Coupling Photophysics, Photochemistry, and Biochemistry for a Complete Mechanistic Modeling and Remote Sensing of Photosynthesis

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Photosynthesis consists of light and carbon reactions. The light reactions can be further divided into the photophysical and photochemical reactions because these two groups of reactions are spatially separated, follow different laws, and operate at vastly contrasting time scales. Recently, we have successfully developed steady-state, mechanistic models for the photophysical and photochemical reactions, respectively. The photophysical model predicts the partitioning of absorbed photon energy among different dissipation pathways. The photochemical model describes the photosynthetic electron transport controlled by the redox reactions between enzyme complexes and electron carriers along the electron transport chain between PSII and PSI. The developed photophysical and photochemical models can be directly coupled with the conventional Farquhar-von Caemmerer-Berry biochemical (carbon reaction) model. This coupling forms a complete model of photosynthesis to predict essentially all light and carbon reaction variables of interest at leaf and canopy scales, such as net and gross photosynthetic rates, actual electron transport rates, state transitions, ratio of cyclic electron transport in PSI, fluorescence emission, redox states of PSII, plastoquinone, and cytochrome b_6f complex, non-photochemical quenching, and constitutive heat dissipation. We have tested the coupled model

with pulse amplitude modulated (PAM) fluorometry and gas exchange measurements made on leaves of C_3 and C_4 species collected in the US, Canada, China, the Netherlands, and Finland. The species tested include lianas, shrubs, boreal deciduous trees, boreal evergreen needle-leaf tree, temperate deciduous trees, tropical deciduous trees, tropical evergreen trees, C_3 grasses, C_4 grasses, and different crop varieties.

The coupled photophysical-photochemical-biochemical model advances photosynthesis research in the following aspects:

- The PAM fluorometry and gas exchange measurements, which are the two most important data sources for studying photosynthesis at the leaf level, can now be used jointly in a unified framework for process understanding and carbon cycle model development.
- The relationship between sun-induced chlorophyll fluorescence and photosynthesis can now be simulated fully mechanistically for remote sensing applications.
- Different energy dissipation pathways can be simulated for better understanding land surface energy balance and temperature dynamics.
- Redox states of major enzymes and mobile electron carriers of the electron transport chain can be inferred directly from PAM fluorometry measurements to study state transition and regulation of electron transport and photosynthesis.
- For the first time, state transitions and ratio of cyclic electron transport are formally represented in photosynthesis modeling.
- The model also provides a logical explanation on why all land plants have a thylakoid with grana stacks.