

Models of Photosynthesis

Graham D. Farquhar*, Susanne von Caemmerer, and Joseph A. Berry

Environmental Biology Group and Cooperative Research Centre for Greenhouse Accounting, Research School of Biological Sciences, Australian National University, Australian Capital Territory 0200, Australia (G.D.F.); Molecular Plant Physiology Group, Research School of Biological Sciences, Australian National University (S.v.C.); and Department of Plant Biology, Carnegie Institution of Washington, Stanford, California 94305 (J.A.B.)

A BRIEF HISTORY

Our model of photosynthesis (8) published some 20 years ago in *Planta* has had an impact and seen application that far exceeded our expectations. Perhaps it is useful to reflect on what this model did and why we published it. It is important to note that our model is not a complete model of photosynthesis. It makes no attempt to treat all of the steps in this important process; rather, it was a synthesis, a simplified view of the already (in 1980) overwhelming knowledge of the contributing mechanisms.

In the years preceding our model a great body of work had accumulated describing the responses of CO₂ exchange by leaves to a wide range of environmental conditions (temperature, CO₂ concentration, light intensity, humidity, and oxygen concentration). These responses were quite reproducible, but difficult to explain. Pieces began to fall into place that informed our ignorance. Perhaps the pivotal event was the finding by George Bowes and Bill Ogren that O₂ was a competitive inhibitor of CO₂ fixation by Rubisco and an alternative substrate leading to a side reaction that fueled photorespiration. Others added findings that integrated photorespiration into photosynthetic carbon metabolism. This synthesis provided a plausible explanation of the manifold interactions between O₂ and CO₂ on the photosynthesis of leaves.

In our model we linked equations describing Rubisco kinetics with others on the stoichiometry of the photosynthetic carbon reduction cycle and the photorespiratory carbon oxidation cycle, particularly on their energetic (electron transport and ATP synthesis) requirements. Building on the pioneering modeling of Hall, Tenhunen, Peisker, Laisk, and others, we then drew together biochemical and organelle level observations of the temperature dependencies of these phenomena, and combined them with an empirical equation for the dependence of "potential" electron transport rate on absorbed irradiance. Our model attempted to match generalized observations of the photosynthetic gas exchange of leaves with

predictions from this mathematical summary of photosynthesis.

We published our paper (8), "A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species," in 1980. Susanne von Caemmerer was, at that stage, a PhD student with Graham Farquhar at the Research School of Biological Sciences, and Joe Berry had earlier been a visitor to Barry Osmond's laboratory there. Many of the principles had been discussed during the earlier visit, including what Joe Berry called the "teeter-totter" (and Graham Farquhar called it a "see-saw") between two flux limitations. That is, that photosynthesis cannot go faster than a carboxylase activity limited rate, and also cannot go faster than an electron transport limited rate, but should move easily from one to another without the overall rate being much smaller than either limitation—few "frictional" losses. A working model of C₃ photosynthesis including these principles was developed before Joe Berry left, and this was integrated into the first publication, a model of the C₄ mechanism (2).

WHY MODEL?

Graham Farquhar was interested in modeling photosynthesis to answer the question raised in his collaboration with Ian Cowan on optimal behavior of stomata: What would the rate of CO₂ assimilation be if stomatal conductance were slightly perturbed? Joe Berry was interested in how the CO₂-concentrating system of C₄ plants influenced CO₂ fixation and photorespiration by Rubisco in the bundle sheath cells. In both cases we needed a mechanism for representing the properties of C₃ plants in the context of a larger analytical framework. Susanne von Caemmerer, who came to this environment with a degree in pure mathematics, used the model as a tool for making quantitative links between leaf biochemistry and gas exchange kinetics (18).

Of course an underlying feeling was that one doesn't really understand something until one can describe it mathematically. The model has been subsequently used for pedagogic purposes, and also as a useful framework for fitting to data, and then extrapolating. All this has provided an interplay between

* Corresponding author; e-mail farquhar@rsbs.anu.edu.au; fax 61-2-6249-4919.

model and measurement that has stimulated development of both fields.

The interplay was also relevant to the direct issue of publishing our paper. It was initially rejected: it contained no data, and it was against *Planta* policy to publish papers that were solely models. Ian Cowan crafted a letter arguing that the modeled response curves were familiar to all the experimentalists who worked on gas exchange. We are grateful to the *Planta* editors for accepting the argument. Later Graham Farquhar was asked to referee all modeling papers sent to *Planta*.

BRINGING BIOCHEMISTRY AND GAS EXCHANGE TOGETHER

The original model development was aided by breakthroughs in understanding Rubisco oxygenase and oxygen inhibition of CO₂ fixation (12) and Rubisco kinetics and their temperature dependence. It was also aided by developments in Rubisco activation, but only in the sense of providing sufficient activity to relate to rates *in vivo*. Understanding the pathway and stoichiometry of the photorespiratory cycle was also important. Improvements in gas exchange technology permitted measurement of photosynthesis, stomatal conductance, and intercellular partial pressure of CO₂. Susanne von Caemmerer discusses many of these issues in her recent text (17). Later, the pool sizes of intermediates and enzyme activities were measured in relation to gas exchange. The parametrization of our model requires estimates of Rubisco kinetic constants and recently, plants with antisense to the small subunit of Rubisco have proved an ideal system for measuring the constants *in vivo*, as these plants are more completely Rubisco-limited than the wild type. Some contemporary gas exchange measurements include those of oxygen and its isotopes (17).

CONTROL OF PHOTOSYNTHESIS

Control of RuBP Regeneration

In our original model, RuBP regeneration was controlled by electron transport, but could also be limited further by other components (lumped together) of the photosynthetic carbon reduction cycle. At higher [CO₂], Tom Sharkey has drawn attention to a third limitation that may come into play, that of triose phosphate utilization. The details of all these interactions are yet to be fully modeled. An interesting, new, and complex approach is being taken by Agu Laisk who has been at the forefront of so much modeling of photosynthesis. He and colleagues are developing a detailed model (13) with dozens of enzymes and electron carriers so that regulation can be examined, as well as control of overall leaf pho-

tosynthesis. It could serve as a working encyclopedia of what is known about enzymes, pathways, and membrane transport. It is perhaps surprising that electron transport in whole-leaf models is still treated largely empirically. Fluorescence studies have been valuable in making progress. Engelbert Weis and Joe Berry (19) used our model to relate the rate of CO₂ exchange to that of electron transport. This permitted a quantitative analysis of the relation between fluorescence quenching properties and electron transport. It separated the role of photochemical quenching and showed that there is a residual role that could be related to non-photochemical quenching. Bernard Genty and colleagues (11) developed a model that has a theoretically satisfying basis and simplicity, built on this finding. They showed that the quantum yield of photosystem II is related to the ratio of steady-state fluorescence to saturated fluorescence ($\Phi_{PS2} = 1 - \Phi/\Phi_m$). The challenge remains that we still don't know the physical mechanism of non-photochemical quenching.

Rubisco Activation and Its Control

Activation/carbamylation and inhibition of Rubisco are an active area of research, experimentally and theoretically (17). Our original model did not include these processes, and with the understanding of that time their inclusion would have kept rates of photosynthesis below those observed in real life. Susanne's thesis work (18) showed that to achieve those rates with subsaturating [CO₂], Rubisco would have to be fully active. Few researchers were allowing for subsaturation and the idea that Rubisco was a storage protein was then wide spread. The subsequent work on tight binding of RuBP and of inhibitors, and on carbamylation, has been an interesting case where model formulation has informed the comparison of *in vitro* and *in vivo* data.

In the steady state, Rubisco activation is now generally thought to be regulated and to place no greater limitation on photosynthesis than is already there because of limited capacity for regeneration of RuBP (typically electron transport). However, a low level of activation may limit, for example, when light intensity suddenly increases.

Transients

Several groups have addressed the issue of transient changes in light intensity and how such changes affect photosynthesis (14, 17). The transients involve the times taken for stomata to respond, for Rubisco activation to increase, and for the pool of phosphorylated intermediates of the PCR cycle to autocatalytically build to the appropriate level.

REGULATION VERSUS LIMITATION: THE SUPPLY OF CO₂ TO RUBISCO

Limitations within the Leaf

Many earlier models of photosynthesis assumed that the kinetics of CO₂ assimilation were determined by resistances to diffusion within the chloroplast. The biochemical models challenged those views. Now the challenge is to modify the biochemical models with appropriate representations relating fluxes to concentrations. We need three-dimensional parameters analogous to the one-dimensional concept of resistance. Dave Parkhurst has made a start with more detailed descriptions of diffusion within the intercellular air spaces of leaves. There appears to be a significant drawdown in [CO₂] from the substomatal cavities to the sites of Rubisco, much of it presumably across the cell walls and membranes, and an unknown contribution from the air spaces (17).

Limitations by Stomata

Chin Wong (20) showed that under many conditions where photosynthetic capacity was caused to change, the ratio of intercellular and ambient CO₂ concentration (C_i/C_a) often remained constant, reducing with increasing leaf-to-air humidity difference. Tim Ball and Joe Berry (1) generalized this finding and effectively produced a succinct relationship between stomatal conductance and rate of photosynthesis. When combined with a biochemical model of photosynthesis, it has formed the basis for many studies modeling whole-leaf and canopy carbon assimilation.

Ian Cowan described stomatal functioning in terms of optimization of carbon gain with respect to water loss, with the free parameter being tied to the statistics of rainfall (3). There is at present insufficient information for a mechanistic model of stomatal functioning.

“Patchiness”

Heterogeneity in stomatal supply has been recognized as a problem when it comes to assigning a concentration of CO₂ at the substomatal level. If the heterogeneity of stomatal opening comes about as the result of some imposed stress, one might be fooled into interpreting the data as a loss of photosynthetic capacity (16). The current quantitative mapping of photosynthesis to address this problem derives from analysis of chlorophyll fluorescence images (4).

HOMOGENEITY OF LIGHT INTENSITY AND PHOTOSYNTHETIC CAPACITY

We originally thought of our model as applying at the chloroplast level and were somewhat surprised

that it seemed to work for a leaf. It assumed a homogeneous light environment, CO₂ concentration, and concentration of Rubisco. It emerged later that the same model should hold if light intensity and photosynthetic capacity co-vary in space (7). Although that can happen within a leaf or canopy when light is averaged over a day (9), it does not hold in detail with changes in light intensity on a time scale far shorter than that of photosynthetic adaptation—particularly a problem with light flecks deep in a canopy. Thus big-leaf models with the total Rubisco per unit ground area treated as a single leaf overestimate canopy photosynthesis. Models that differentiate sun and shade leaves largely overcome these problems (5) for broad-leaved species and grasses like wheat. Nevertheless, there is a need to introduce penumbral effects, especially for coniferous species. The analogous problem exists considering the internal volume of a leaf as well.

SCALING TO THE GLOBAL LEVEL

Models of photosynthesis and stomatal conductance are becoming embedded in larger models of the global carbon cycle and of land surface feedbacks on climate. The physiological properties affect atmospheric temperature and the hydrological cycle (10). Models now strive to simulate the mass and energy balance of the land surface with changing meteorological conditions over time—especially in climate models. Use of our model of photosynthesis has resulted in development of theory to couple satellite remote sensing of spectral reflectance to estimate the absorbed photosynthetically active radiation and the efficiency of its use by chloroplasts at a global scale with spatial resolution of about 1 km². The coupling of these with stomatal models has improved the simulation of heat and water exchange between vegetated surfaces of continents and the atmosphere (15). The significance for quantitative understanding of the bioenergetics of our planet is just beginning to have an impact.

MOVING TO LONGER TIME SCALES

There is a need for longer-term modeling of photosynthesis. There is little known about and thus little predictive modeling of how Rubisco activity and electron transport capacity change with environmental conditions. In practice most applications follow the observed changes in leaf properties, either from direct observations or from measurements of leaf nitrogen levels, as the latter often give reasonable measures of capacity once the nitrogen tied up in cell walls is accounted for (6). Future developments are inextricably linked with modeling of growth and development and will necessarily involve considerations of cell division and expansion and of hormonal and other controls of gene expression.

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