Elements of a dynamic systems model of canopy photosynthesis

Xin-Guang Zhu[1,2], Qingfeng Song[1,2] and Donald R Ort[3]

Improving photosynthesis throughout the full canopy rather than photosynthesis of only the top leaves of the canopy is central to improving crop yields. Many canopy photosynthesis models have been developed from physiological and ecological perspectives, however most do not consider heterogeneities of microclimatic factors inside a canopy, canopy dynamics and associated energetics, or competition among different plants, and most models lack a direct linkage to molecular processes. Here we described the rationale, elements, and approaches necessary to build a dynamic systems model of canopy photosynthesis. A systems model should integrate metabolic processes including photosynthesis, respiration, nitrogen metabolism, resource re-mobilization and photosynthate partitioning with canopy level light, CO_2, water vapor distributions and heat exchange processes. In so doing a systems-based canopy photosynthesis model will enable studies of molecular ecology and dramatically improve our insight into engineering crops for improved canopy photosynthetic CO_2 uptake, resource use efficiencies and yields.

Addresses
[1] State Key Laboratory of Hybrid Rice Research, CAS-MPG Partner Institute for Computational Biology, Shanghai Institutes for Biological Sciences, Chinese Academy of Sciences, Yueyang Road 320, Shanghai, 200031, China
[2] CAS Key Laboratory of Computational Biology, Chinese Academy of Sciences, CAS-MPG (Chinese Academy of Sciences-German Max Planck Society) Partner Institute for Computational Biology, Shanghai Institute of Biological Sciences, Chinese Academy of Sciences, Shanghai, 200031, China
[3] Global Change and Photosynthesis Research Unit, USDA ARS, Departments of Plant Biology and Crop Sciences, Institute of Genomic Biology, University of Illinois, Urbana, IL 61801, United States

Corresponding author: Zhu, Xin-Guang (zhuxinguang@picb.ac.cn)

Introduction

On or near the 31st of October 2011, the global population reached 7 billion (http://www.worldometers.info/world-population/). Before plateauing in the middle of this century, the global population will have increased by another 2–4 billion humans [1], which along with improving economic conditions in large parts of the developing world creates an unprecedented demand for food and energy [2]. An element of meeting the challenge of doubling the global food production will have to be increasing the efficiency of crop canopy photosynthesis [3•]. Crop yield is inherently related to the seasonal integral of net canopy photosynthesis. Canopy photosynthetic CO_2 uptake rate (A_c) is the integral of photosynthetic CO_2 uptake from both sunlit and shaded leaves. A_c changes over the growing season as well as over the diurnal cycle. The difference in the light intensity dependence between canopy and leaf photosynthesis is shown in Figure 1. Photosynthesis of an individual leaf saturates at about 700 μmol m^{-2} s^{-1} PPFD for a typical C3 and about 1000 μmol m^{-2} s^{-1} PPFD for a C4 leaf. However, for a crop canopy containing several leaf layers, the A_c for either C3 or C4 canopies shows little sign of saturation even at 2000 μmol m^{-2} s^{-1} PPFD that is higher than full sunlight at most locations. Because of this fact, photosynthetic CO_2 uptake by shaded leaves can account for up to about 50% of A_c [4]. The historical misunderstanding of the relationship between photosynthesis and crop yields is largely owing to considering leaf instead of full canopy photosynthesis to derive the relationship [5•,6].

Given that photosynthesis generates carbon and energy required for plant growth and development, photosynthesis is usually assumed to be optimized given that it has had >3.5 billion years of evolutionary fine tuning [7]. However, there is now a great deal of evidence to suggest that many photosynthetic components of crop plants, for example, Rubisco specificity factor [8], enzyme distributions [9], leaf chlorophyll concentration [10], leaf angle [11], and leaf nitrogen distribution [12•] are not optimized to achieve maximum A_c (i.e. maximum net primary productivity). This lack of optimization to achieve maximum A_c should not come as a surprise in that maximizing A_c does not derive from selection for good competitors in natural ecosystems; maximizing A_c is a unique goal of agriculture. For example, an individual plant taller [13,14], greener [10], and having more horizontal leaves [15] than required for maximum A_c usually has a competitive advantage over its neighbors. Thus, plants adopt features beneficial for the individual at the cost of the community and therefore use resources, including light, inefficiently compared to strategies designed to maximize net primary productivity. Furthermore, selection in natural habitats favor individuals that invest resources to maintain sufficient defensive [16] or in preventative mechanisms to ensure their survival and competitive advantage when facing stress and other unpredictable environmental fluctuations [17,18•]. Additionally elements of global climate change, most notably increasing

Figure 1
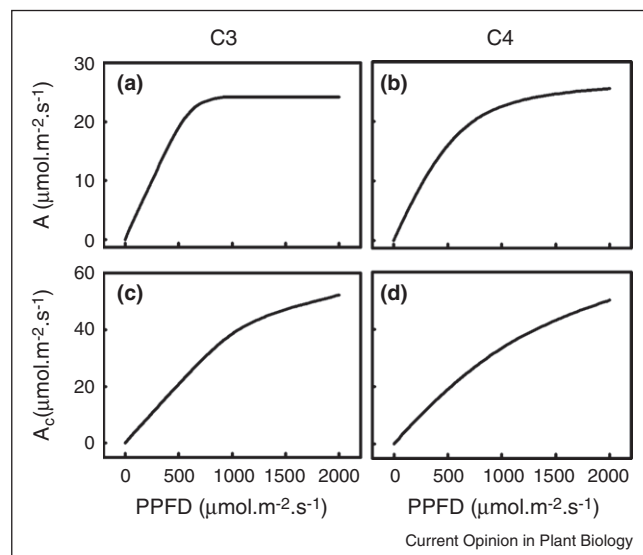
The light response curves for both leaf (**a** and **b**) and canopy (**c** and **d**) photosynthesis in C3 (**a** and **c**) and C4 (**b** and **d**) plants. Simulations were conducted using WIMOVAC [44]. The canopy was assumed to have leaf area index of 4, random leaf distribution and inclination, solar zenith angle of $30°$ with 70% of incident light as direct light. Photosynthetic parameters for C3 plants were from [25] and for C4 plants were from [76]. PPFD: photosynthetic photon flux density.

atmospheric CO_2 concentration and temperature, are occurring at a pace that far exceeds the rate at which evolution of new adaptive features can occur. Indeed, the current Rubisco specificity factor in typical C3 plants is adapted to the CO_2 levels that existed for the ~ 20 M years that preceded the industrial revolution [8]. Finally, the boost of photosynthesis and biomass attendant to the insertion of a 'photorespiratory bypass' into plant chloroplasts using enzymes from *E. coli* [28] illustrates that there are more efficient alternatives for certain photosynthetic processes and enzymes that can be found in genetic resources to which plants do not have access without biotechnological intervention.

The deviation of photosynthesis from optimum and the difficulty of measuring canopy photosynthesis (A_c) in the field necessitate development of canopy photosynthesis models. Since the publication of the first mathematical model for estimating canopy photosynthesis [19], many models had been developed for agro-ecology or forest-ecology research for which there are several excellent reviews [20–22]. Our purpose here is to consider what is required to take the important next step of developing a full systems model of canopy photosynthesis. Such a model would enable studies of molecular ecology and provide insight to guide the engineering of crops for improved canopy photosynthetic CO_2 uptake, crop yield and resource use efficiencies.

## Lessons learned from current canopy photosynthesis models

Among current canopy photosynthesis models the most well known are the: maximal productivity model, resource-use efficiency model, big-leaf model, sunlit–shaded model, and multi-layer model. These models vary in the amount of physiological and environmental mechanism and detail that they incorporate [20]. Comparatively, the sunlit–shaded model is the best performer over a broad range of different time scales for which it has been validated, although other modeling approaches have specific advantages including simplicity of implementation and the ability to be combined with remote sensing data related to the interception of light by vegetation [20,23**,24*]. One major advantage of the sunlit–shaded model is its scalability and in particular its ability to directly incorporate leaf level physiological properties [23**]. Furthermore, important canopy architectural parameters, such as ratio of horizontal versus vertical projected leaf area ratios, leaf area index, and randomness of leaf angle distribution, are also represented in the model [24*], thereby providing it with the power to identify potential targets to engineer a higher A_c, for example, a decrease rather than increase in Rubisco specificity factor [8], decreasing leaf current chlorophyll concentration [10], and implementing a faster recovery from the photoprotective state to its full efficiency state [4]. Improving the light distribution inside a canopy through manipulating leaf angles is another approach to enhance A_c predicted by the sunlit–shaded model [11].

Current canopy photosynthesis models have also been used to study the interaction between canopy processes and environmental factors in both natural or managed ecosystems. For example, a sunlit–shaded canopy model has been used to predict that elevated CO_2 can alter the magnitude or even the direction of responses of A_c to increase in temperature [25]. Changes in the fraction of diffuse light caused by clouds or other atmospheric particles were also forecast by this model to strongly influence A_c [26]. The influence of canopy height on A_c can also be explored within current canopy models [27]. However, other important factors that impact canopy photosynthesis are not captured in current canopy photosynthesis models. For example, in cereal crops spike photosynthesis is known to play a significant role in determining crop yields [28], but this aspect has not been effectively represented in current canopy photosynthesis models for cereal crops.

Elements of a dynamic systems model of canopy photosynthesis

The sunlit–shaded model, although clearly the most powerful of the existing canopy models, nevertheless has important constraints, which limit its accuracy in predicting canopy photosynthesis CO_2 uptake rates (A_c) under numerous conditions of interest. Topping

Figure 2
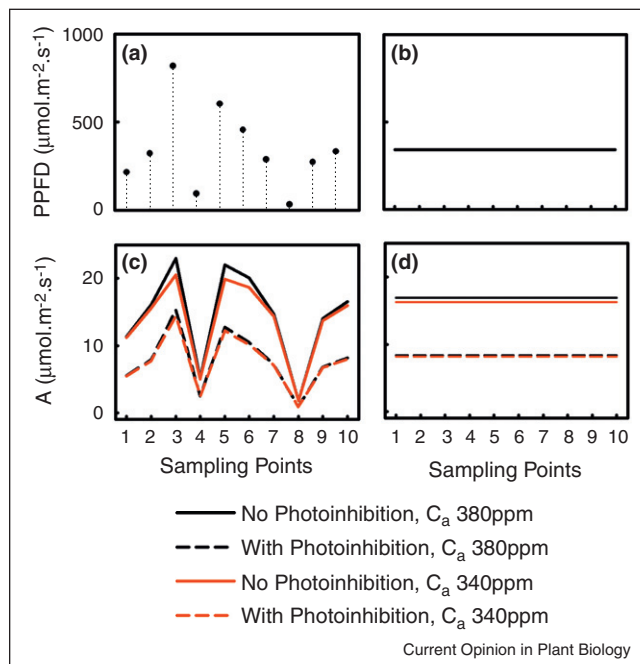
The influence of light and CO_2 heterogeneities on the estimates of total C3 canopy CO_2 uptake rate (A_c). **(a)** Hypothetical PPFD at 10 different depths within a canopy of leaves; **(b)** the average PPFD of the 10 depths; **(c)** estimated A_c using actual PPFD at the different depths; **(d)** estimated A_c with the average PPFD. C_a: atmospheric CO_2 concentration. The leaf photosynthetic rates were calculated based on light response curve following [3]. The parameters used are: A_{sat} of 24.2 μmol m^{-2} s^{-1} at [CO_2] concentrations of 380 ppm and 21.4 μmol m^{-2} s^{-1} at 340 ppm. The convexity factors are 0.71 with and 0.95 without photoinhibition. The initial slopes of CO_2 uptake versus light curves are 0.028 with and 0.055 without photoinhibition. A simplification used in this calculation is the assumption of the same extent of photoinhibition for leaves at all 10 depths in the canopy.

the list of its limitations is that the sunlit–shaded model predicts the 'average' light intensities for both sunlit and shaded leaves within a canopy [23$^{\bullet\bullet}$,24$^{\bullet}$], that is, the high level of spatial and temporal heterogeneity of light environments inside a canopy is not considered. The influence of this heterogeneity on the calculation of A_c is illustrated in Figure 2. Assuming no photoinhibition (i.e. no photoprotection), A_c calculated with the average light level is 17% higher than that estimated with the actual light levels inside a canopy (Figure 2). With photoinhibition (i.e. photoprotective mechanisms engaged), the estimated A_c using the average light level is 7% higher than the estimate with actual light level (Figure 2). Here we used the simplification that the level of photoinhibition was same for all leaves regardless of depth within the canopy; had we included the gradient in photoinhibition that would actually exist it would have resulted in an even greater difference in A_c calculated using average versus actual light levels. Furthermore, as with light levels, CO_2 levels within a canopy are also

highly heterogeneous both temporary and spatially, for example, a 40 ppm gradual decrease of CO_2 concentration from the top to the center of a canopy height is common in deep maize or soybean canopies [29,30]. Given that mesophyll resistance can further decrease CO_2 concentration in chloroplast stroma [31] and the non-linear response of photosynthesis to CO_2 [32], ignoring the CO_2 gradient inside a canopy overestimated A_c by ~4% for a C3 crop (Figure 2). Another limitation of current canopy photosynthesis models, as also discussed in [33], is their lack of linkage between leaf physiological processes to molecular processes. As a result, such models cannot be used to identify molecular targets to engineer for higher A_c.

Figure 3a illustrates the key elements required for a mechanistic systems model of canopy photosynthesis to overcome the above-mentioned limitations. A brief summary of the differences between current canopy photosynthesis models and a fully mechanistic dynamic systems model of canopy photosynthesis is shown in Table 1. The basic components of the dynamic systems model of canopy photosynthesis include physical models of canopy microclimate, systems models of metabolic processes representing photosynthesis, respiration, nitrogen metabolism, resource re-mobilization and photosynthate partitioning in a plant, and algorithms for integrating these components to develop the complete model. In the past few decades, tremendous progress has been made in each of these different aspects. The most notable of the major advances are summarized here. First, models representing 3-D canopy architectures have been developed for different crops including maize [34–36], rice [37,38], and wheat [39]. Various forward and reverse light ray tracing algorithms combined with such 3D canopy architecture models have been developed to predict the light environment inside a canopy [27,40–42]. Compared to the large number of light distribution models, the CO_2 distribution inside a canopy has only been modeled in a limited number of crops, for example, in soybean [43]. The temperature and humidity profiles are usually predicted by canopy models based on the energy balance and stomatal conductance [43,44].

Major advances have also been made in developing mechanistic models of plant metabolic processes. So far, a number of kinetic models of photosynthesis and of plant primary metabolism have been developed [9,45,46]. To enable simulation of canopy photosynthesis during the growing season, various models of photosynthate partitioning were also developed, including descriptive allometry models, functional equilibrium models, and sink regulation models with different levels of mechanistic underpinnings [47,48$^{\bullet}$,49]. Recently, a mechanistic model of starch metabolism and sugar partitioning between shoot and root was developed, where measurable parameters, including maximal leaf growth rates, minimal levels of sugar in the leaves, and relationship between the minimal

Figure 3
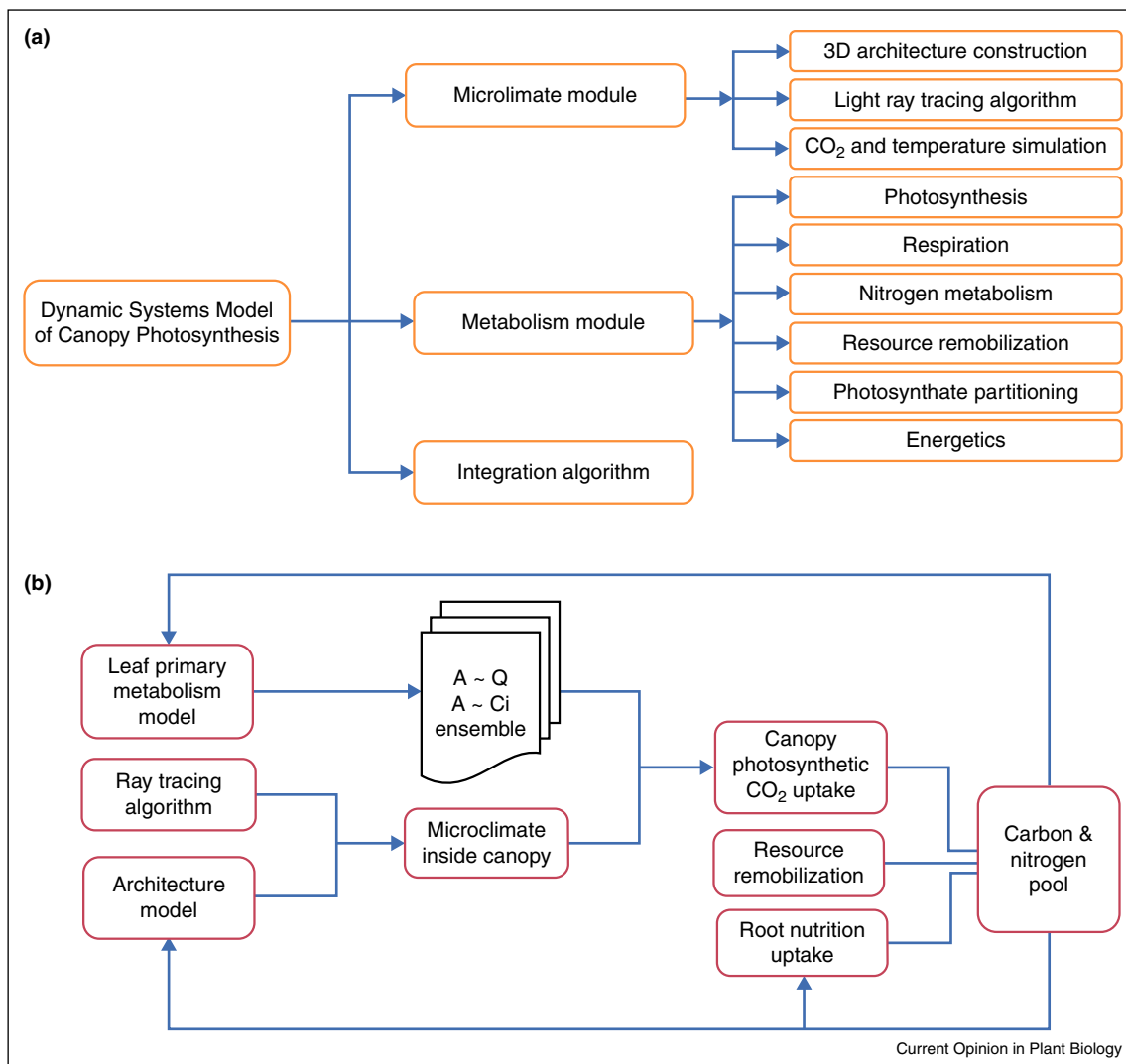
The major elements of a systems model of canopy photosynthesis **(a)** and algorithms used to integrate metabolic model with canopy microclimate model **(b)**. The major elements include physical models of canopy microclimate, systems models of metabolic processes representing photosynthesis, respiration, nitrogen metabolism, resource re-mobilization and photosynthate partitioning, and algorithms for integrating these components to develop the complete model **(a)**. A hierarchical multi-scale approach is used to integrate these different models to develop the complete systems model of canopy photosynthesis **(b)**.

sugar levels and maintenance respiration rates, were used as key parameters [50•]. This model can predict the growth retardation of both starch-less and starch excess mutants compared to wildtype [50•], which represent a major advance toward building a mechanistic source-sink model.

In addition to the photosynthate partitioning, plants remobilize carbon and nitrogen from senescencing leaves at the lowest layers of a canopy for re-use to grow new leaves at the top of the canopy, which usually happens when the photosynthetic CO_2 uptake of shaded leaves is less than its respiratory cost [12•,51]. This remobilization

is correlated with leaf longevity, leaf mass per area and density [51,52], with leaf age potentially being used to program nitrogen allocation to maximize carbon gain [53]. Recently, these different aspects, that is, photosynthesis, respiration, cost of protein turnover and other mainten-ance processes, have been incorporated into dynamic canopy photosynthesis models [54] and used to explain the response of trees to elevated CO_2 [55,56]. Also a new robust method to estimate the energetic cost for building plant primary metabolism studies has been developed [57•], which is an important step toward a complete mechanistic systems model.

Table 1

Comparison of current canopy photosynthesis models and emergent dynamic systems model of canopy photosynthesis. In the section labeled as 'Availability of features in different models', the '×' represents 'not available' and '√' represents 'available'. In the section labeled as 'Applications of the model', the '×' represents 'incapable to do' and '√' represents 'capable to do'

		Radiation use efficiency model [77]	Big leaf model [78–80]	Sunlit–shaded model [23[••],24[•]]	Structural Function model [22,27,60]	Dynamic systems model
Availability of features in different models	Canopy architecture	×	×	×	√	√
	Leaf photosynthetic properties at different layers of the canopy	×	×	√	√	√
	Interaction between photosynthesis, respiration and nitrogen metabolism	×	×	×	×	√
	Source sink interaction	×	×	×	√	√
Applications of the model	Predict canopy photosynthetic CO_2 uptake	√	√	√	√	√
	Identify genes to modify for increased canopy photosynthesis	×	×	×	×	√
	Study mechanisms underlying plant adaptation to different environments	×	×	√	√	√

How is it possible to integrate a canopy microclimate model with these different metabolic models to develop a complete dynamic systems model of canopy photosynthesis? This is computationally challenging since the involved processes in the models occur at drastically different time scales spanning from picoseconds (10^{-9} s) for the primary events in photosynthesis to metabolic processes at millisecond scale (10^{-3} s) up to processes occurring at minutes scale ($\sim10^2$ s), for example, changes in light environments inside the canopy. To overcome this difficulty, we are adopting a hierarchical multi-scale approach [58] (Figure 3). Briefly, first a 'divide-and-conquer' strategy is used to develop individual metabolic models and these models will then be combined to form an integrated plant primary metabolism model [3[•]]. Then, we will run the complete metabolic model for a variety of parameter sets to generate an ensemble of photosynthetic rates under diverse parameter sets. This ensemble of data will then be used as a lookup table when we run the complete model of canopy photosynthesis (Figure 3b). Finally, the photosynthate produced will be used within the model to grow new organs with full consideration of both the construction cost and also the allometrical constraints observed in nature [58,59]. Recently, a novel aspect oriented functional structural plant modeling approach has also been proposed to deal with the complex interactions among different processes in plant growth and development [60].

Parameterization and validation of such a complex multi-scale model is equally challenging. Fortunately, a number of critical measurement techniques required to parameterize and validate such models have also recently emerged. For example, a versatile stereo imaging system has been developed to obtain 3D canopy architectural parameters [61]. A number of physiological parameters, for example, stomatal conductance, biomass, biomass composition, and so on, have been measured with high throughput spectroscopic methods [62–65]. At the leaf level, activities of multiple key enzymes involved in plant primary metabolism are being measured with robot-based platforms [66]. Development of advanced canopy photosynthesis chambers to measure total photosynthetic CO_2 uptake for model validation is also on-going. Combined these provide the means to generate a complete and robust data set required to parameterize, test and validate systems models of canopy photosynthesis.

What a highly mechanistic systems model of canopy photosynthesis can offer in the post-genomic era

A complete systems model of canopy photosynthesis linking processes from the molecular level through to the canopy level will provide a powerful new tool to both test and generate hypotheses regarding mechanisms underlying plant growth and survival strategies in natural environments. A global scale survey of leaf economic traits showed that relationships between leaf mass per area,

longevity, leaf nitrogen content and photosynthetic parameters, were remarkably conserved [67]. Furthermore, when facing stress, plants usually respond by taking one of three well-conserved strategies, that is, competitive, stress tolerant or ruderal, each with different combinations of canopy architecture, leaf form, longevity, and leaf turnover rates [68]. One intriguing hypothesis underlying these conserved relationships is that plants can potentially utilize many different strategies to grow and survive, and thus the particular strategy chosen might be an optimal solution of the dynamic systems model constrained by the growth environment and the genetic background of the plant. Though ecological and physiological models coupled with optimization routines have been developed to study relationships between these features [12•,51,69,70], these models offer little opportunity to explore the molecular mechanisms behind these relationships. By linking molecular process to leaf and canopy processes, a dynamic systems model of canopy photosynthesis can offer new avenues to study ecological and physiological processes or phenomena from a molecular perspective.

A systems model of canopy photosynthesis can also be a major new tool to guide crop engineering to improve A_c. Although considerable effort has gone into engineering higher rates and more efficient photosynthesis, the success to date has been modest [71–74]. A dynamic systems model of photosynthesis as envisioned here, which incorporates the interactions among canopy microclimate, primary metabolism, resource re-mobilization in senescencing leaves, and associated energetic costs for maintaining existing tissues and constructing new tissues [57•,75•], would provide a robust framework to systematically re-evaluate the potential of different canopy features, for example, leaf nitrogen content, leaf thickness, leaf composition, enzyme distributions, enzyme kinetics and so on to improve A_c from a whole systems' energy and resource use efficiency perspective.

A persistent dream of plant biotechnology has been the ability to accurately predict the consequences of modifying different molecular, cellular, leaf and canopy level properties on total canopy CO_2 uptake rates, on canopy light, water and nitrogen use efficiencies and ultimately on the yield of crops before ever conducting a field experiment. While this dream may never be entirely fulfilled, with the rapid advances in plant science, model building algorithms and computation capacity, it is timely now to develop a heuristic integrative model that will take a large step toward that goal.

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