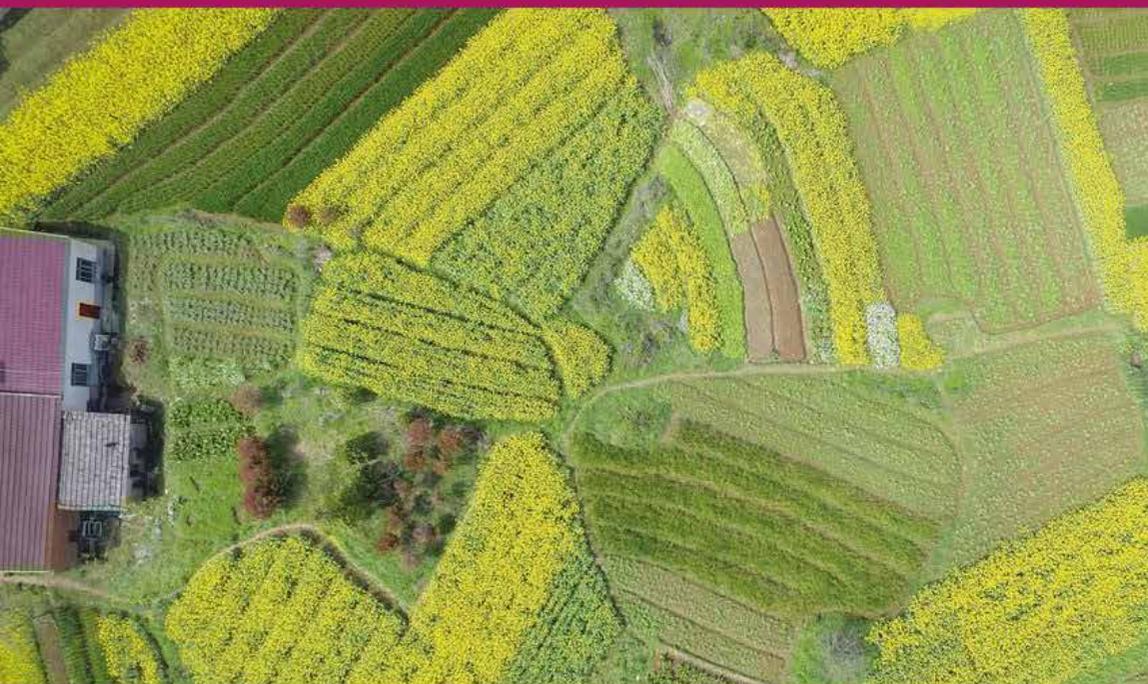


BURLEIGH DODDS SERIES IN AGRICULTURAL SCIENCE

Advances in crop modelling for a sustainable agriculture

Edited by Emeritus Professor Kenneth Boote
University of Florida, USA



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Introduction

This collection summarises key advances in crop modelling, with a focus on developing the next generation of crop and whole-farm models to improve decision making and support for farmers. Chapters in Part 1 review advances in modelling individual components of agricultural systems, such as plant responses to environmental conditions, crop growth stage prediction, nutrient and water cycling as well as pest/disease dynamics.

Building on topics previously discussed in Part 1, Part 2 addresses the challenges of combining modular sub-systems into whole farm system, landscape and regional models. Chapters cover topics such as integration of rotations and livestock, as well as landscape models such as agroecological zone (AEZ) models. Chapters also review the performance of specific models such as APSIM and DSSAT and the challenges of developing decision support systems (DSS) linked with such models. The final part of the book reviews wider issues in improving model reliability such as data sharing and the supply of real-time data, as well as crop model inter-comparison.

Part 1 Modelling sub-systems

Chapter 1 discusses advances and improvements in modelling plant processes. It provides an overview of the advances made historically and today in modelling key plant processes. It focuses on the processes associated with carbon acquisition and allocation, such as photosynthesis, stomatal conductance, respiration and assimilate partitioning, and provides a section on modelling phenology, the timing of plant developmental events.

Moving on to Chapter 2, advances in functional-structural plant (FSP) modelling of plants and crops are discussed. Crop models have been instrumental in predicting yields in wide ranges of current and future environmental conditions. However, they encounter problems in representing spatial heterogeneity of a plant stand and the associated plant responses under competition from other plants including weeds and intercrops. The FSP models simulate the effects of specific plant traits, management choices that influence plant architecture, and lighting regimes such as those in greenhouses. For such purposes, functional-structural plant (FSP) models have been developed, which simulate individual plants that interact with each other in 3D, with the changes in plant architecture feeding back on the distribution of environmental drivers that make them grow and develop (light, water, nutrients). With this in mind, the authors outline the purposes of FSP models, the components they need to

have to serve these purposes and provide an account of recent applications of FSP models.

Chapter 3 reviews improving the modelling of nutrient cycles in crop cultivation. Agricultural productivity depends on crops receiving adequate amounts of essential nutrients from the soil and supplied fertilizers and manures. Through the biogeochemical cycling of nutrients, fertile soils supply the following essential nutrients to plants: nitrogen, phosphorus, potassium, sulfur, calcium, magnesium, iron, zinc, copper, manganese, boron, molybdenum, cobalt, and nickel. Deficiency of any of these nutrients results in lower productivity. The chapter focuses primarily on the nutrient cycle modelling for nitrogen, phosphorus and potassium and their relationships to soil organic matter decomposition. Given the importance of nitrogen in global food production and its impact on the environment, the major emphasis of the chapter is on nitrogen modelling.

The subject of Chapter 4 is improving the modelling of water cycles in crop cultivation. Adequate representation of the water cycle in cropping systems remains as one of the major concerns for crop model developers as it is involved in many critical processes such as the determination of the energy balance and crop temperature, the determination of crop productivity, and the movement of nutrients in the soil and their uptake. The chapter begins by discussing crop water availability and its linkage to weather, soil and management at point, field and watershed scales. It then reviews the determination of the potential and actual crop evapotranspiration and soil water availability in crop models. The chapter also discusses modelling crop water uptake and the integration of soil water balance components in crop models. Finally, the chapter reviews crop water use and atmospheric carbon dioxide concentration effects on transpiration and concludes by highlighting the main limitations of modelling water cycles that are currently observed.

The final chapter of Part 1, Chapter 5, discusses improving crop pest/disease modelling. Dissemination of crop pests and diseases occurs through both natural and anthropogenic processes, facilitated by the increasing interconnectedness of the global food chain. Food security depends on our ability to manage crop pests and diseases effectively. The chapter offers a brief overview of approaches to coupling of models in order to better predict and manage crop pests and diseases. The chapter explains the PEST subroutine in the CROPGRO family of models, and shows how a strategy of keeping the crop model separate from disease/pest models, and coupling through Message Passing Interface (MPI) functionality, can be effective. It also provides a section on insect pest and disease management, specifically focusing on the CROPGRO-soybean simulation model. Finally, the chapter looks ahead to future research trends in this area.

Part 2 Developing whole farm system, landscape and regional models

Part 2 begins with Chapter 6 which reviews whole farm system models in practice. The challenges of contemporary agriculture are causing farmers to seek models directed at whole-farm goals, which requires mathematically-based models grounded in the latest scientific understanding of animal growth and reproduction, crop physiology, soil and environmental sciences, as well as economics and human relations. Such models are often invaluable tools in the process of undertaking nuanced, multifaceted management decisions at the farm system level. The chapter explores model selection and, through a series of case studies, whole farm modelling in both smallholder systems and single enterprise farm businesses. Finally, the chapter looks ahead to future research trends in this area.

Moving on to Chapter 7, the chapter describes the DSSAT crop modelling ecosystem. It begins by providing the history of the DSSAT model development and goes on to discuss the creation of multiple crop models and tools for data preparation, analysis and applications. The chapter also provides an overview of the structure and science of the crop simulation models included in DSSAT. The tools and utilities for weather, soil, and experimental data entry are also discussed, and a section on crop model calibration and evaluation is included. Finally, the chapter reviews the range of applications and concludes by discussing the future of the DSSAT crop modelling ecosystem.

The next chapter of Part 2 reviews modelling crop rotations and capturing short- and long-term feedbacks for sustainability and soil health. Crop rotation is a critical management strategy available to farmers to sustain soil fertility, combat pests, and improve crop yields. Because of the complex feedbacks occurring in the soil-plant-atmosphere continuum, legacy effects and their interactions with climate are generally not well understood, and their ultimate influence on yields and environmental quality is difficult to predict. Crop simulation models offer a way of parsing through this complexity. Chapter 8 illustrates how crop models account for the interactions between soil, cultivars, management, and climate, on crops grown in various rotations, and their effects on yield and environmental outcomes (e.g. nitrate leaching, soil organic carbon sequestration) under current and future climate scenarios by presenting two different case studies and modelling approaches. The chapter concludes by summarizing the advantages and disadvantages of the modelling approaches and offers some recommendations for how to best capture legacy effects.

Chapter 9 examines the integration of livestock production into whole-farm system models of mixed crop-livestock systems. Crop-livestock farming systems integrate various biophysical components with farm decision-making. Whole-farm system models help to understand the complexity arising from this

integration and are useful tools to explore effects of interventions and to design improved systems. After describing the generic characteristics of crop-livestock systems, the chapter gives an account of the separate component models, from which whole-farm models are usually assembled. Most attention goes to the wide diversity in pasture, livestock and manure models, while approaches to represent farm management in models are also discussed. The interactions between farm components strongly determine model functioning and performance, and often present modelling challenges to capture them. With a focus on grazing, manure dynamics and animal mobility, the chapter assesses the key processes governing these interactions and reviews how models represent them. The representation of feed quality in crop model outputs and the management of time scales and carry-over effects is also discussed. Finally, the chapter concludes by providing two examples of common whole-farm model applications from contrasting environments.

Moving on to Chapter 10, the chapter examines the integration of economic simulation models with whole-farm system models for ex ante technology impact assessment. The key analytical challenge to developing agricultural system models is to predict the behaviour of agricultural systems in the multiple dimensions that are relevant to their economic, environmental and social sustainability, under recent historically observed conditions and when they are modified to improve economic performance. The chapter discusses ex ante technology impact assessment, defined as forward-looking efforts at technology design and evaluation. Supported by a case study, the chapter reviews methods to combine process-based and economic production models to overcome some of the limitations of each approach. Finally, the chapter looks ahead to future research trends in this area and provides detailed guidance on further reading.

Chapter 11 addresses developing climate-based decision support systems (DSS) from agricultural systems models. Decision support systems (DSSs) in production agriculture are computer software programs that make use of models and other information to make site-specific recommendations for farm management-related activities. Major advances have been made in developing DSS for agriculture, particularly with respect to incorporating climate forecasts into farmers' decision-making process. The chapter describes DSSs in agriculture, focusing on the importance of a participatory approach in DSS development. The chapter offers examples of climate-based DSS for crop and land management, pest and disease management, and livestock (dairy) management. The chapter reflects on lessons learned in the process of developing climate-based DSS. Finally, the chapter looks ahead to future research trends in this area.

The subject of Chapter 12 is the use of landscape models to support sustainable intensification of agroecological systems. Intensification of

agriculture to meet the growing demand of food and renewable resources is contrasted with a decrease in species diversity, pollution in water bodies and a decline in freshwater resources. To protect our resources, the natural functioning of ecosystems and the diversity of landscapes, agricultural land use must reduce its resource use and its impact on biodiversity and ecosystems. Addressing both challenges simultaneously requires a perspective that takes a more detailed look into the heterogeneity of climate and soils and their role in agroecosystem functioning, the interactions between flora and fauna, the interdependencies with the green infrastructure at landscape scale and the role of humans and how they organise themselves in this system. In this chapter the authors reflect on the different social, economic and natural features of agricultural landscapes that govern important processes in agro-ecosystems and discuss current approaches for modelling ecosystem services using a landscape approach.

The concluding chapter of Part 2 discusses agroecosystem models for delivering ecosystem services. Agroecosystems are complex representations of the interactions occurring among multiple biological systems at the field and landscape scale. Models simulating these interactions across time and space are not very mature and expanding our current knowledge on crop, pest, and soils models provides a framework for how we use agroecological models to quantify a range of ecosystem services. Chapter 13 examines the need for an agroecosystem approach, outlining the importance of plants, soils, pests, diseases, weeds and pollinators as part of the agroecosystem. Finally, the chapter looks ahead to future research trends in this area.

Part 3 Modelling issues

The first chapter, Chapter 14, examines data for developing, testing and applying crop and farm models. It reviews the kinds of data available to crop and farm modellers. The chapter highlights practices concerning storage, exchanging and combining data from various sources, examining the socio-economic and ethical implications. It also looks at the role of companies in data flows and generating recommendations, and presents examples of successful use of agricultural data, both for science and agricultural practice. The chapter concludes by looking ahead to future research trends in the area.

Moving on to Chapter 15, this chapter examines how to deal with uncertainty in crop models. There is increasing awareness in crop modelling of the importance of uncertainty. The modeller needs uncertainty information to prioritize improvements, while the user needs uncertainty information to make informed decisions. The chapter introduces the concept of model uncertainty, considering such factors as model structure, inputs and parameters. The chapter then looks at ways to reduce uncertainty in crop modelling and looks ahead to

future trends in the area. Finally, the chapter provides detailed guidance on further reading on the subject.

Chapter 16 focuses on crop simulation model inter-comparison and improvement. Crop modelling is an integrated discipline of agricultural sciences that contributes to agricultural research, including the areas of agronomic management, precision agriculture, environmental impacts and externalities, input efficiency, managing climate variability and seasonal forecasting, breeding, climate change impacts and adaptations, and agricultural policy. More recently, the crop modelling community has begun to exchange models, model routines, and data in coordinated and protocol-based crop model inter-comparison and improvement projects. The chapter summarises crop model inter-comparison studies and their contribution to sustainable agriculture and discuss gaps and trends in crop simulation model inter-comparisons and improvements. It covers crop model inter-comparison, crop model uncertainty, crop model improvement, and crop model application, respectively. A case study from the Agricultural Model Inter-comparison and Improvement Project for Wheat (AgMIP-Wheat) is included. The chapter concludes with a review of future trends in research.

The final chapter of the book examines the future of crop modelling for sustainable agriculture. Crop growth simulation models have become increasingly important as accepted tools with uses in education, research, crop management, industry, and government policy decisions related to improving and sustaining agricultural production of food, feed, fibre, and ecosystem services. The chapter begins with a brief review of history of crop modeling that has led to excellent collaborations among the world's crop modeling community. It discusses present and future potential uses of crop models in education, academic research, plant breeding, strategic crop management, in-season advisory tools, famine risk tools, climate change impact assessment, ecosystem services, sustaining long-term soil fertility, and integration with livestock and economic models. The chapter concludes with a look to the future with a review of what is new in crop models, the processes that need improvement, along with suggestions of new features needed

Part 1

Modelling sub-systems

Chapter 1

Advances and improvements in modeling plant processes

Soo-Hyung Kim and Jennifer Hsiao, University of Washington, USA; and Hannah Kinmonth-Schultz, University of Kansas, USA

- 1 Introduction
- 2 Modeling photosynthesis and stomatal conductance for carbon acquisition
- 3 Modeling respiration and assimilate partitioning
- 4 Modeling phenology: the timing of crop developmental events
- 5 Conclusion and future trends
- 6 Where to look for further information
- 7 References

1 Introduction

The growth of a crop is coordinated by multiple physiological processes. Process-based crop models (PBCMs) simulate growth, development, and performance of crop plants by modeling their underlying physiological processes, and the coordination and integration of these processes at the whole-plant and canopy scales. The physiological processes incorporated into PBCMs can include photosynthesis, transpiration, respiration, organ development, and assimilate transport. Most PBCMs are explanatory models by nature as they integrate sub-models that represent the mechanisms and processes at lower levels of biological organization into the whole-crop level responses (Boote et al., 2013; Marcelis et al., 1998; Thornley and Johnson, 1990). For example, in some maize PBCMs the dynamics of total leaf area is simulated by modeling growth and senescence of individual leaves (Kim et al., 2012; Lizaso et al., 2003). A key strength of PBCMs is their ability to mechanistically integrate multiple physiological processes and their interactions into crop performance with respect to environmental, management, and genetic factors. Much progress has been made in our understanding of individual physiological processes; yet, current understanding of some processes may be more advanced than others. This discrepancy is reflected in the degree to which individual physiological

mechanisms are implemented into PBCMs – some more thorough and reductionistic (e.g. photosynthesis and floral development) than others (e.g. sink regulations). Using a modular crop model structure (Acock and Reddy, 1997), the sub-models for different processes may be updated periodically to reflect, and include new biological knowledge, thus requiring minimal effort for revamping and restructuring the entire model.

Modeling the processes involved in carbon acquisition and allocation is fundamental in PBCMs. *Carbon dynamics* are determined by the rate of CO₂ assimilation through photosynthesis, release of CO₂ and energy production through respiration, and allocation of assimilated carbon to internal and external sinks (e.g. growing organs and symbionts). Many models and modeling approaches with varying degrees of mechanism and reductionism exist for plant carbon fixation (e.g. Farquhar et al., 1980; Monteith, 1977; Zhu et al., 2013). On the other hand, models for how the carbon assimilates are distributed within plants are less common. Modeling *phenology* is another top priority in PBCMs because accurate prediction of the timing of crop development can dictate the model's ability to simulate subsequent growth and other physiological processes as well as final biomass and yield. Phenology models are also critical for making timely management decisions in season. Crop phenology models have evolved from simple models relating observations of growing-season temperatures to specific plant processes such as the timing of anthesis (Lehenbauer, 1914), to models that routinely incorporate multiple layers of plant organization, specifically, organ initiation, expansion and senescence (Wang et al., 2017).

This chapter provides an overview of the advances made historically and today in modeling key plant processes with a focus on the processes associated with carbon acquisition and allocation (photosynthesis, stomatal conductance, respiration, and assimilate partitioning), and the timing of plant developmental events (phenology). Areas for further improvement are also addressed.

2 Modeling photosynthesis and stomatal conductance for carbon acquisition

Photosynthesis is a key physiological process that determines plant growth, performance, and crop yield. It responds to various environmental factors such as light, temperature, humidity, atmospheric CO₂ concentrations, soil water and nitrogen availability, and is arguably one of the most studied physiological processes within plants. Stomatal conductance controls the exchange of carbon and water that occurs through the simultaneous process of photosynthesis and transpiration. Accurate representations of photosynthesis and stomatal conductance within models are critical in linking plant water relations with carbon gain, and can be considered as one of the critical foundations in crop

modeling. Here, we introduce several key modeling approaches developed to describe these processes.

2.1 Models of photosynthesis

2.1.1 Brief history

Some of the earliest attempts to model photosynthesis focused on describing the light interception and distribution within the canopy. Leaf-level photosynthetic rates were modeled as a function of the intercepted light level at different canopy layers, commonly through a rectangular hyperbola function (de Wit, 1965; Duncan et al., 1967; Monsi and Saeki, 1953; Monteith, 1965). Subsequently, several field observations demonstrated biomass accumulation to be proportional to intercepted radiation (Monteith, 1972; Warren Wilson, 1967). Specifically, Monteith (1977) presented how dry-matter production of various economically important crops in Great Britain linearly correlated with the intercepted radiation under ideal growing conditions, leading to the theory that carbon gain in crops through photosynthesis can be estimated based on the amount of sunlight intercepted during the growing season and on the efficiency with which it is converted into biomass. This concept is commonly known as radiation use efficiency (RUE) and has been adopted into many crop simulation models due to its elegance and simplicity (White et al., 2011).

In 1980, Farquhar and colleagues published a biochemical model for C_3 plants that attempted to incorporate and simplify the expanding understanding of mechanisms behind photosynthesis (The FvCB model; Farquhar et al., 1980). The FvCB model was further modified by Harley and Sharkey (1991), and was later expanded for C_4 photosynthesis by von Caemmerer and Furbank (1999). Despite being published nearly four decades ago, the FvCB model is still one of the most frequently used methods for studying photosynthetic response to different environmental perturbations (e.g. Farquhar et al., 2001; Field, 2002; Rogers et al., 2017; Sellers et al, 1997).

To date, a majority of the crop models for staple crops (e.g. maize, rice, wheat, potato) use RUE as the primary method for modeling biomass production, but an increasing number of models have been adopting or transferring to photosynthesis-based approaches at the leaf or canopy level (Asseng et al., 2013; Bassu et al., 2014; Fleisher et al., 2017; Li et al., 2015).

2.1.2 A mechanistic modeling approach for photosynthesis

The FvCB model captures the biochemical demand for CO_2 assimilation at the chloroplast that is scalable to a leaf. The leaf net photosynthetic rate (A) is determined by describing the rate of three key processes within the Calvin cycle:

(1) the rate of carboxylation, which is catalyzed by Rubisco (A_c), (2) the rate of RuBP regeneration, which is controlled by the electron transport rate within the light-dependent reaction of photosynthesis (A_j), and (3) the rate of synthesizing photosynthetic end products (A_p), mainly, converting triose phosphates into sucrose and starch, also known as triose phosphate utilization (TPU; Fig. 1). Since the three processes (i.e., A_c , A_j , A_p) are continuous components within the Calvin cycle, the most rate-limiting process eventually determines the net photosynthetic rate (Eqn. 1):

$$A = \min(A_c, A_j, A_p) \quad (1)$$

The rate of each process responds to enzymatic properties as well as environmental variables such as temperature, light levels, and CO_2 and oxygen concentrations. Here, we briefly describe how the FvCB model individually describes A_c , A_j , and A_p .

A_c represents photosynthetic rates limited by the carboxylation capacity of Rubisco and is calculated based on Rubisco kinetics (Eqn. 2):

$$A_c = V_{cmax} \left(\frac{C_c - \Gamma^*}{C_c + K_c (1 + O/K_o)} \right) - R_d \quad (2)$$

V_{cmax} describes the maximal rate of carboxylation for Rubisco, and K_c and K_o are the Michaelis-Menten constants for Rubisco reacting with CO_2 and oxygen, respectively. These parameters describe the enzymatic properties of Rubisco, which are temperature dependent. C_c and O denote the CO_2 and oxygen partial

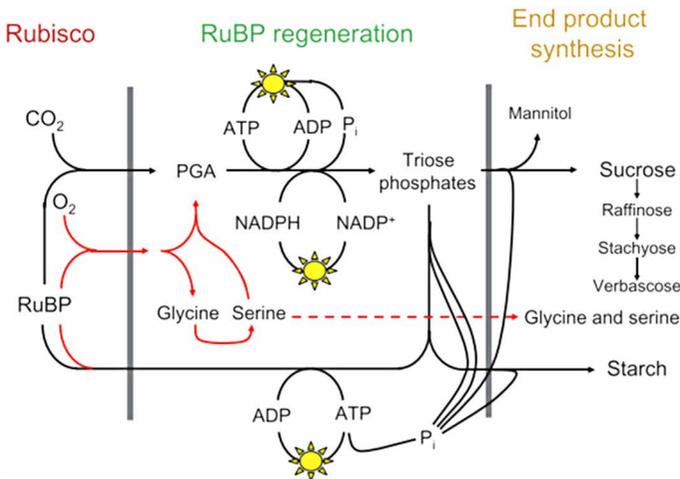


Figure 1 Scheme showing some of the processes that affect photosynthetic rate (Sharkey et al., 2007, Figure 1).

pressure at the chloroplast, and Γ^* is the CO_2 compensation point, defined as the CO_2 concentration level at which carbon uptake through photosynthesis is balanced by CO_2 released through photorespiration. Finally, the calculation accounts for leaf-level daytime respiration, R_d , which is the respiratory release of CO_2 excluding that from photorespiration.

A_j describes the CO_2 assimilation rate limited by RuBP regeneration and is calculated based on the electron transport rate within the light reaction of photosynthesis that generates ATP and NADPH to fuel RuBP regeneration (Eqn. 3):

$$A_j = J \frac{C_c - \Gamma^*}{4C_c + 8\Gamma^*} - R_d \quad (3)$$

$$J = \frac{\alpha_{LL} I_{abs} + J_{max} - \sqrt{(\alpha_{LL} I_{abs} + J_{max})^2 - 4\theta J_{max} \alpha_{LL} I_{abs}}}{2\theta} \quad (4)$$

J describes the electron transport rate that is a function of light absorbed in photosynthetically active radiation, usually modeled as shown in Eqn. (4). J depends on the maximum capacity of electron transport (J_{max}), the amount of light absorbed (I_{abs}), the quantum yield of electron transport under light-limiting conditions (α_{LL}), and an empirical parameter θ that represents the convexity of the J to I_{abs} response curve.

Finally, A_p represents photosynthetic rates limited by TPU and is calculated based on the rate at which photosynthetic end products are being utilized and transported out of the chloroplast (Eqn. 5):

$$A_p = 3TPU - R_d \quad (5)$$

in which the photosynthetic rate is determined by TPU and R_d .

2.1.3 Scaling photosynthesis from leaf to canopy

The main question to consider when attempting to scale photosynthesis from a single-leaf level up to a canopy level is the distribution of light within the canopy. Monsi and Saeki (1953) published the very first mathematical model for canopy-level photosynthesis, applying the Beer-Lambert optic law to describe light attenuation within a plant canopy affected by leaf area index and the optical properties of the leaves. This concept of radiation penetration through the canopy set the foundation for several canopy photosynthesis models that divided the plant canopy into multiple layers with different light-level and leaf-angle classes and calculated the canopy-level photosynthetic rate by numerically integrating photosynthetic rates throughout the canopy layers (de Wit, 1965; Duncan et al., 1967; Monsi and Saeki, 1953; Monteith, 1965).

Further improvements of the original Monsi and Saeki model included acknowledging the importance of direct versus diffuse light within the canopy (de Wit, 1965; Duncan et al., 1967; Spitters et al., 1986). Subsequent observations also revealed the difference in photosynthetic capacities between sunlit and shaded leaves. Specifically, photosynthetic rates typically increased linearly with light levels for shaded leaves, while these responses were often saturated in sunlit leaves (Boardman, 2003). This allowed the multilayer model to be simplified by classifying the leaves within a canopy into two types, sunlit and shaded leaves, while still being able to accurately capture the canopy-level photosynthetic rate (de Pury and Farquhar, 1997). Methods exist to further simplify the canopy structure into just a single photosynthetic layer (known as the big leaf model). While computationally efficient, the big leaf model was prone to overestimating canopy-level photosynthesis, particularly for dense canopies. Introducing empirical coefficients or fitting with observations helped correct for this issue, but applications tend to be limited to the calibrated conditions (de Pury and Farquhar, 1997).

Alternatively, Functional-Structural Plant Models (FSPM) took a different approach in the level of complexity when modeling the plant architecture. Detailed descriptions of the plant structure, including the branching system, leaf angle, and leaf curvature allow for a more realistic representation of the plant canopy and the light distribution within it (Allen et al., 2005; Godin and Sinoquet, 2005; Vos et al., 2010). Such approaches require significantly more work to compute parameters, but can be very useful, especially when asking research questions that link plant function and structure. Further information on FSPMs can be found in Chapter 2 by Evers and Marcelis.

2.1.4 Recent advances

First published in 1980, the FvCB photosynthesis model has gained widespread impact through time (Farquhar et al., 2001). Its elegance in capturing fundamental mechanistic processes within photosynthesis has led to broad applications in terrestrial, ecosystem, and Earth system modeling communities (Farquhar et al., 2001; Field, 2002; Rogers et al., 2017; Sellers et al., 1997). Nevertheless, the FvCB model has not been widely adopted within the crop modeling community (Yin and Struik, 2009) likely due to perceived complexity in the model structure and the level of required parameter information when compared to the commonly used RUE approach (Cannell and Thornley, 1998). RUE remains a useful approach in crop simulation models, especially due to its simple form. Factors that are known to affect RUE, such as CO₂ concentrations, can also be accounted for if explicitly calibrated (White et al., 2011). However, RUE remains a largely empirical approach, and its ability to capture dynamic interactions between different environmental effects on photosynthesis and

biomass production can be limited, especially when projecting conditions under a changing climate in which current relationships between crops and environmental factors may not remain the same.

Since the development of the FvCB model, sophisticated portable instruments for leaf gas-exchange measurements have become readily available, providing much more information to aid the parameterization process for the FvCB model, and composites of estimated parameter values now exist within the literature for a wide range of C_3 and C_4 plant species (Bellasio et al., 2017; Wullschleger, 1993; Yin and Struik, 2009). In addition, it is commonly assumed that enzyme kinetic parameters of Rubisco are relatively conserved between plant species and crop cultivars that share the same photosynthetic pathway (Sharkey et al., 2007; von Caemmerer, 2000), which can reduce the number of unknown parameters within the model. However, the FvCB model was not intended to capture all the steps within photosynthesis; rather, it synthesizes key components in order to simulate the steady-state photosynthetic rate. Recent advances in process-based photosynthesis models have incorporated more dynamic and explicit mechanisms, with an increasing interest in representing the whole photosynthesis process.

A mechanistically detailed and comprehensive photosynthetic model requires a series of interconnected biochemical and biophysical reactions that dynamically shift under different environmental conditions; these models are regulated by specific conditions at the photosynthetic site, such as pH levels, redox state, concentrations of key ions, etc. (Zhu et al., 2013). Developing such model requires extensive knowledge of the photosynthetic system as well as computational power and numerical algorithms to solve for it, and such methods have recently started to become more available. Laisk et al. (2006) developed a photosynthesis model for C_3 plants that described in detail both the light-dependent and independent reactions. The model compartmentalized a leaf into the thylakoid membranes, thylakoid lumen, chloroplast stroma, and the cytosol, while tracking the intermediate compounds that occur throughout the photosynthesis process through a system of differential equations. This approach showed the growing interest in mechanistically modeling the photosynthetic process as a whole. In 2013, Zhu and colleagues published a mechanistic and dynamic photosynthesis modeling platform, *e-photosynthesis*, that built upon several previous works on this topic (Laisk et al., 2006; Zhu et al., 2005, 2007, 2013) and is likely one of the most comprehensive models of its kind to date.

The detailed mechanisms captured within such models make them great tools for exploring breeding and genetic modification targets to improve photosynthesis, with implications for improving yield for major food crops. However, the level of information in such models requires expansive parameter sets and considerable computation power, which can pose challenges when

incorporated into a whole-plant crop model structure. Nevertheless, studies have proposed ideas of scaling such models up to canopy levels (Zhu et al., 2012). While this process remains informationally and computationally challenging, new tools and approaches have been proposed to tackle the complex interactions between different processes at varying time scales as well as the difficulty in parameterizing and validating such models (Zhu et al., 2012). If successful, a complete model linking molecular-level mechanisms to canopy level can be used as a powerful tool both for hypothesis testing and for crop engineering.

2.2 Models of stomatal conductance

Stomata have long been a subject of interest for scientists. Early documentation can be dated back to 1898, when Francis Darwin, Charles Darwin's son, published detailed observations on stomatal responses to various environmental variables (Darwin, 1898). Up to this day, stomatal behavior and the processes behind them still remain an active field of research; while the primary signals controlling stomatal opening and closing are understood, a full mechanistic understanding of these responses still remains a work in progress, especially in stomatal hydraulic responses (Buckley, 2016, 2017). Because of the tightly coupled relationship between CO₂ uptake for photosynthesis and water loss from transpiration through stomata, modeling stomatal conductance is critical for mechanistic representation of plant carbon-water relations and also to fully utilize the FvCB photosynthesis model (Eqn. 1) for which [CO₂] inside the leaf (C_i) or at the chloroplast (C_c) is the driving variable. We will summarize here several modeling approaches with varying degrees of complexity that attempt to capture these stomatal responses.

2.2.1 Empirical approaches

One of the earliest attempts to model stomatal conductance (g_s) was an empirical approach published by Jarvis (1976). The model described stomatal conductance of illuminated leaves as a function of leaf temperature (T_l), vapor pressure deficit (VPD), leaf water potential (ψ_l), and ambient CO₂ concentrations (C_a), and modeled their responses as independently multiplicative (Eqn. 6). The simplicity of this model made it easy to incorporate into whole-plant models, but the model provided little mechanistic information on stomatal function, thus requiring parameterization under new environmental conditions. Observed interactions between the model inputs also have led to criticism of its assumption of independent model input (Tardieu et al., 1996).

$$g_s = f_1(Q) \cdot f_1(T_l) \cdot f_1(VPD) \cdot f_1(C_a) \cdot f_1(\psi_l) \quad (6)$$

Around the same time, Cowan and Farquhar (1977) approached the problem through a different school of thought. They described stomatal functioning from a top-down method with concepts that largely stem from economic theories of optimality and the general idea that stomatal responses are selected over evolutionary time to achieve an optimal behavior of maximizing carbon gained through photosynthesis (A) while minimizing water lost through transpiration (E). This concept can be described by minimizing the integrated sum of the following equation between time-steps t_1 and t_2 :

$$\int_{t_1}^{t_2} (E(t) - \lambda A(t)) dt \quad (7)$$

Where the empirical λ parameter describes the marginal cost (in this case, water lost) for carbon gain. A few studies have attempted to implement this theory to model stomatal behavior (Lloyd et al., 2002; Mencuccini, 2003). However, overall usage of such a modeling approach was limited, mostly due to the ambiguity in parameterizing λ , the difficulty in determining the time interval in which to capture the optimal stomatal behavior (t_1 - t_2 in Eqn. 7), and the model's inaccuracy in capturing stomatal responses to CO_2 concentrations.

2.2.2 Semi-empirical approaches

The initial proposal of an optimality-based stomatal conductance model was not widely applied, but various leaf-level observations supported its prediction of a conservative ratio of intercellular to ambient CO_2 concentrations (Wong et al., 1979). These observations helped shape the development of a semi-empirical (or semi-mechanistic) stomatal model developed by Ball et al. (1987), which has since become one of the most commonly used stomatal conductance models up to this day, and is often referred to as the Ball-Berry model.

The Ball-Berry model was developed based on leaf-level observations, typically showing stomatal conductance correlated with photosynthetic rate (Wong et al., 1979) and modified by relative humidity. This led to a simple model formulation that describes g_s as a function of net photosynthetic rate (A), the CO_2 concentration at the leaf surface (c_s), and the relative humidity at the leaf surface (h_s ; Eqn. 8):

$$g_s = g_o + m \frac{Ah_s}{c_s} \quad (8)$$

The two free parameters within the model, g_o and m , represent minimal stomatal conductance when A equals zero and an empirical parameter that describes the sensitivity of stomatal conductance to environmental variables, respectively. The model has been further modified by Leuning in 1995 by

incorporating the concept of a CO₂ compensation point including respiration (Γ), modifying the original relative humidity response into VPD (D_s), which has been shown to better describe the stomatal response to humidity (Aphalo and Jarvis, 1991), and including an additional free parameter, D_o (Eqn. 9):

$$g_s = g_o + \frac{mA}{(c_s - \Gamma) \left(1 + \frac{D_s}{D_o}\right)} \quad (9)$$

Note that g_s is not defined when c_s equals Γ (Eqn. 9). Similarly, g_s is not defined when c_s equals zero in Eqn. (8).

While still largely empirical, the Ball-Berry model and its variations were elegant and simple in form and easy to test and parameterize with leaf gas-exchange measurements. When using it to dynamically predict stomatal conductance from environmental variables, the Ball-Berry model required an input of photosynthetic rate calculated through a separate model (e.g. often the FvCB photosynthesis model). Thus, the model structure represents the strong dependence and coupling between photosynthesis and stomatal conductance. We describe the coupling process in further detail in Section 2.3.

The simplicity and mechanistic behavior of this coupled g_s - A approach has led to a wide range of applications (Egea et al., 2011). However, a common criticism of the approach relates to the empirical parameter m , also referred to as the Ball-Berry slope. The m parameter within the model represents a composite sensitivity of g_s to photosynthetic rate, humidity, CO₂ concentrations, and temperature (indirectly through photosynthesis). The lack of a specific biological meaning within this term can require re-parameterization whenever applying the model for a new species or under new environmental conditions. Miner et al. (2017) surveyed m values published through the past three decades, which showed a wide range of variability within and between plant functional groups. These results pointed out some outstanding debates on whether m changes under adaptation to a change of environmental conditions such as elevated CO₂ levels and water stress and whether the wide range of values we see in the literature represents the true variability within this value, or whether it stems from the range of different measurement methods.

Recently, Medlyn et al. (2011) demonstrated that a model directly analogous to the Ball-Berry model and its variations can be derived and approximated by combining the optimal stomatal behavior theory (Cowan and Farquhar, 1977) with parts of the FvCB photosynthesis model (Farquhar et al., 1980). They termed this model as the unified stomatal model (Eqns. 10 and 11):

$$g_s \approx g_0 + 1.6 \left(1 + \frac{g_1}{\sqrt{D}}\right) \frac{A}{C_a} \quad (10)$$

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