



How to misinterpret photosynthesis measurements and develop incorrect ecosystem models

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It is becoming widely accepted that current land ecosystem models (dynamic global vegetation models and land-surface models) rest on shaky foundations and are in need of rebuilding, taking advantage of huge data resources that were hardly conceivable when these models were first developed. It has also become almost a truism that next-generation model development should involve observationalists, experimentalists and modellers working more closely together. What is currently lacking, however, is open discussion of specific problems in the structure of current models, and how they might have arisen. Such a discussion is important if the same mistakes are not to be perpetuated in a new generation of models.

I will focus on the central processes governing leaf-level gas exchange, which powers the land carbon and water cycles. I will show that a broad area of confusion exists – as much in the empirical ecophysiological literature as in modelling research – concerning the interpretation of gas-exchange measurements and (especially) their scaling up from the narrow temporal and spatial scales of laboratory measurements to the broad-scale research questions linked to global environmental change. In particular, I will provide examples (drawing on a variety of published and unpublished observations) that illustrate the benefits of taking a “plant-centred” view, showing how consideration of optimal acclimation challenges many (often unstated) assumptions about the relationship of plant and ecosystem processes to environmental variation.

- (1) Photosynthesis is usually measured at light saturation (implying Rubisco limitation), leading to temperature and CO₂ responses that are completely different from those of gross primary production (GPP) under field conditions.
- (2) The actual rate of electron transport under field conditions depends strongly on the intrinsic quantum efficiency, which is temperature-independent (within a broad range) and unrelated to the maximum electron transport rate.
- (3) Because leaf nitrogen (per unit area) correlates with photosynthetic capacity, it is often assumed that the former controls the latter. But this correlation is often weak and causality appears to be the other way round.
- (4) Ecosystem respiration does not increase during daytime, but the standard methods of flux partitioning assume that it does. The result is a systematic bias in gross primary production “data” derived from flux measurements.
- (5) Stomatal conductance and assimilation rate are closely coupled. Neglect of this coupling can lead to incorrect interpretations of stomatal behaviour. Consideration of this coupling, however, leads to strongly supported predictions of the ratio of leaf-internal to ambient carbon dioxide.
- (6) The photosynthetic capacities for carboxylation and electron transport vary spatially and seasonally (which most models neglect) but not systematically with plant functional types (as most models assume).
- (7) “Down-regulation” of photosynthetic capacity (and even leaf nitrogen) with enhanced carbon dioxide represents optimal acclimation.
- (8) The fertilization effect of enhanced carbon dioxide is not universally dependent on nutrient supply, and can account for the observed land carbon sink.

I will end on an optimistic note: rapid recent developments in formalizing optimality hypotheses, and their translation into explicit, quantitative predictions that can be tested using measurements (available through data synthesis or new experiments and measurement campaigns), offer extraordinary promise for the building of new and more secure foundations for terrestrial ecosystem science.