

Photosynthetic Research in Plant Science

Ayumi Tanaka¹ and Amane Makino²

¹Institute of Low Temperature Science, Hokkaido University, Sapporo, Japan

²Graduate School of Agricultural Science, Tohoku University, Sendai, Japan

Photosynthesis is a highly regulated, multistep process. It encompasses the harvest of solar energy, transfer of excitation energy, energy conversion, electron transfer from water to NADP⁺, ATP generation and a series of enzymatic reactions that assimilate carbon dioxide and synthesize carbohydrate.

Photosynthesis has a unique place in the history of plant science, as its central concepts were established by the middle of the last century, and the detailed mechanisms have since been elucidated. For example, measurements of photosynthetic efficiency (quantum yield) at different wavelengths of light (Emerson and Lewis 1943) led to the insight that two distinct forms of Chl must be excited in oxygenic photosynthesis. These results suggested the concept of two photochemical systems. The reaction center pigments of PSII and PSI (P680 and P700, respectively) were found by studying changes in light absorbance in the red region (Kok 1959, Döring et al. 1969). Chls with absorbance maxima corresponding to these specific wavelengths were proposed as the final light sink. These Chls were shown to drive electron transfer by charge separation. The linkage of electron transfer and CO₂ assimilation was suggested by studies on Hill oxidant (Hill 1937). A linear electron transport system with two light-driven reactions (Z scheme) was proposed based upon observations of the redox state of cytochromes (Hill and Bendall 1960, Duysens et al. 1961), and photophosphorylation was found to be associated with thylakoid fragments (Arnon et al. 1954). The metabolic pathway that assimilates carbon by fixation of CO₂ was discovered by Calvin's group who used ¹⁴CO₂ radioactive tracers in the 1950s (Bassham and Calvin 1957). This was the first significant discovery in biochemistry made using radioactive tracers. The primary reaction of CO₂ fixation is catalyzed by Rubisco (Weissbach et al. 1956), initially called Fraction 1 protein (Wildman and Bonner 1947). Rubisco is the most abundant protein in the world, largely because it is also the most inefficient with the

lowest catalytic turnover rate (1–3 s⁻¹). Another CO₂ fixation pathway was then found in sugarcane (Kortschak et al. 1964, Hatch and Slack 1965) and named C₄ photosynthesis.

Although photosynthesis plays the central role in the energy metabolism of plants, historically there have not been strong interactions between photosynthesis research and other fields of plant science. Many techniques and tools developed for photosynthesis research have not been widely used in other fields because they were developed to examine phenomena unique to photosynthesis. For example, excitation energy transfer and charge separation are fundamental but unique processes of photosynthesis. Another reason for the historic isolation of photosynthesis research within plant science is that it was long believed that CO₂ fixation and carbohydrate production are the sole function of photosynthesis, with carbohydrates representing the only link between photosynthesis and other biological phenomena.

However, this situation has begun to change. Recent research has revealed that photosynthesis is closely related to a variety of other physiological processes. It is a major system for controlling the redox state of cells, playing an important role in regulating enzyme activity and many other cellular processes (Buchanan and Balmer 2005, Hisabori et al. 2007). Photosynthesis also generates reactive oxygen species, which are now appreciated as being regulatory factors for many biological processes rather than inevitable by-products of photosynthesis (Wagner et al. 2004, Beck 2005). Precursor molecules of Chl, which are a major component of photosynthesis, act as a chloroplast-derived signal, and are involved in regulating the cell cycle (Kobayashi et al. 2009). In light of this new information, it seems important to re-evaluate the function(s), both potential and demonstrated, of photosynthesis from a variety of view points. Photosynthesis research now employs the methods and tools of molecular biology and genetics, which are central methods for plant science in general. Meanwhile, Chl fluorescence and gas exchange

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measurements, developed especially for photosynthesis research, are now widely used in stress biology and ecology.

Photosynthesis research also contributes to our understanding of ecological phenomena and even the global environments (Farquhar et al. 1980, de Pury and Farquhar 1997, Monsi and Saeki 2005). Indeed, photosynthesis is now an integral component of simulation models used to predict the future of our planet. Improving the efficiency of photosynthesis by artificial modification of photosynthetic proteins and pathways has long been considered impossible or at best problematic, because, over evolutionary time, photosynthesis has become complex and tightly regulated. However, recent advances have made it possible to manipulate photosynthesis using molecular genetic technology (Andrews and Whiney 2003, Raines 2006). These advances may have positive influences on crop productivity (Parry et al. 2007) as photosynthetic rates have frequently been correlated with biomass accretion (Kruger and Volin 2006). Thus, we can expect many more novel concepts to be added to this history of photosynthetic research.

As photosynthesis research tackles new challenges, we should also continue to re-evaluate past research. Oxygen evolution, energy dissipation and cyclic electron transport are crucial processes during photosynthesis, yet their mechanisms still remain to be clarified. We have very limited knowledge of the formation and degradation of photosynthetic apparatus. Also, although photosynthesis plays a central role in C and N metabolism in plants, we do not yet understand how potential photosynthesis is related to crop productivity.

Plant and Cell Physiology would like to contribute to the development of novel concepts, pioneering new fields and solving the unanswered questions of photosynthesis. This special issue covers a wide range of topics in photosynthesis research. Terashima et al. (pp. 684–697) readdress the enigmatic question of why leaves are green. They show that the light profile through a leaf is steeper than that of photosynthesis, and that the green wavelengths in white light are more effective in driving photosynthesis than red light. Evans (pp. 698–706) proposes a new model using Chl fluorescence to explore modifications in quantum yield with leaf depth. This new multilayered model can be applied to study variations in light absorption profiles, photosynthetic capacity and calculation of chloroplastic CO₂ concentration at different depths through the leaf.

Singlet oxygen, ¹O₂, is produced by the photosystem and Chl pigments. ¹O₂ not only causes physiological damage but also activates stress response programs. The *flu* mutant of *Arabidopsis thaliana* overaccumulates protochlorophyllide that upon illumination generates singlet oxygen, causing growth cessation and cell death. Coll et al. (pp. 707–718) have isolated suppressor mutants, dubbed 'singlet oxygen-linked death activator' (soldat), that specifically abrogate

¹O₂-mediated stress responses in young *flu* seedlings, and they discuss the processes of acclimation to stresses. Pheophorbide *a* is a degradation product of Chl and one of the most powerful photosensitizing molecules. Mutants defective in pheophorbide *a* oxygenase, which converts pheophorbide *a* to open tetrapyrrole, accumulate pheophorbide *a* and display cell death in a light-dependent manner. Hirashima et al. (pp. 719–729) report that pheophorbide *a* is involved in this light-independent cell death.

Plants regulate the redox level of the plastoquinone pool in response to the light environment. In acclimation to high-light conditions, the redox level is kept in an oxidized state by the plastoquinone oxidation system (POS). Miyake et al. (pp. 730–743) investigated the mechanism of POS using the Chl fluorescence parameter, qL.

Nagai and Makino (pp. 744–755) examine in detail the differences between rice and wheat, the two most commercially important crops, in the temperature responses of CO₂ assimilation and plant growth. They find that the difference in biomass production between the two species at the level of the whole plant depends on the difference in N-use efficiency in leaf photosynthesis and growth rate. Sage and Sage (pp. 756–772) examine chlorenchyma structure in rice and related *Oryza* species in relation to photosynthetic function. They find that rice chlorenchyma architecture includes adaptations to maximize the scavenging of photorespired CO₂ and to enhance the diffusive conductance of CO₂. In addition, they consider that the introduction of Kranz anatomy does not require radical anatomical alterations in engineering C₄ rice.

Bioinformatics has become a powerful tool, especially in photosynthetic research, because photosynthetic organisms have a wide taxonomic distribution among prokaryotes and eukaryotes. Ishikawa et al. (pp. 773–788) present the results of a pilot study of functional orthogenomics, combining bioinformatic and experimental analyses to identify nuclear-encoded chloroplast proteins of endosymbiotic origin (CRENDOS). They conclude that phylogenetic profiling is useful in finding CPRENDOS, although the physiological functions of orthologous genes may be different in chloroplasts and cyanobacteria.

We hope you enjoy this special issue, and would like to invite you to submit more excellent papers to *Plant and Cell Physiology* in the field of photosynthesis.

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