Nutrient limitation: theories and empirical support

Jinyun Tang and William J. Riley

Lawrence Berkeley National Laboratory

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- Biomolecules are made of carbon and other nutrients.
- Nutrients are naturally in short supply.

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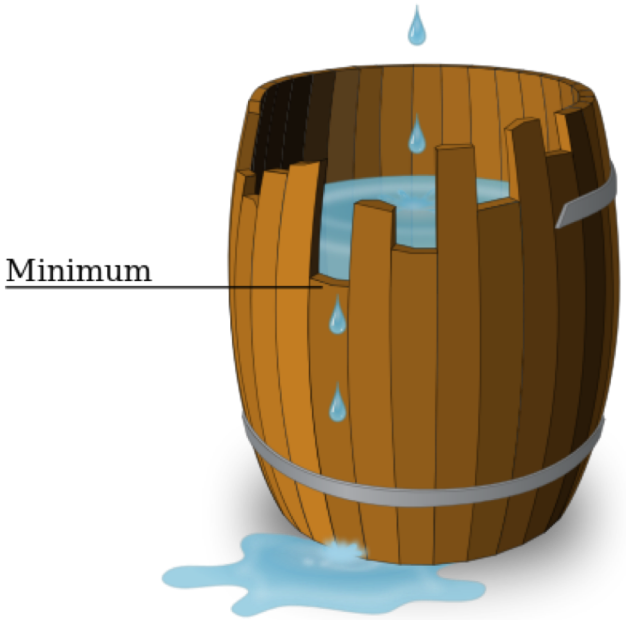
It is therefore important to know

- How does nutrient limitation operate in biological growth?
- How to interpret empirical supports?
- What are the implications to different models?

Classical hypothesis: Liebig's aw of the minimum

The shortest stave determines the level of water a bucket can hold!



Liebig's bucket

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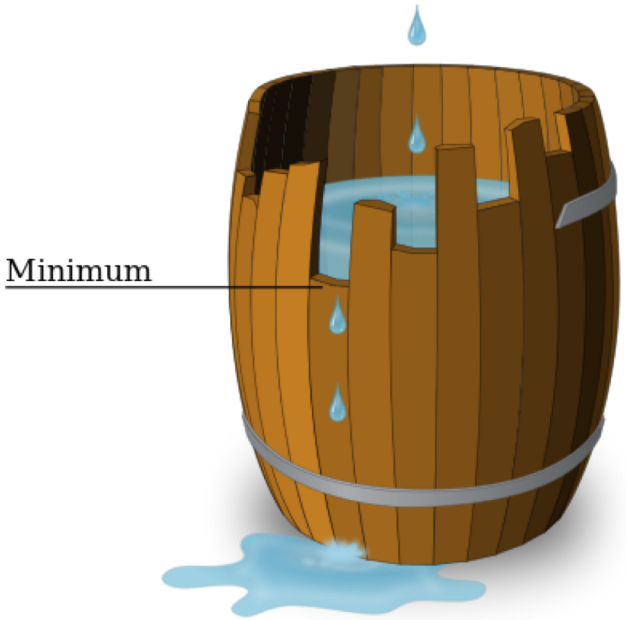

Liebig's bucket

van der Ploeg, R. R., W. Bohm, and M. B. Kirkham. 1999. On the origin of the theory of mineral nutrition of plants and the law of the minimum. A very nice historical account of LLM.

LLM is widely applied

- Nutrient limitation.
- Photosynthesis: flux limitation.

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LLM is occasionally questioned

- Thomas R. Sinclair and Wayne R. Park (1993) "Inadequacy of the Liebig limiting-factor paradigm for explaining varying crop yields.
- The duo of the Ball-Berry equation and Farquhar model occasionally do not converge. (My hypothesis).

Where is the law of the minimum (mechanistically) from?

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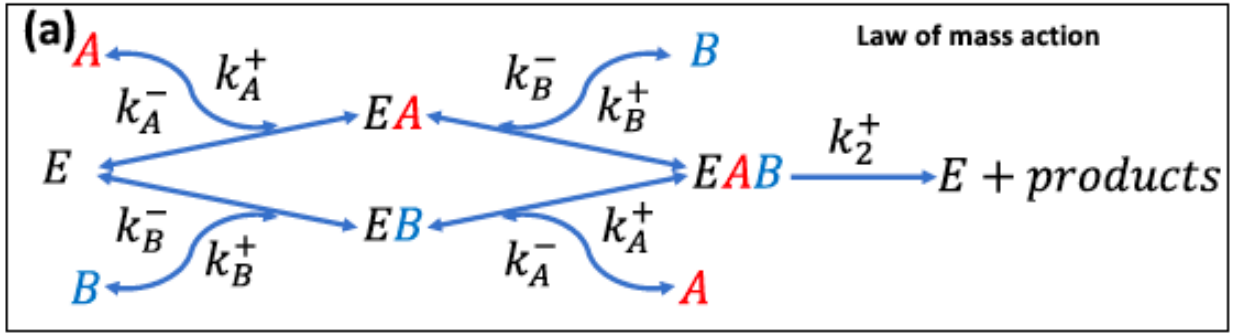
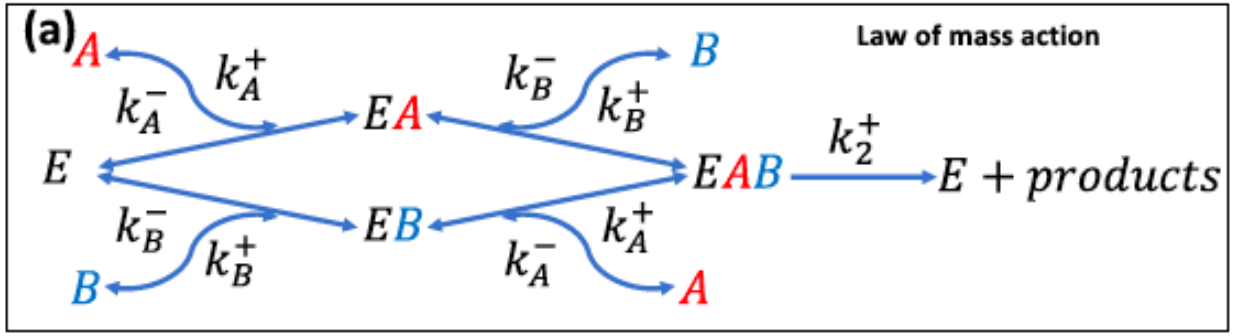
Because nutrient limitation is biochemistry, if LLM is legitimate, then it can be derived from the law of mass action.

Law of mass action



Law of mass action



$$k_A^+[E][A] + k_B^-[EAB] = (k_A^- + k_B^+[B])[EA]$$

$$k_B^+[E][B] + k_A^-[EAB] = (k_B^- + k_A^+[A])[EB]$$

$$k_A^+[EB][A] + k_B^+[EA][B] = (k_A^- + k_B^- + k_2^+)[EAB]$$

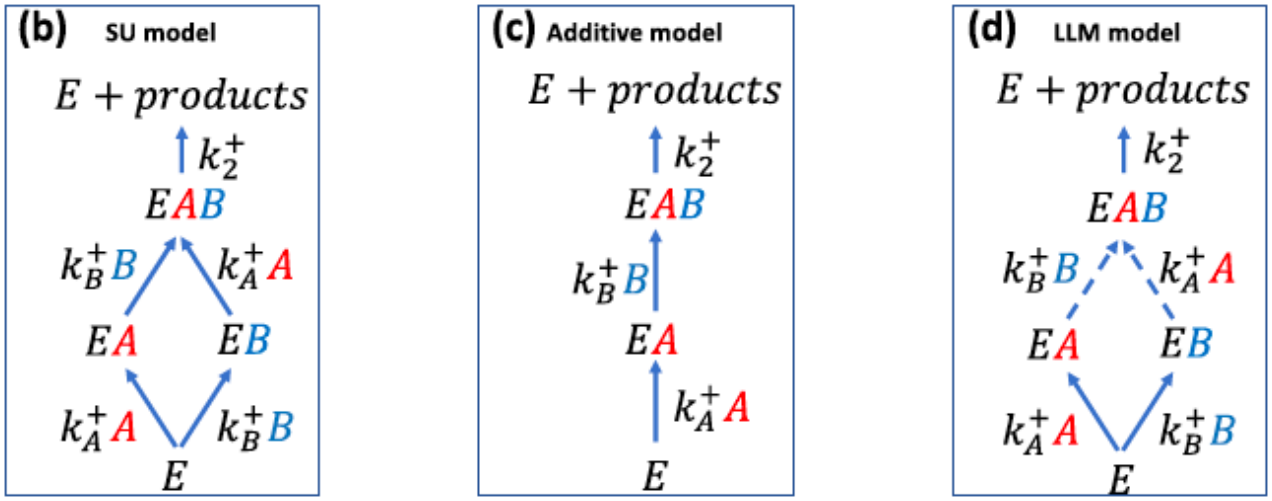
$$[E]_T = [E] + [EA] + [EB] + [EAB]$$

$$[A]_T = [A] + [EA] + [EAB]$$

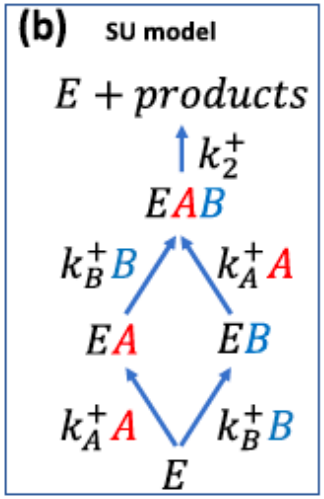
$$[B]_T = [B] + [EB] + [EAB]$$

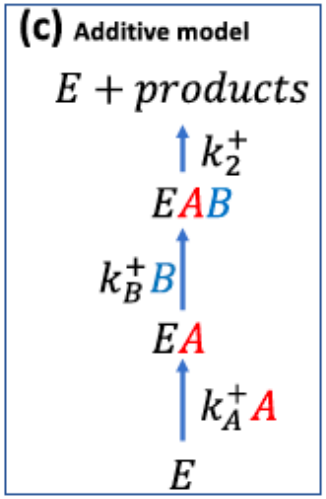
$$F = k_2^+[EAB]$$

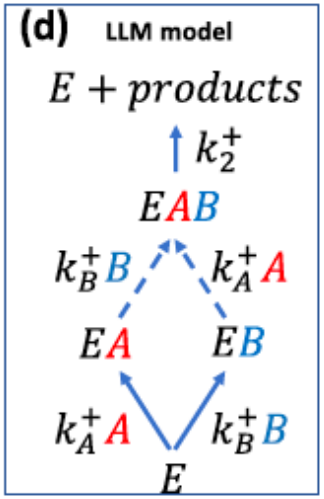
Three approximate models: graph representations



Three approximate models: mathematical representations







$$F_{SU} = \frac{k_2^+[E]_T}{1 + \frac{K_A}{[A]} + \frac{K_B}{[B]} - \frac{1}{[A]/K_A + [B]/K_B}}$$

$$F_{ADD} = \frac{k_2^+[E]_T}{1 + \frac{K_A}{[A]} + \frac{K_B}{[B]}}$$

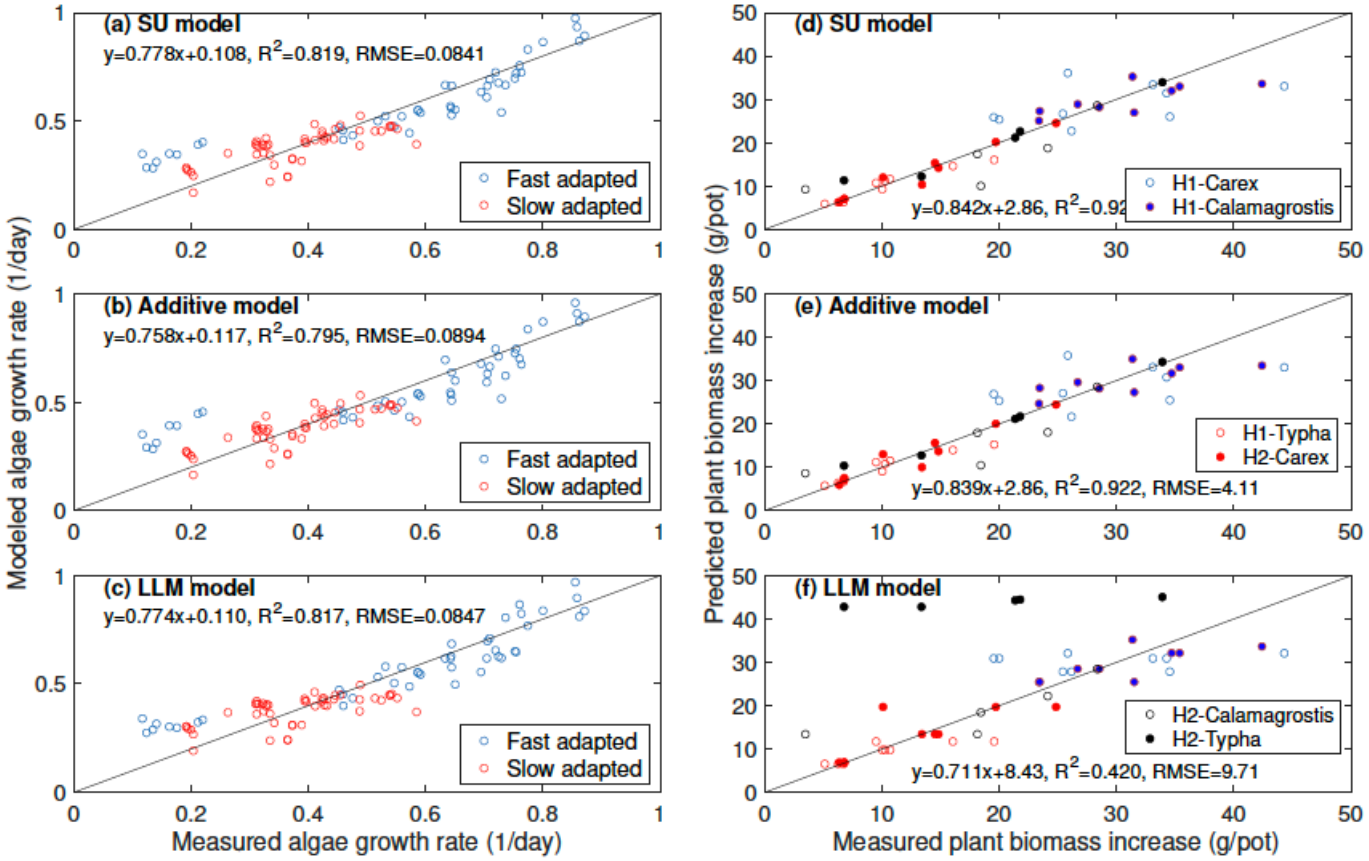
$$F_{LLM} = min\left(\frac{k_2^+[E]_T}{1 + \frac{K_A}{[A]}}, \frac{k_2^+[E]_T}{1 + \frac{K_B}{[B]}}\right)$$

Apply to empirical data: algae and plant growth

- Algae growth data (Droop, 1974)
  - Phosphorus and B_{12} vitamin as limiting nutrients.
  - growth rate as a function of cell quota, i.e. internal concentration
  - fast and slow groups

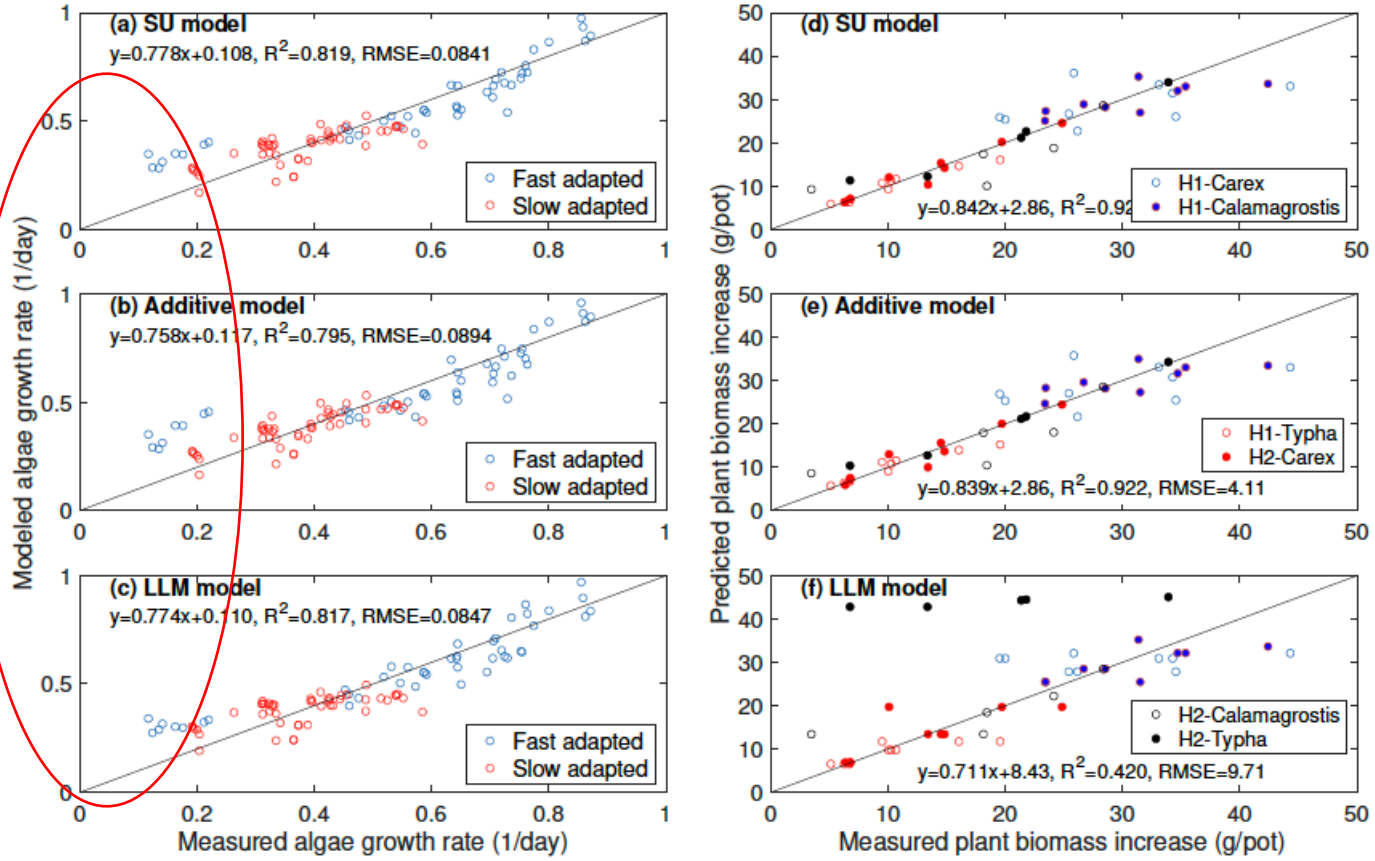
- Plant growth data (Shaver and Mellilo, 1984)
  - nitrogen and phosphorus as limiting nutrients
  - growth rate as a function of soil concentration
  - three genra and six harvests

The interpreting power of three models



The interpreting power of three models

Very similar performance



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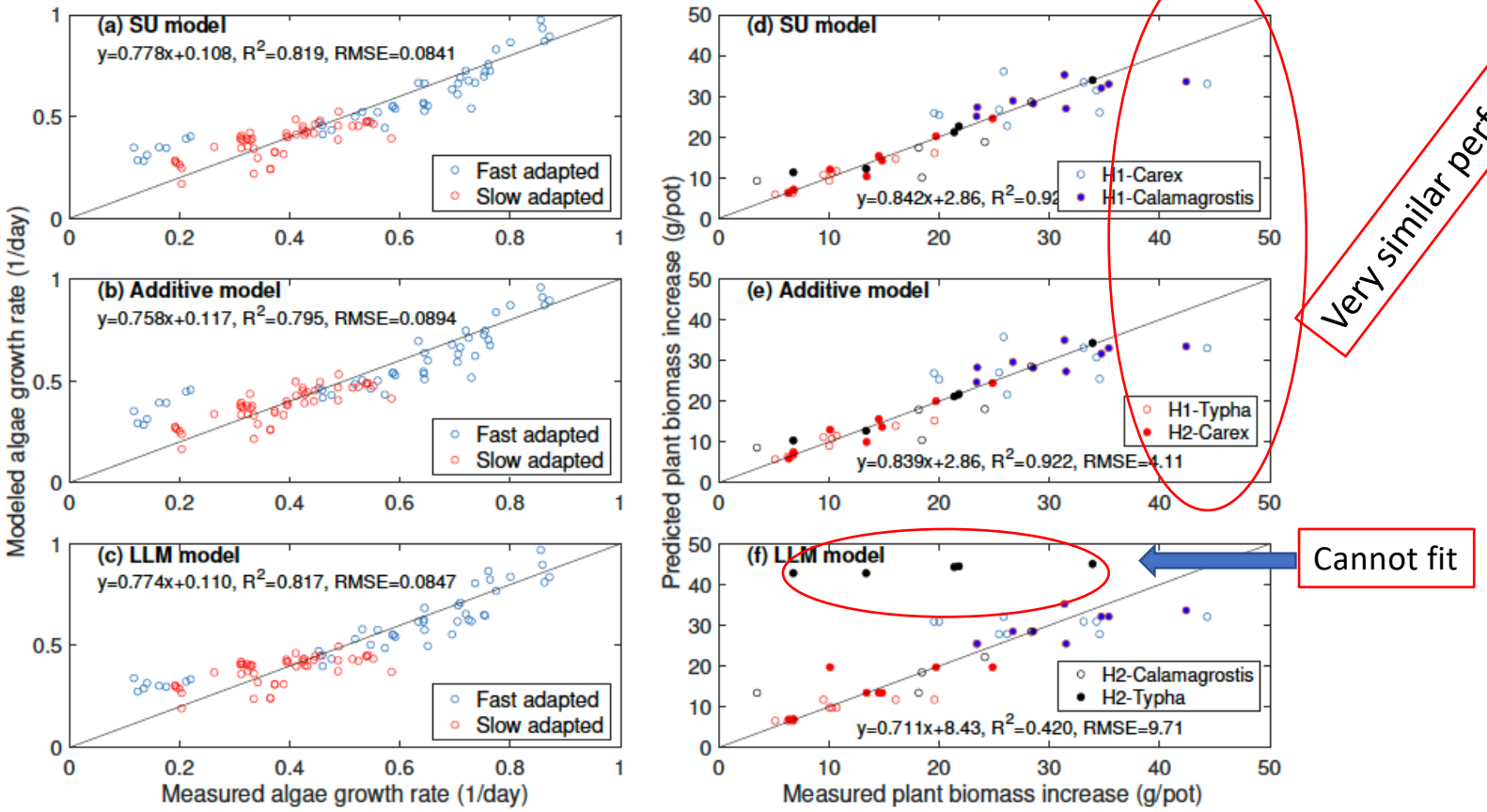
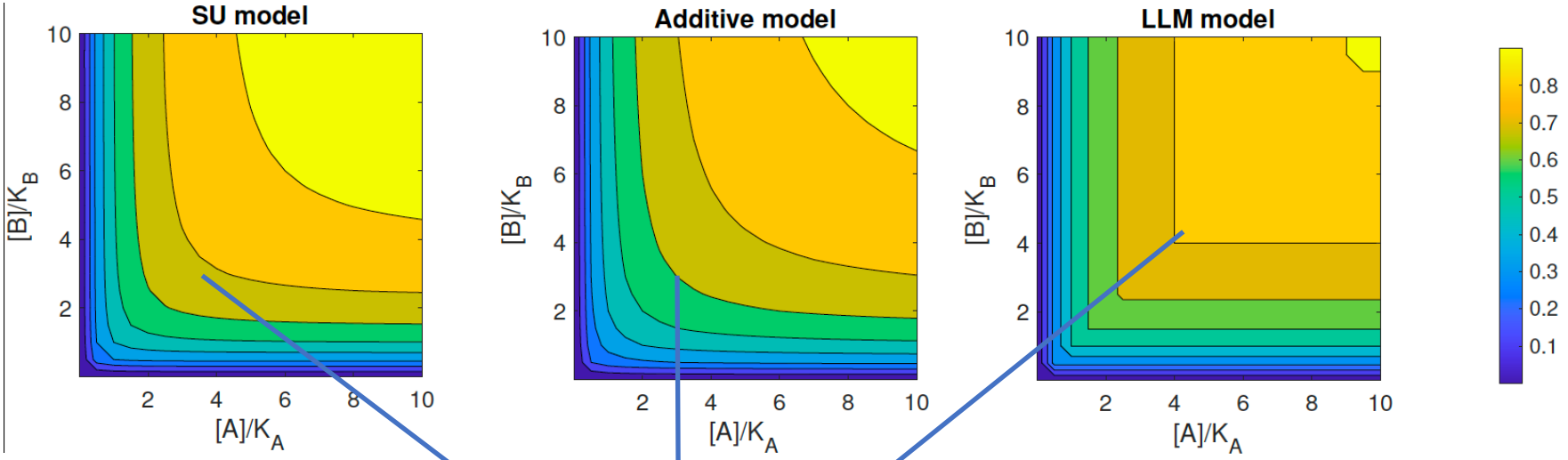
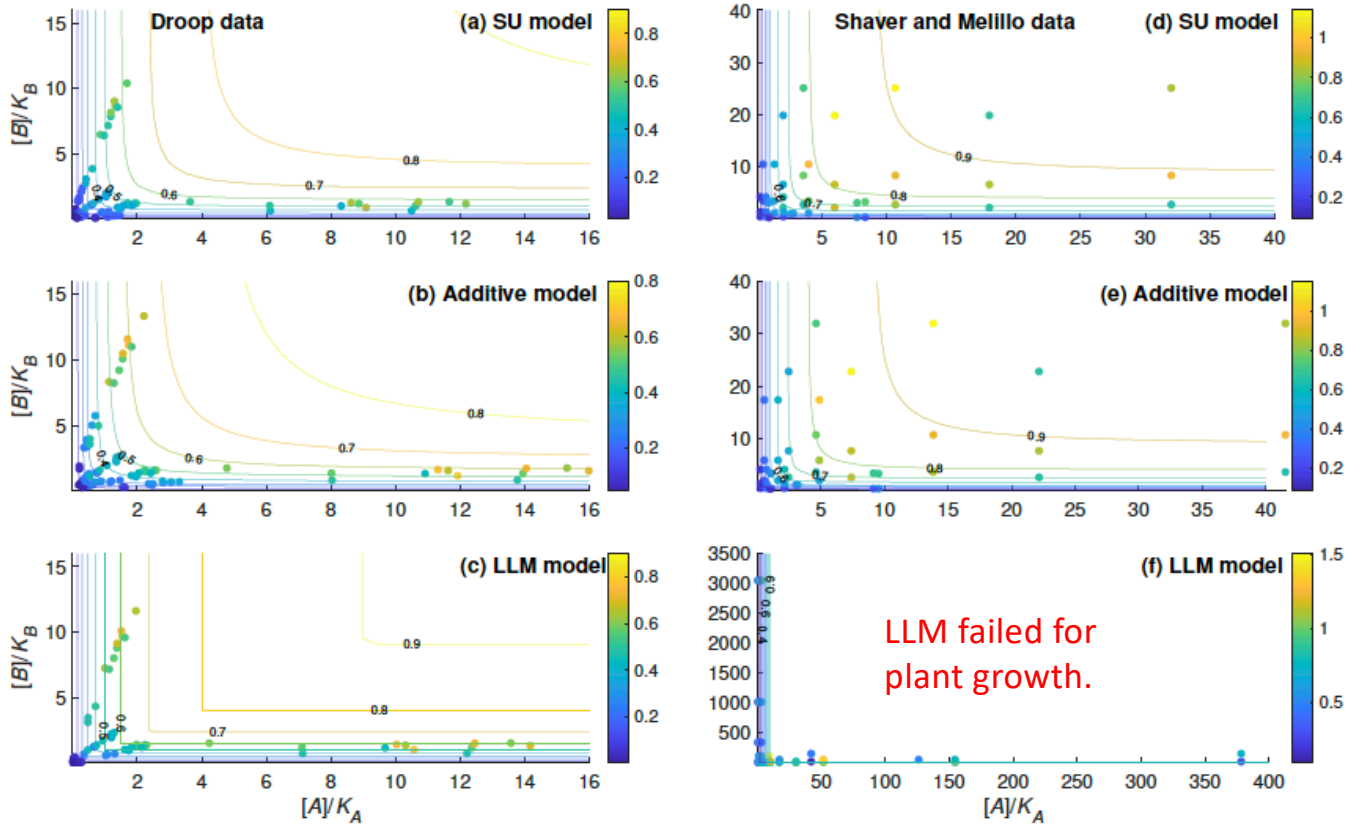


The co-limitation pattern for normalized growth

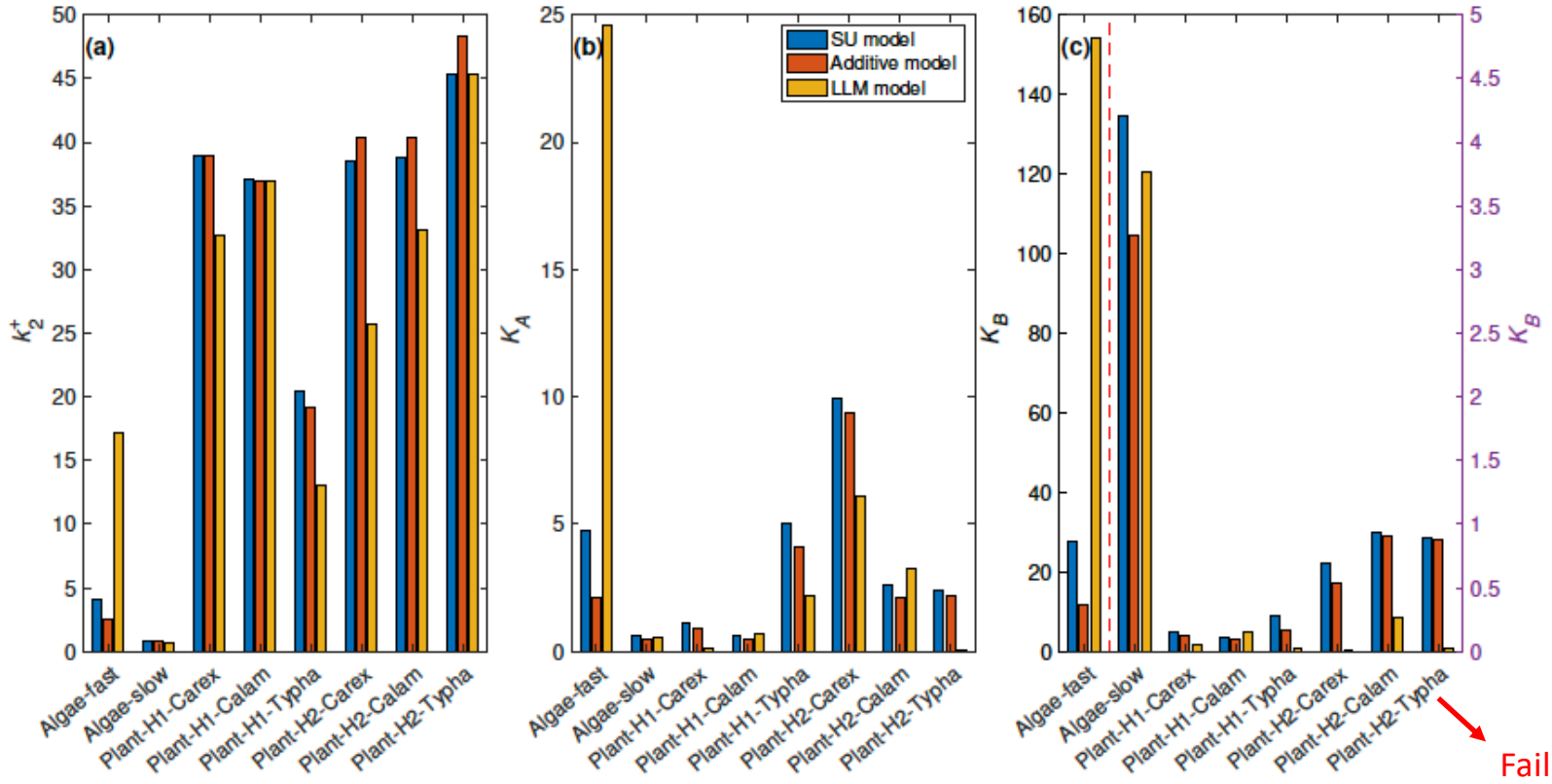


Growth co-limited region

The co-limitation pattern for normalized growth

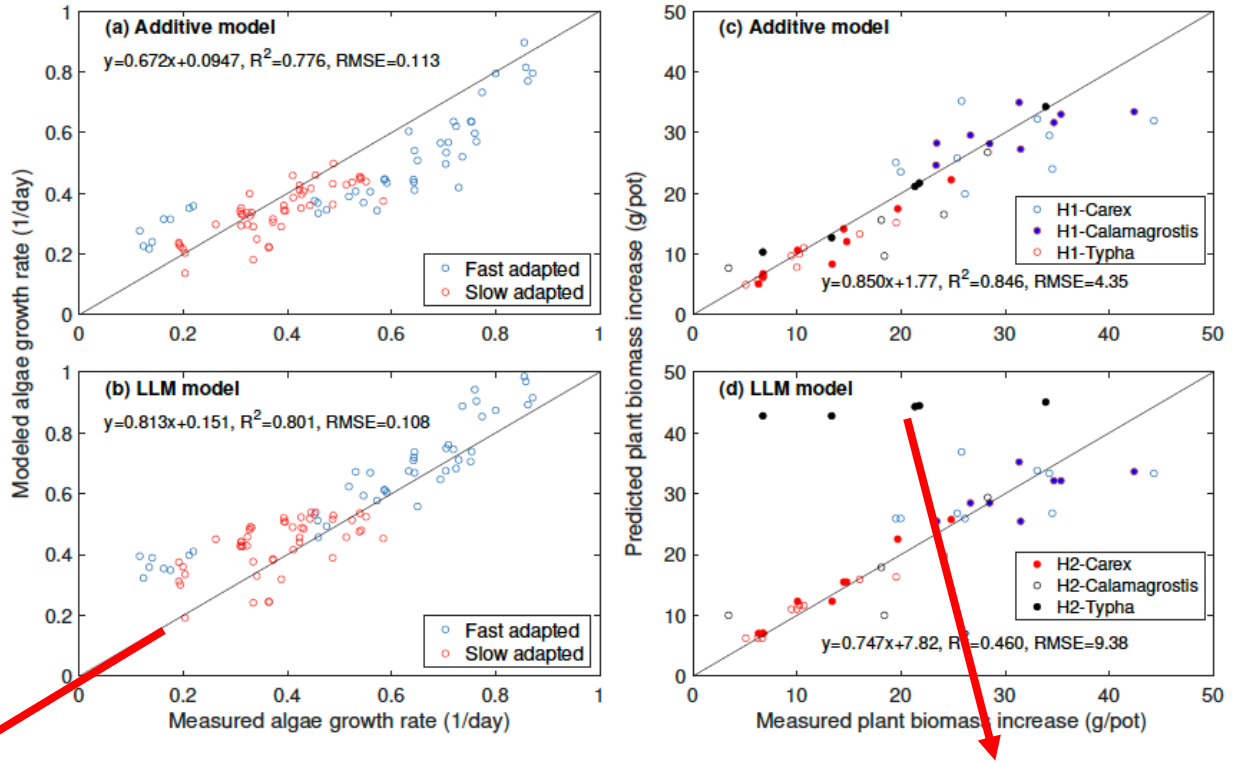


Implication of model parameters



Very different parameters for the LLM model

Model parameters vs model performance



Wrong parameters make wrong model right!

Wrong parameters make wrong model wrong!

Summary

- Liebig's law of the minimum (LLM) is a very/too crude approximation to the law of mass action.
- Synthesizing unit model and additive model are more accurate, and similarly good.
- The structural deficiency in LLM can occasionally be fixed using wrong parameters (as compared to true parameters from the SU model).
- LLM has other conceptual problems: e.g., implication of stoichiometric homeostasis when growth is modeled as a function of nutrient flux.
- Nutrient quota is a better concept for quantifying nutrient limitation.