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Biochemical Models of Leaf Photosynthesis

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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_2. Interest in predicting net primary productivity has restored interest in leaf photosynthetic models to predict and assess changes in photosynthetic CO_2 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_2 relate to rubisco's preference for $^{12}CO_2$ rather than $^{13}CO_2$. The oxygen isotope composition of atmospheric CO_2 is influenced by the amount of carbonic anhydrase in the chloroplast of C_3 species and the mesophyll cytosol of C_4 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_2 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_2 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_2 uptake was completely limited by diffusion processes at low CO_2 partial pressures and that biochemical processes became important only at high CO_2 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_2 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_2 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_2 fixation, even at low CO_2 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 CO_2 and the nitrogen content of leaves, and later related it to different concentrations of rubisco. Furthermore, following earlier discoveries of the O_2 sensitivity of photosynthesis, viz. an enhancement of CO_2 assimilation rate at low O_2, Gauhl and Björkman (1969) showed very elegantly that, while oxygen partial pressures did affect CO_2 assimilation rate, water vapour exchange was not affected (i.e. stomata had not responded). Clearly, the increase in CO_2 assimilation rates seen with a decrease in O_2 partial pressures could not be explained by a limitation on CO_2 diffusion. Mathematical models of leaf photosynthesis based on Gaastra's resistance equation could not accommodate this O_2 sensitivity of 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 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 O_2 exchange that occurs during C_3 photosynthesis.

Though the C_3 pathway of photosynthesis dominates most of the terrestrial ecosystem, the 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 C_4 pathway is common amongst species native to tropical and subtropical grasslands. It took some very energetic grinding of C_4 leaves before rubisco was recognized as a key player in the C_4 photosynthetic pathway (Hatch 1997; Osmond 1997). It is now well recognized that the C_4 photosynthetic pathway functions as a CO_2 concentrating mechanism that provides rubisco, located in the bundle sheath, with a high CO_2 atmosphere where it can function at near 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 C_3–C_4 intermediate species. Different biochemical variants give rise to the syndrome of C_3–C_4 intermediacy, but all such plants have a C_4-like leaf anatomy. C_3–C_4 species are sometimes considered to be evolutionary intermediates between C_3 and C_4 species. The pathways revolve around efficient

refixation of photorespiratory CO_2. Their leaf gas exchange shows a reduced oxygen sensitivity in comparison with that of C_3 species and improved photosynthetic rates at low 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.

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