

TECHNIQUES IN PLANT SCIENCES

No 2

# Biochemical Models of Leaf Photosynthesis

S. von Caemmerer



CSIRO  
PUBLISHING

National Library Cataloguing in Publication entry

von Caemmerer, S. (Susanne).

Biochemical models of leaf photosynthesis.

Bibliography.

ISBN 0 643 06379 X.

1. Botanical chemistry.

2. Photosynthesis – Measurement.

I. Title. (Series : Techniques in plant sciences ; no. 2).

572.460723

© CSIRO 2000

This book is available from:

CSIRO PUBLISHING

PO Box 1139 (150 Oxford Street)

Collingwood VIC 3066

Australia

Tel: (03) 9662 7666 Int: +(613) 9662 7666

Fax: (03) 9662 7555 Int: + (613) 9662 7555

Email: [sales@publish.csiro.au](mailto:sales@publish.csiro.au)

<http://www.publish.csiro.au>

Printed in Australia by Brown Prior Anderson

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## Preface

Increasing concerns about global climate change have revived research interests in all aspects of carbon exchange. Natural ecosystems form an important part of the global carbon balance as sinks for atmospheric CO<sub>2</sub>. Interest in predicting net primary productivity has restored interest in leaf photosynthetic models to predict and assess changes in photosynthetic CO<sub>2</sub> assimilation in different environments. Photosynthetic processes of leaves have a remarkable influence on our global atmosphere. Seasonal and latitudinal variations in the carbon isotope ratio of atmospheric CO<sub>2</sub> relate to rubisco's preference for <sup>12</sup>CO<sub>2</sub> rather than <sup>13</sup>CO<sub>2</sub>. The oxygen isotope composition of atmospheric CO<sub>2</sub> is influenced by the amount of carbonic anhydrase in the chloroplast of C<sub>3</sub> species and the mesophyll cytosol of C<sub>4</sub> species (Francey and Tans 1987; Yakir et al. 1992; Farquhar et al. 1993). This book deals exclusively with the photosynthetic processes of leaves. The models discussed are based on the underlying biochemical processes of photosynthesis and were designed to help in the interpretation of leaf gas-exchange measurements. However, because of their simplicity they have also proved valuable as submodels in a variety of other larger scale applications such as canopy photosynthesis and climate models.

At present, the techniques of genetic and molecular biology, which allow the modulation of individual plant characters, enable new questions to be asked in ecophysiology about photosynthesis and plant growth. The steady-state leaf-photosynthetic models have become an invaluable guide for the analysis of such genetic manipulation, where they are frequently used in conjunction with gas-exchange measurements to provide *in vivo* estimates of biochemical parameters.

Leaf gas-exchange measurements were first developed in the late 1950s. Penman and Schofield (1951) put the theories of diffusion of CO<sub>2</sub> and water vapour through stomata on a firm physical basis. Gaastra took up their ideas in the 1950s and modern analytical gas exchange is often attributed to his seminal work (Gaastra 1959). His work was a landmark because it examined CO<sub>2</sub> assimilation and water vapour exchange rates of individual leaves under different environmental conditions, and he distinguished between stomatal and internal resistances. Gaastra at the time concluded that the rate of CO<sub>2</sub> uptake was completely limited by diffusion processes at low CO<sub>2</sub> partial pressures and that biochemical processes became important only at high CO<sub>2</sub> partial pressures. Thus, gas-exchange studies focused initially on physical limitations to diffusion. Based on Gaastra's ideas, early models of leaf gas exchange had been developed as analogues of electrical resistances, and this proved useful in making a distinction between stomatal and mesophyll limitations on CO<sub>2</sub> assimilation. Mesophyll, or 'residual', resistance was a collective term that embodied non-stomatal diffusive factors, and included both physical and biochemical constraints.

In Australia, particularly, there was a great interest in determining the relative importance of stomatal and mesophyll resistance in limiting CO<sub>2</sub> assimilation rates under adverse conditions of high temperature and frequent water stresses (Bierhuizen and Slatyer 1964; Troughton and Slatyer 1969). It was not long, however, before persuasive arguments were being brought forward to show that leaf biochemistry had an important influence on the rate of CO<sub>2</sub> fixation, even at low CO<sub>2</sub> partial pressures. For example, Björkman and Holmgren (1963) made careful gas-exchange measurements of sun and shade ecotypes of *Solidago*, and noted a strong correlation between

photosynthetic rate measured at high irradiance and ambient  $\text{CO}_2$  and the nitrogen content of leaves, and later related it to different concentrations of rubisco. Furthermore, following earlier discoveries of the  $\text{O}_2$  sensitivity of photosynthesis, viz. an enhancement of  $\text{CO}_2$  assimilation rate at low  $\text{O}_2$ , Gauh and Björkman (1969) showed very elegantly that, while oxygen partial pressures did affect  $\text{CO}_2$  assimilation rate, water vapour exchange was not affected (i.e. stomata had not responded). Clearly, the increase in  $\text{CO}_2$  assimilation rates seen with a decrease in  $\text{O}_2$  partial pressures could not be explained by a limitation on  $\text{CO}_2$  diffusion. Mathematical models of leaf photosynthesis based on Gaastra's resistance equation could not accommodate this  $\text{O}_2$  sensitivity of  $\text{CO}_2$  assimilation. They were quickly superseded by the development of more biochemical models in the early 1970s. The discoveries by Bowes et al. (1971) that rubisco was responsible for both carboxylation and oxygenation of ribulose-1,5-bisphosphate put rubisco in the limelight. Laing et al. (1974) and Peisker (1974) were first to compare the gas exchange of leaves with the *in vitro* kinetics of rubisco.

In this book rubisco takes centre stage. Although there are many chloroplast components essential for the operation of photosynthesis, successful mathematical descriptions of photosynthesis are inevitably linked to rate equations of rubisco carboxylation and oxygenation. Chapter 1 thus deals with the kinetic properties of rubisco and these equations form the basis for the biochemical models presented in this book. In Chapter 1, *in vitro* and *in vivo* responses of rubisco are compared and analysed. Since the leaf photosynthetic models are based on rubisco's kinetic properties they have also proved a useful tool for examining the *in vivo* activity of rubisco. This is taken up in the later part of the chapter where transgenic plants with impaired photosynthetic properties are used to unravel the mysteries of *in vivo* regulation of rubisco.

Chapter 2 is a straightforward treatment of the now frequently used photosynthesis model of Farquhar et al. (1980). The chapter contains many examples of applications of the model to the analysis of transgenic plants with altered photosynthetic properties. It identifies some of the existing gaps in our knowledge, which need to be addressed because of the present need to model photosynthesis with respect to global climate change.

Chlorophyll fluorescence has emerged as a powerful, non-destructive tool for the analysis of photosynthesis and is providing insights into chloroplast electron transport rates. It is particularly useful as a field measure of photosynthetic performance and has thus stimulated considerable interest in comparisons with photosynthetic  $\text{CO}_2$  exchange. In Chapter 3 a comparison is made between the use of measurements of chlorophyll fluorescence to estimate chloroplast electron transport rate and estimates made from gas-exchange measurements. Furthermore, the model of Farquhar et al. (1980) is used to derive rate equations for the  $\text{O}_2$  exchange that occurs during  $\text{C}_3$  photosynthesis.

Though the  $\text{C}_3$  pathway of photosynthesis dominates most of the terrestrial ecosystem, the  $\text{C}_4$  pathway of photosynthesis is important in certain agricultural and natural ecosystems and accounts for as much as 20% of global carbon fixation. The  $\text{C}_4$  pathway is common amongst species native to tropical and subtropical grasslands. It took some very energetic grinding of  $\text{C}_4$  leaves before rubisco was recognized as a key player in the  $\text{C}_4$  photosynthetic pathway (Hatch 1997; Osmond 1997). It is now well recognized that the  $\text{C}_4$  photosynthetic pathway functions as a  $\text{CO}_2$  concentrating mechanism that provides rubisco, located in the bundle sheath, with a high  $\text{CO}_2$  atmosphere where it can function at near  $\text{CO}_2$  saturation with minimal oxygenase activity. This requires the cooperation between mesophyll and bundle-sheath cells, and the involvement of two cell types has complicated biochemical analysis. Here, the photosynthetic models provide an important quantitative tool to predict bundle-sheath function.

The fifth chapter discusses biochemical models of leaf photosynthesis of  $\text{C}_3$ - $\text{C}_4$  intermediate species. Different biochemical variants give rise to the syndrome of  $\text{C}_3$ - $\text{C}_4$  intermediacy, but all such plants have a  $\text{C}_4$ -like leaf anatomy.  $\text{C}_3$ - $\text{C}_4$  species are sometimes considered to be evolutionary intermediates between  $\text{C}_3$  and  $\text{C}_4$  species. The pathways revolve around efficient



refixation of photorespiratory  $\text{CO}_2$ . Their leaf gas exchange shows a reduced oxygen sensitivity in comparison with that of  $\text{C}_3$  species and improved photosynthetic rates at low  $\text{CO}_2$  partial pressure. Since many of the details of these pathways remain unexplored the photosynthetic models are, of necessity, experimental. Perhaps this chapter provides the best examples of how the biochemical models presented in this book can aid in the formulation of ideas. Each photosynthesis model provides a set of hypotheses brought together in a quantitative form that can be used to design and interpret experiments.

## Acknowledgments

I wish to thank C. Barry Osmond for inviting me to contribute to this series of Techniques in Plant Sciences. I have greatly enjoyed this opportunity and appreciate the encouragement and support he has provided throughout my scientific career. With his never-ending enthusiasm for science he has been a source of inspiration for me. I had the great fortune to have Graham D. Farquhar as my PhD supervisor and have been irrevocably influenced by his rigorous approach to science. I am fortunate to be able to work within the stimulating environment of the Molecular Plant Physiology Group at the Research School of Biological Science. I am indebted to John Andrews for many fascinating discussions on the mechanism and regulation of rubisco. I thank Murray Badger, John Andrews and Dean Price for the opportunity to collaborate on the analysis of transgenic plants with impaired photosynthesis. Lastly I would like to thank John R. Evans for his friendship. I am thankful for his helpful, energetic and apposite criticisms.