have been developed for precision agriculture. Currently, there are several representative categories of crop and agro-ecosystem models, including the de Wit school models, the DSSAT series models and the APSIM series models, which have contributed substantially to improvement of agricultural practices. However, these models are weak in predicting performances of crops under environmental and genetic perturbations are generally weak, which severely limits the application of these models in guiding precision agriculture. We need to develop the next generation crop and agro-ecosystems models with a high level of mechanistic basis, which can be integrated with high throughput data and can predict the heterogeneity of environmental factors inside canopy and dynamic canopy photosynthesis. In developing such a model close collaboration is inevitably required among scientists from different disciplines. The successful development and application of such models will undoubtedly advance precision agriculture through providing better agronomical practices tailored for different growing environments. These models will also form a basis to identify breeding targets for increased productivity at given location with given soil and climatic conditions.

Keywords crop models, ecosystem models, crop yields, nonlinear analysis, photosynthesis

Citation Zhu X G, Zhang G L, Tholen D, et al. The next generation models for crops and agro-ecosystems. *Sci China Inf Sci*, 2011, 54: 589–597, doi: 10.1007/s11432-011-4197-8

1 Introduction

Ensuring food security is a key challenge facing our society. During the past few decades, the crop yield per unit area has been dramatically increased through breeding better germplasm and improving agricultural practices, such as better pest and weeds control, increased irrigation and fertilization, etc. Unfortunately, though global population continues increasing, crop yield per unit area shows little, if any, increase in the past ten years [1, 2]. There are a number of other factors endangering global food

*Corresponding author (email: zhuxinguang@picb.ac.cn)

security, e.g., the global climate change, in particular the increased frequencies of extreme weather events such as flooding, drought, and the increased proportion of protein-rich diet in developing countries. In 2008, a rumor about the potential shortage of rice production caused riots in many countries across the world. Given the increased urbanization, it is also unlikely to increase crop productivity through increased arable land area; as a result, increasing crop yield per unit land area becomes a major challenge facing plant biologists and agronomists. Precision agriculture holds great potential to dramatically increase crop productivity through tailoring agricultural practices and germplasms to fit the particular weather and soil conditions in each crop growing area.

The core of precision agriculture is to manage agricultural practices, such as sowing density, fertilizer needs, and other input parameters, based on the variability in field conditions [3], which correspondingly heavily relies on the capacity to accurately predicting responses of crop growth and development under different weather, soil, and other environmental conditions using models. In this paper, we first analyze the significance of crop models in guiding improving crop yields, then we explain the status quo of crop and agro-ecosystem modeling, and demonstrate that modern agronomy, plant biology, and computational sciences enable development of the next generation models of crops and agro-ecosystems. Several research areas that need to be advanced to develop the next generation models of crops and agro-ecosystems are then briefly listed. In the end, we call for a close collaboration between scientists working in related disciplines.

2 The next generation crop and agro-ecosystems models will play important roles in modern precision agriculture and plant biology research

The exploration of crop and agro-ecosystem models will play important roles in helping control crop growth and development through designing proper irrigation and fertilization practices, and correspondingly in helping improve yields under different field conditions. Crop yields not only depend on intrinsic properties of plant growth and development, but also rely on the nonlinear interaction between plants and external environments. For example, canopy photosynthesis, which generates material required for the growth and development of crops, is influenced by such intrinsic properties as leaf nitrogen content, leaf photosynthetic properties, and leaf area index, and extrinsic properties including humidity, light, and temperature [4, 5]. Temperature influences canopy photosynthesis in a highly nonlinear manner. For example, under low temperatures, increasing temperature increases photosynthetic rates; while under high temperatures, increasing temperature decreases photosynthetic rates [6]. Water and light conditions also influence photosynthesis similarly [5, 7, 8]. The influence of one environmental (stress) factor on photosynthesis may depend on other environmental factors. For example, under low or high temperature, or drought conditions, leaves are more prone to photoinhibition [9]. Such nonlinearities between influences of different factors on photosynthesis and various other crop growth and developmental processes make it challenging to empirically select the best agricultural practices (mainly the scheduling of irrigation and fertilizer application) for different field conditions.

Developing mechanistic models of crops and agro-ecosystems will help coordinate vegetative growth and reproductive growth, which are also critical to gaining high crop yields. If vegetative growth is more than necessary, the reproductive growth might be hampered due to either shortage of time, or shortage of nutrients available for construction of the reproductive organs. In contrast, if vegetative growth is deficient, reproductive growth will also be hampered simply due to low supply of carbohydrate from vegetative growth [10, 11]. Developing mechanistic models of crop growth and development, which can predict timing and duration of different development stages under different soil and weather conditions, will be critical to coordinating vegetative and reproductive growth through selecting optimal agronomical practices, i.e. scheduling of irrigation and fertilization scheduling based on the differential impacts of water and nutrients on plant developmental progression [12].

Thirdly, models of crops and agro-ecosystems with a high level of mechanistic basis will help identify breeding targets to increase crop potential yields. More and more field and theoretical evidence has suggested that increasing crop photosynthetic energy conversion efficiency (ε_c), i.e. the efficiency of plant

converting light energy into chemical energy using photosynthesis, represents a feasible and rewarding approach to increasing potential yields [5, 13]. However, identification of potential approaches to increasing ε_c is extremely challenging. First, more than 100 proteins are involved in various aspects of photosynthesis [14–16]. Even if we assume that a) only 10 genes in photosynthesis are closely related to ε_c ; b) the activity of each enzyme or protein coded by photosynthetic gene can only be doubled or halved, the identification of the optimal combination of genes for ε_c under a particular environment would require 2^{10} transgenic experiments. Adding to this complexity, photosynthesis interacts closely with respiration, nitrogen metabolism, water transport, etc., and can be influenced by a number of environmental factors in a highly nonlinear way [5]. So, ε_c reflects the coordination of whole plant central metabolism [17]. Furthermore, plant productivity is not determined by the photosynthesis of a single leaf, but rather by the total photosynthesis of a whole plant canopy over a whole growing season [5]. The photosynthesis in the field is influenced by the variability of weather (light, temperature, humidity, precipitation), soil conditions (soil type, soil water content, water table), and changes in photosynthetic physiological properties over the growing season. Given this complexity, experimental approaches to identifying targets to engineer higher productivity are not feasible, or not economical. Mathematical modeling, combined with optimization techniques, provides a feasible approach to tackle this challenge. In this regard, a model of photosynthetic carbon metabolism has been developed and combined with an evolutionary algorithm to identify engineering targets for higher photosynthetic CO₂ uptake rate [5, 18].

In addition to supporting application research, the next generation models of crops and agro-ecosystems also hold great potential in basic research of plant biology. One major feature of a highly mechanistic model of crops and agro-ecosystems is its ability to link high throughput genomic data, e.g. genomic sequences, RNA expression data, proteomics data, and metabolomics data, to observable macroscopic phenotypes. Such a direct linkage makes it possible to test molecular mechanisms underlining macroscopic phenomena, such as molecular changes responsible for adaptation of photosynthesis under different light and CO₂ conditions [19]. Such models will also help evaluate the ability of our current crop systems to provide food, energy, and other ecosystem services in various predicted global climate change scenarios.

2.1 Representative crop and agro-ecosystem models

Many crop and agro-ecosystem models have been developed since the 1960s, which contributed substantially to our understanding of the interaction of crops and environments, crop management and crop improvements [20, 21]. Here we briefly introduce a number of representative models of crops and agro-ecosystems. At the end of this section, the needs for further development of crop and agro-ecosystem models are discussed.

2.1.1 *School of de Wit models*

Dr. de Wit of Wageningen Agricultural University started developing crop growth and development models, usually termed “School of de Wit” models [22]. These models predict the crop potential yields, which are further modified by the availability of water, nitrogen and nutrients. Representative models in this series include ELECROS [23], BACROS [24, 25], SUCROS [26], WOFOST [27], MACROS [28], LINTUL [29]. These models can be used for hypothesis testing to predict plant growth and development under various scenarios of global climate change or altered agronomical practices.

2.1.2 *DSSAT model series*

The DSSAT (decision support system for agro-technology transfer) models developed specialized modules for different crops [21] in modeling the vegetative and reproductive growth process, detailed physiological processes including photosynthesis, respiration, photosynthate allocation, plant growth and senescence, and also the soil nitrogen cycle. Currently, the series of models have already included modules for 16 different crop species, e.g. wheat, maize, rice, sorghum, soybean, millet, peanut, sugarcane, and cassava. DSSAT models have also been combined with geography information systems (GIS) [30].

2.1.3 *APSIM model*

APSIM (agricultural production system simulator) is an agro-ecosystem modeling platform that integrates various crop models developed by Australia scientists [31]. Compared to DSSAT and school of de Wit model series, APSIM focuses on simulating soil processes, especially the effects of different climatic and management factors on soil processes. Another feature of APSM is its modularized design: modules describing processes related to climate, soil, water, nutrition, and crop physiology are individually developed and used as basic building blocks for whole models. Users can assemble different modules to create customized models that fit particular environments and crops. APSM can support crop agronomical practice selection and soil management [31].

Besides these three model series, a number of other models also have contributed much to either basic or applied researches in crop or agronomic sciences. In particular, the CENTURY model simulates the dynamics of carbon, nitrogen, phosphorus and sulfur in soil [32], which has been adopted in many crop simulation models, e.g. DSSAT models [21] and WIMOVAC [33]. So far, though these different models have substantially contributed to agriculture and plant biology research, an accurate description of the mechanisms underlying growth and development and the mechanisms underlying the interaction of plants with their environments is still lacking. This severely inhibits the potential of these models to predict responses of plant growth and development under new environments for which these models are yet to be parameterized. In the next section, we will demonstrate that the advances in plant biology make it ready to develop the next generation models of crops and agro-ecosystems, which has improved capacity to predict the responses of crop growth and development under environmental changes.

2.2 It is time to develop the next generation models of crops and agro-ecosystems

The mechanistic biochemical model of photosynthesis [34] has been used in many crop and agro-ecosystem models [21, 33]. Though Farquhar model has proven extremely successful in predicting photosynthesis at leaf and canopy levels [34], it fails to simulate the complex interactions between photosynthesis and other plant physiological processes including respiration, nitrogen metabolism, and water movement through the soil-root-stem-leaf-atmosphere continuum. Recent years have seen many rapid advances in molecular mechanisms underlying interactions of photosynthesis with other physiological processes, e.g. photosynthesis and respiration [7, 17, 35], photosynthesis and nitrogen metabolism [36], photosynthesis, stomatal conductance and leaf water status [37], which forms the basis to develop new models to simulate the interaction between these different metabolic and physiological processes. Well-established algorithms for developing mechanistic models of plant metabolism have already been used to develop various metabolic models [5, 18, 38].

In addition to the close linkage between different metabolic processes, the expression of key enzymes involved in different metabolic processes is constantly adjusted or regulated in responses to various environments. For example, sugars, in particular sucrose and glucose, regulate expression of photosynthetic genes [39–41]. The carbon and nitrogen metabolisms closely interact and regulate each other [42, 43]. The molecular mechanisms underlying crop flowering timing [44] and molecular mechanisms underlying the leaf shape and size [45] have also been gradually revealed. But, how to integrate these molecular mechanisms into models of crops and agro-ecosystem? One approach is directly linking quantitative trait loci (QTL) to model parameters [46–48], as already used in the model of flowering timing [46] and the model of leaf growth and expansion [48]. Another approach is to directly develop models of genetic regulatory network related to metabolism and development. This approach, however, still needs a long time to show its feasibility. This is because though many bioinformatics algorithms have been developed to construct genetic regulatory network [49–58], the accuracy of these identified networks still needs substantial experimental validation. Minimally, however, these algorithms and the availability of massive amount of high throughput data make it possible to develop models of genetic regulatory network.

As discussed earlier, crop yields are more closely related to more than leaf photosynthesis, canopy photosynthesis, which are influenced by a number of environmental factors, including light, humidity, and temperature [59]. More and more experimental evidence and modern cultivars have demonstrated

that canopy architecture influences canopy photosynthesis and crop yields [60], very possibly due to its influence on environmental factors, especially light distribution inside canopy [5, 60]. To accurately estimate canopy photosynthesis, accurate information of these environmental factors around each leaf in the canopy is required. In the field, obtaining environmental parameters for different leaves is extremely challenging due to high level of temporal and spatial heterogeneities in these different factors [4, 59, 61, 62]. In this regard, three-dimensional models of plant architecture in trees [63] and maize [64] have already been developed. Specialized measurement techniques to digitize the three-dimensional canopy architecture, e.g. fastSCAN (Polhemus Incorporation, <http://www.polhemus.com>), have also been developed in recent years; all these advances help develop more advanced canopy photosynthesis models with detailed and more realistic representation of the three-dimensional canopy architecture.

Besides canopy photosynthesis, another crucial factor influencing crop yields is the source sink interaction. For many grain crops, such as rice, maize, and wheat, leaf and grain are the main source and sink organs respectively. The transport of photosynthate from source to sink tissues goes through vascular bundles. Admittedly, though the interaction between source and sink has been studied for many decades, our understanding of the molecular mechanism behind regulation of the source sink interaction is still rather limited [65, 66]. But, many important empirical observations have been made, e.g. a) source activities, representing the total photosynthetic CO₂ uptake rates, are mainly influenced by not only canopy architecture, but also activities of many enzymes and proteins involved in photosynthesis, including Rubisco, SBPase (sedoheptulose-1,7-bisphosphatase), FBPase (fructose-1,6-bisphosphatase) [16, 18]; b) the sink capacity is mainly affected by the activity of key enzymes associated with starch synthesis and sucrose synthesis, including sucrose synthase, ADP-glucose pyrophosphorylase, starch synthase, starch branching enzyme and starch debranching enzymes [18, 67, 68]; c) hormone influences sink activities, as shown in rice grain filling [69, 70]. Sugar levels control expression of genes involved in photosynthetic, nitrogen metabolism, sucrose and starch metabolism [71, 72], correspondingly plays an important role in regulating source and sink interaction. Again, though our understanding of the molecular mechanisms underlying source sink interaction and also means for partitioning of photosynthate into different organs are still far from complete, the recent advances regarding regulation of genes involved in source and sink capacities need to be incorporated into existing models of crop and agro-ecosystems.

3 Components of the next generation models for crops and agro-ecosystems

Given the needs and feasibility of developing improved models with more mechanistic basis, we suggest a number of research areas to expediate generation of the next generation models of crops and agro-ecosystems.

First, a number of core models need to be developed (Figure 1). These models include: a) models of plant central metabolism and its regulation, models of flowering timing, and models of source sink interaction; b) models of microclimatic factors inside three-dimensional canopies, which can predict light, CO₂, temperature, humidity and ozone conditions in the canopy and, in the long run, simulate the influence of mechanical forces on canopy architecture and correspondingly on microclimatic conditions; c) models of nitrogen and water movements through the soil-root-stem-leaf-atmosphere continuum; models simulating soil nitrogen, carbon and phosphorus cycles also need to be further improved; d) models of organ (leaf, flower, and root) formation.

Secondly, to facilitate application of these models in new crop design and quantitative studies of plant molecular and physiological processes, a number of methods (Figure 2) are needed, which include: a) methods to identify breeding targets for particular crops under a given environment; b) methods to identify molecular basis for a macroscopic phenotype; c) methods for model analysis, including sensitivity analysis, parameter estimation and bifurcation analysis.

Finally, to maximize the application of models in research and education, supporting databases and online portals specifically tailored for the next generation models of crops and agro-ecosystems are also needed.

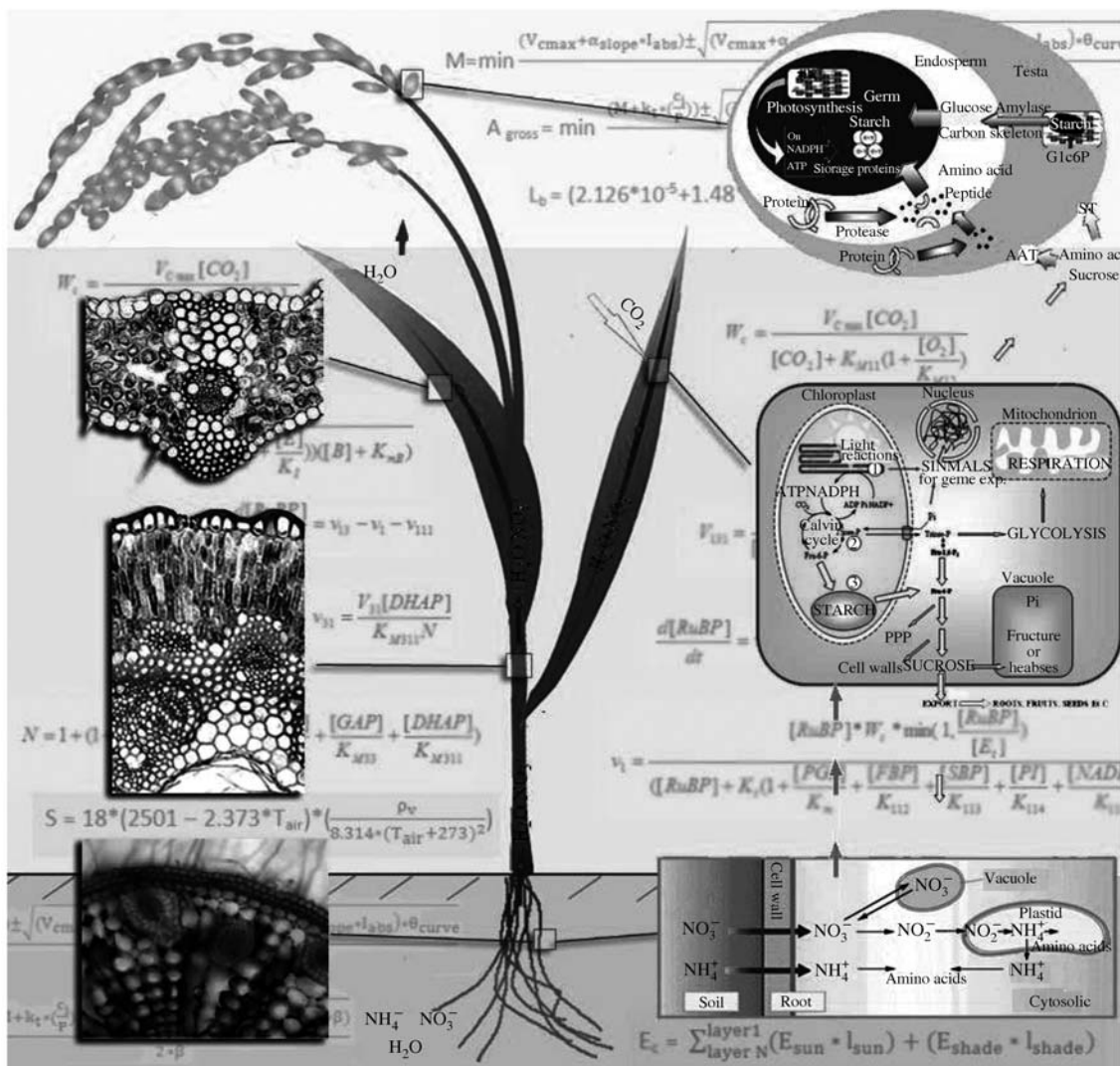


Figure 1 Diagram showing processes involved in a plant used in the next generation models of crops and agro-ecosystems. The models will simulate the central metabolism including photosynthesis, respiration, nitrogen transport, assimilation and partitioning, water uptake, transport and evaporation, interaction among these different processes, and also interaction of these processes with environments. The next generation models of crops and agro-ecosystems will also simulate the growth and development process of crops.

4 Summary

With the global population increase, climate change, and decrease in arable areas, identifying new approaches to increase crop productivity is one critical challenge facing our society. Developing the next generation of crop and agro-ecosystem models will not only help us identify better farming practices and breeding targets for increased productivity, but also help study mechanistic basis behind observable macroscopic phenotypes, and predict responses of plants or crops to future climate change. The next generation crop and agro-ecosystem models will incorporate recent advances of mechanisms underlying many aspects of crop growth and development, and interactions between plants and their environments. Developing the next generation crop and agro-ecosystem models requires close collaboration between scientists in different disciplines including but not limited to agronomy, mathematics, information sciences, plant sciences, earth sciences, geology sciences and even social sciences. It is foreseeable that once such models are developed, they will play an important guiding role in precision agriculture, where the bottle-

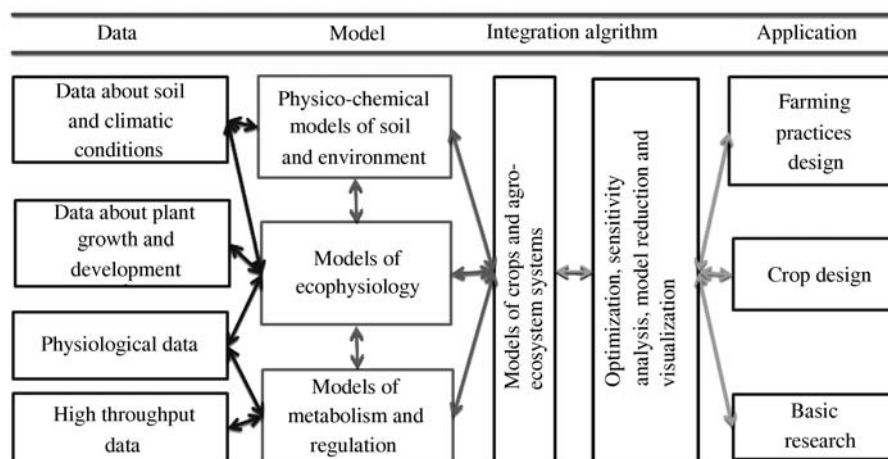


Figure 2 Major components of the next generation models of crops and agro-ecosystems. These models include models of the plant central metabolism and regulation, models of crop eco-physiology, physical and chemical models of soil processes and the environmental processes. These models will be directly linked to high throughput data, data about crop physiology, crop growth and development, and climatic data. To effectively use the models to identify better farming practices, targets for crop improvements, and to explore systems properties, tailored algorithms for optimization, sensitivity analysis, model reduction and visualization will be developed.

neck is indeed the lack of robust models of interaction of plants with their environments.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (Grant No. 30970213), and the Young Talent Frontier Program of Shanghai Institutes for Biology Sciences/Chinese Academy of Sciences (Grant No. 09Y1C11501). The authors thank Steve Long, Don Ort, Eric Sturler for collaborations.

References

- 1 Conway G, Toenniessen G. Feeding the world in the twenty-first century. *Nature*, 1999, 402: C55–C58
- 2 Peng S B, Tang Q, Zou Y. Current status and challenges of rice production in China. *Plant Prod Sci*, 2009, 12: 3–8
- 3 Stafford J V. Implementing precision agriculture in the 21st century. *J Agr Eng Res*, 2002, 76: 267–275
- 4 Niinemets U L O. Photosynthesis and resource distribution through plant canopies. *Plant Cell Environ*, 2007, 30: 1052–1071
- 5 Zhu X G, Long S P, Ort D R. Improving photosynthetic efficiency for greater yield. *Ann Rev Plant Biol*, 2010, 61: 235–261
- 6 Sage R F, Kubien D S. The temperature response of C3 and C4 photosynthesis. *Plant Cell Environ*, 2007, 30: 1086–1106
- 7 Atkin O K, Macherel D. The crucial role of plant mitochondria in orchestrating drought tolerance. *Ann Bot*, 2009, 103: 581–597
- 8 Cornic G, Fresneau C. Photosynthetic carbon reduction and carbon oxidation cycles are the main electron sinks for photosystem II activity during a mild drought. *Ann Bot*, 2002, 89: 887–894
- 9 Long S P, Humphries S W, Falkowski P G. Photoinhibition of photosynthesis in nature. *Ann Rev Plant Physiol Plant Mol Biol*, 1994, 45: 633–662
- 10 Slafer G A. Genetic basis of yield as viewed from a crop physiologist's perspective. *Ann Appl Biol*, 2003, 142: 117–128
- 11 Murchie E H, Pinto M, Horton P. Agriculture and the new challenges for photosynthesis research. *New Phytol*, 2008, 181: 532–552
- 12 Gibson S. Control of plant development and gene expression by sugar signaling. *Cur Opin Plant Sci*, 2005, 8: 93–102
- 13 Zhu X G, Long S P, Ort D R. What is the maximum efficiency with which photosynthesis can convert solar energy into biomass? *Current Opin Biotech*, 2008, 19: 153–159
- 14 Cramer W A, Zhang H M, Yan J S, et al. Transmembrane traffic in the cytochrome b6f complex. *Ann Rev Biochem*, 2006, 75: 769–790
- 15 Nelson N, Yocum C F. Structure and function of photosystems I and II. *Ann Rev Plant Biol*, 2006, 57: 521–565

- 16 Raines C A. The calvin cycle revisited. *Photosyn Res*, 2003, 75: 1–10
- 17 Lawlor D W, Tezara W. Causes of decreased photosynthetic rate and metabolic capacity in water-deficient leaf cells: a critical evaluation of mechanisms and integration of processes. *Ann Bot*, 2009, 103: 561–579
- 18 Zhu X G, De Sturler E, Long S P. Optimizing the distribution of resources between enzymes of carbon metabolism can dramatically increase photosynthetic rate: A numerical simulation using an evolutionary algorithm. *Plant Physiol*, 2007, 145: 513–526
- 19 Rogers A, Humphries S W. A mechanistic evaluation of photosynthetic acclimation at elevated CO₂. *Glob Change Biol*, 2000, 6: 1005–1011
- 20 Lin Z H, Mo X G, Xiang Y Q. Research advances on crop growth models. *Acta Agron Sin*, 2003, 29: 750–758
- 21 Jones J W, Hoogenboom G, Porter C H, et al. The DSSAT cropping system model. *Europ J Agron*, 2003, 18: 235–265
- 22 Bouman B A M, Van Keulen H, Van Laar H H, et al. The ‘School of de Wit’ crop growth simulation models: a pedigree and historical overview. *Agri Syst*, 1996, 52: 171–198
- 23 de Wit C T, Penning de Vries F W T. The simulation of photosynthetic systems. In: *Prediction and Management of Photosynthetic Productivity, Proceedings of the International Biological Program/Plant Production Technical Meeting*. Wageningen, 1970. 47–70
- 24 de Wit C T. *Simulation of assimilation, respiration and transpiration of crops*. Simul Monographs, 1978
- 25 Penning de Vries F W T, Laar H H. Simulation of plant growth and crop production. In: *PUDOC, Wageningen*, 1982, 1–308
- 26 Van Keulen H, Penning de Vries F W T, Drees E M. A summary model for crop growth. In: Penning de Vries F W T, van Laar H H, eds. *Simulation of Plant Growth and Crop Production*. Simulation Monograph, PUDOC, Wageningen, 1982. 87–98
- 27 Keulen H, Wolf J. Modelling of agricultural production: weather, soils and crops. In: *PUDOC, Wageningen*, 1986, 1–478
- 28 Penning de Vries F W T, Jansen D M, M. Ten Berge H F M, et al. Simulation of ecophysiological processes of growth in several annual crops. In: *Simulation Monograph, PUDOC, Wageningen*, 1989. 1–280
- 29 Spitters C J T, Schapendonk A. Evaluation of breeding strategies for drought tolerance in potato by means of crop growth simulation. *Plant Soil*, 1990, 123: 193–203
- 30 Lal H, Hoogenboom G, Calixte J P, et al. Using crop simulation modles and GIS for regional productivity analysis. *Trans ASABE*, 1993, 36: 175–184
- 31 Mccown R L, Hammer G L, Hargreaves J N G, et al. APSIM: a novel software system for model development, model testing and simulation in agricultural systems research. *Agr Syst*, 1996, 50: 255–271
- 32 Parton W J, Stewart J W B, Cole C V. Dynamics of C, N, P and S in grassland soils: a model. *Biogeochemistry*, 1988, 5: 109–131
- 33 Humphries S W, Long S P. WIMOVAC: a software package for modelling the dynamics of plant leaf and canopy photosynthesis. *Comput Appl Biosci*, 1995, 11: 361–371
- 34 Farquhar G D, Von Caemmerer S, Berry J A. A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta*, 1980, 149: 78–90
- 35 Lawlor D W, Cornic G. Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant Cell Environ*, 2002, 25: 275–294
- 36 Stitt M, Krapp A. The interaction between elevated carbon dioxide and nitrogen nutrition: the physiological and molecular background. *Plant Cell Environ*, 1999, 22: 583–621
- 37 Buckley T N, Mott K A, Farquhar G D. A hydromechanical and biochemical model of stomatal conductance. *Plant Cell Environ*, 2003, 26: 1767–1785
- 38 Morgan J A, Rhodes D. Mathematical modeling of plant metabolic pathways. *Metabol Eng*, 2002, 4: 80–89
- 39 Rolland F, Baena-Gonzalez E, Sheen J. Sugar sensing and signaling in plants: conserved and novel mechanisms. *Ann Rev Plant Biol*, 2006, 57: 675–709
- 40 Rolland F, Moore B, Sheen J. Sugar sensing and signaling in plants. *Plant Cell*, 2002, 14: S185–205
- 41 Rolland F, Sheen J. Sugar sensing and signalling networks in plants. *Biochem Soc Trans*, 2005, 33: 269–271
- 42 Stitt M, Muller C, Matt P, et al. Steps towards an integrated view of nitrogen metabolism. *J Exp Bot*, 2002, 53: 959–970
- 43 Scheible W R, Lauerer M, Schulze E D, et al. Accumulation of nitrate in the shoot acts as a signal to regulate shoot-root allocation in tobacco. *Plant J*, 1997, 11: 671–691
- 44 Yin X Y, Struik P C, Van Eeuwijk F A, et al. QTL analysis and QTL-based prediction of flowering phenology in recombinant inbred lines of barley. *J Exp Bot*, 2005, 56: 967–976
- 45 Tsukaya H. Mechanisms of leaf shape determination. *Ann Rev Plant Biol*, 2006, 57: 477–496
- 46 Yin X Y, Struik P C, Tang J J, et al. Model analysis of flowering phenology in recombinant inbred lines of barley. *J Exp Bot*, 2005, 56: 959–965
- 47 Yin X Y, Struik P C, Kropff M J. Role of crop physiology in predicting gene-to-phenotype relationships. *Trends Plant Sci*, 2004, 9: 426–432

- 48 Yin X Y, Al E. Coupling estimated effects of QTLs for physiological traits to a crop growth model: predicting yield variation among recombinant inbred lines in barley. *Heredity*, 2000, 85: 539–549
- 49 Bailey T L, Elkan C. Unsupervised learning of multiple motifs in biopolymers using expectation maximization. *Mach Learn*, 1995, 21: 51–80
- 50 Lawrence C E, Altschul S F, Boguski M S, et al. Detecting subtle sequence signals—A Gibbs sampling strategy for multiple alignment. *Science*, 1993, 262: 208–214
- 51 Siddharthan R, Siggia E D, Van Nimwegen E. PhyloGibbs: A Gibbs sampling motif finder that incorporates phylogeny. *Plos Comput Biol*, 2005, 1: 534–556
- 52 Friedman N, Linial M, Nachman I, et al. Using Bayesian networks to analyze expression data. *J Comput Biol*, 2000, 7: 601–620
- 53 Segal E, Yelensky R, Koller D. Genome-wide discovery of transcriptional modules from DNA sequence and gene expression. *Bioinformatics*, 2003, 19 Suppl.: i273–i282
- 54 Segal E, Shapira M, Regev A, et al. Module networks: identifying regulatory modules and their condition-specific regulators from gene expression data. *Nat Genet*, 2003, 34: 166–176
- 55 Lee T I, Rinaldi N J, Robert F, et al. Transcriptional regulatory networks in *Saccharomyces cerevisiae*. *Science*, 2002, 298: 799–804
- 56 Bar-Joseph Z, Gerber G K, Lee T I, et al. Computational discovery of gene modules and regulatory networks. *Nat Biotech*, 2003, 21: 1337–1342
- 57 Harbison C T, Gordon D B, Lee T I, et al. Transcriptional regulatory code of a eukaryotic genome. *Nature*, 2004, 431: 99–104
- 58 Jin V X, Rabinovich A, Squazzo S L, et al. A computational genomics approach to identify cis-regulatory modules from chromatin immunoprecipitation microarray data—A case study using E2F1. *Genome Res*, 2006, 16: 1585–1595
- 59 Niinemets U, Valladares F. Photosynthetic acclimation to simultaneous and interacting environmental stresses along natural light gradients: Optimality and constraints. *Plant Biol*, 2004, 6: 254–268
- 60 Long S P, Zhu X G, Naidu S L, et al. Can improvement in photosynthesis increase crop yields? *Plant Cell Environ*, 2006, 29: 315–330
- 61 Leakey A D B, Scholes J D, Press M C. Physiological and ecological significance of sunflecks for dipterocarp seedlings. *J Exp Bot*, 2005, 56: 469–482
- 62 Percy R W, Roden J S, Gamon J A. Sunfleck dynamics in relation to canopy structure in a soybean (*Glycine max* (L.) Merr) canopy. *Agr Forest Meteorol*, 1990, 52: 359–372
- 63 Percy R W, Yang W M. A three-dimensional crown architecture model for assessment of light capture and carbon gain by understory plants. *Oecologia*, 1996, 108: 1–12
- 64 Espana M L, Baret F, Aries F, et al. Modeling maize canopy 3D architecture—Application to reflectance simulation. *Ecol Model*, 1999, 122: 25–43
- 65 Fischer R A. Understanding the physiological basis of yield potential in wheat. *J Agr Sci*, 2007, 145: 99–113
- 66 Reynolds M, Calderini D, Condon A, et al. Association of source/sink traits with yield, biomass and radiation use efficiency among random sister lines from three wheat crosses in a high-yield environment. *J Agr Sci*, 2007, 145: 3–16
- 67 Martha G J, Kay D, Alan M M. Starch synthesis in the cereal endosperm. *Curr Opin Plant Biol*, 2003, 6: 215–222
- 68 Geigenberger P, Stitt M, Fernie A R. Metabolic control analysis and regulation of the conversion of sucrose to starch in growing potato tubers. *Plant Cell Environ*, 2004, 27: 655–673
- 69 Clifford P E, Offler C E, Patrick J W. Growth-regulators have rapid effects on photosynthate unloading from seed coats of *Phaseolus vulgaris* L. *Plant Physiol*, 1986, 80: 635–637
- 70 Jones R J, Brenner M L. Distribution of abscisic-acid in maize kernel during grain filling. *Plant Physiol*, 1987, 83: 905–909
- 71 Jang J C, Leon P, Zhou L, et al. Hexokinase as a sugar sensor in higher plants. *Plant Cell*, 1997, 9: 5–19
- 72 Sheen J. Feedback control of gene expression. *Photosynth Res*, 1994, 39: 427–438