“Towards the role of plant-microbial symbiosis on patterns expected from photosynthetic least-cost theory”

**Abstract**

Photosynthesis represents the largest carbon flux between the atmosphere and biosphere and is a process that links terrestrial carbon, water, and nutrient cycles. Photosynthetic least-cost theory provides a framework for understanding variability in photosynthetic processes across environments, positing that variance in leaf photosynthetic capacity across environmental gradients is the product of (1) climate-driven demand to build and maintain photosynthetic enzymes and (2) modifications in the ratio of intercellular CO2 to atmospheric CO2 that result from changes in the cost of acquiring nutrients relative to water. Recent work is beginning to show consistent empirical support for theoretical expectations across environmental gradients and in manipulative experiments; however, results from such studies largely ignore impacts of plant-microbial symbioses on patterns expected from the theory. Plants rely on symbioses with soil microbial communities such as arbuscular mycorrhizal or ectomycorrhizal fungi for nutrient acquisition, water uptake, and pathogen defense. Plant-microbial symbioses are typically maintained on the basis of nutrient exchange, where plants allocate carbon derived from photosynthesis belowground in exchange for nutrients mined by microbial symbionts. The relationship between belowground carbon allocation and nutrient acquisition, or the carbon cost for acquiring nitrogen, varies in species that form associations with different microbial symbionts, indicating that plant-microbial symbioses may be an important factor to consider when evaluating patterns expected from theory. Here, we review evidence for patterns expected from photosynthetic least-cost theory across environmental gradients, synthesize a conceptual framework for understanding the role of plant-microbial symbioses on photosynthetic least-cost expectations, and use this framework to propose experiments that will help elucidate the role of plant-microbial symbioses on patterns expected from the theory.

**Crude Outline**

1. Field and experimental evidence for patterns and mechanisms expected from photosynthetic least-cost theory
   1. Overview of theory (conceptual figure below, microbial symbioses effect included as “black box”)
      1. Evokes eco-evolutionary principles: uncompetitive plant trait combinations are rapidly eliminated from environment through both short (e.g., acclimation) and long (e.g., species replacement) timescales
      2. Eco-evolutionary frameworks implies that competitive plant trait combinations are therefore predictable based on growing environment, providing testable hypotheses that can be used to assess variance in trait combinations across envrionments
      3. Photosynthetic least-cost theory leverages eco-evolutionary optimality, suggesting that photosynthetic processes should acclimate to changing environments by maximizing light-use efficiency at the lowest summed cost of using nutrients and water
         1. Nutrient and water use is substitutable such that a given minimal summed cost of using nutrients and water can be achieved by trading inefficient use of a relatively more abundant (less costly) resource for more efficient use of a relatively less abundant (more costly) resource
      4. Photosynthetic responses to environment are therefore determined either through climate-driven demand to build and maintain photosynthetic enzymes or through changes in the cost of using nutrients or water across resource availability gradients
   2. Evidence across environmental gradients
      1. Summary of results from Dong et al. (2017, 2020, 2022a, 2022b), Smith et al. (2019), Peng et al. (2020), Paillassa et al. (2020), Westerband et al. (2023), Perkowski et al. (in prep)
   3. Evidence from manipulative experiments
      1. Summary of results from Bialic-Murphy et al. (2020), integrate findings from Perkowski et al (2021) and Waring et al. (2023), Perkowski et al. (in prep) x 2
   4. Applications of the theory (a lead-in for conceptual framework for plant-microbial symbioses)
      1. Field evidence documented across biomes with varying climate regime -> suggests broad applicability of the theory across climates
      2. Evidence from field manipulation studies (Bialic-Murphy et al. 2021; Perkowski et al. *in review*) suggest that patterns expected from the theory apply to finer spatiotemporal scales than global gradient analyses
         1. Belowground disruption of arbuscular mycorrhizal fungi is connected with nitrogen-water use tradeoffs predicted by the theory (Bialic-Murphy et al. 2021)
            1. Suggests that belowground soil microbial communities may play an important role in mediating patterns expected from theory, though such symbioses are largely ignored in studies evaluating patterns expected from photosynthetic least-cost theory (but see Smith & Keenan 2020 and Perkowski et al. in prep)
         2. *A. saccharum* individuals maintained net photosynthesis rates along a nitrogen fertilization gradient by sacrificing inefficient nitrogen use for increasingly efficient water use (Perkowski et al. *in review*)
2. Conceptual framework for understanding the role of plant-microbial symbioses on patterns expected from theory
   1. The framework (reference conceptual figure from “Overview of the theory”)
      1. Could alternatively draw a tree diagram like the one in MANE framework paper from Phillips et al. (2013)
      2. Microbial symbioses modify costs of nutrient and water acquisition, thus altering the cost of using nutrients relative to water
      3. Theory suggests that increasing costs of using nutrients relative to water is positively related to the ratio of intercellular CO2 to atmospheric CO2 (leaf Ci:Ca)
         1. Increased costs of using nutrients relative to water increases nutrient use efficiency at the expense of reduced water use efficiency
      4. Thus, species that form associations with microbial symbioses that have greater costs of nutrient acquisition may exhibit increased leaf Ci:Ca, increased nutrient use efficiency, and reduced water use efficiency in a given environment compared to species that form associations with microbial symbioses that have reduced costs of nutrient acquisition
      5. Alternatively, species that form associations with microbial symbioses that have greater costs of water acquisition may exhibit decreased leaf Ci:Ca, decreased nutrient use efficiency, and increased water use efficiency compared to a species that form associations with microbial symbioses that have reduced costs of water acquisition
   2. Existing empirical evidence supporting a potential role of microbial symbioses on theoretical expectations
      1. Need some help here
3. Open research questions and proposed experiments that will help elucidate role of plant-microbial symbioses on theoretical expectations (2 main research avenues)
   1. Few studies quantify costs of nutrient or water acquisition
   2. Costs of nutrient acquisition are rarely scaled to leaf or whole plant physiology, limiting inferences about impacts of microbial symbioses on patterns expected from theory

Diagram of a diagram of a plant

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