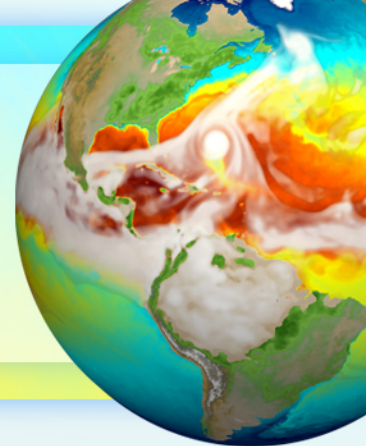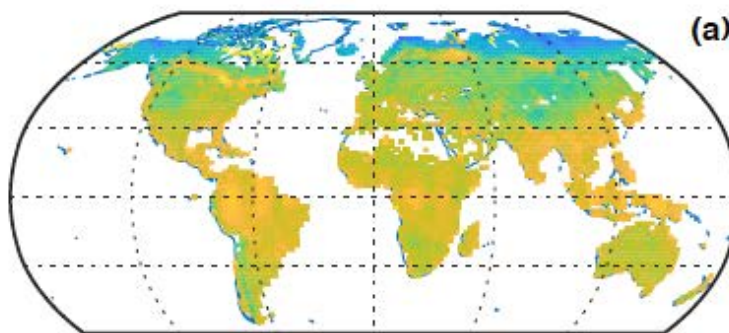# Weaker land–climate feedbacks from nutrient uptake during photosynthesis inactive periods

William J. Riley

Qing Zhu, Jinyun Tang

Lawrence Berkeley National Laboratory

(a)

Overview

- Background
  - Global-scale land C cycle and nutrient constraints
  - Plant and microbial dynamics and nutrient competition
  - Observations of Photosynthesis Inactive Period (PIP) plant nutrient uptake

- Modeling approaches and concepts
  - CMIP-class models and Relative Demand approach
  - Enzyme mediated reactions
  - ELMv1-ECA approach

- Results and Implications

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Global C Budget

Ciais et al. (2013); IPCC FAR Chpt. 6
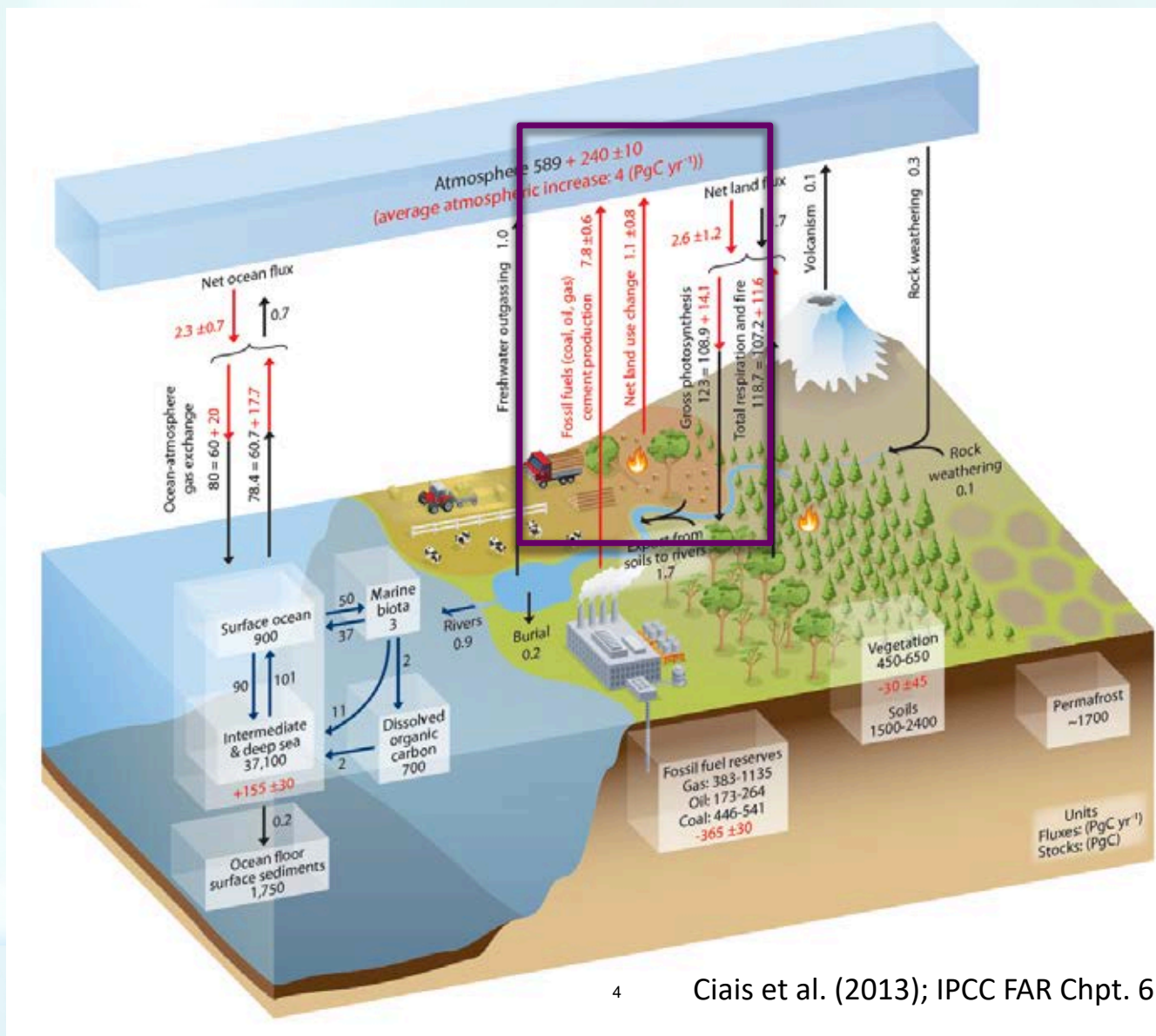
Global C Budget

Ciais et al. (2013); IPCC FAR Chpt. 6
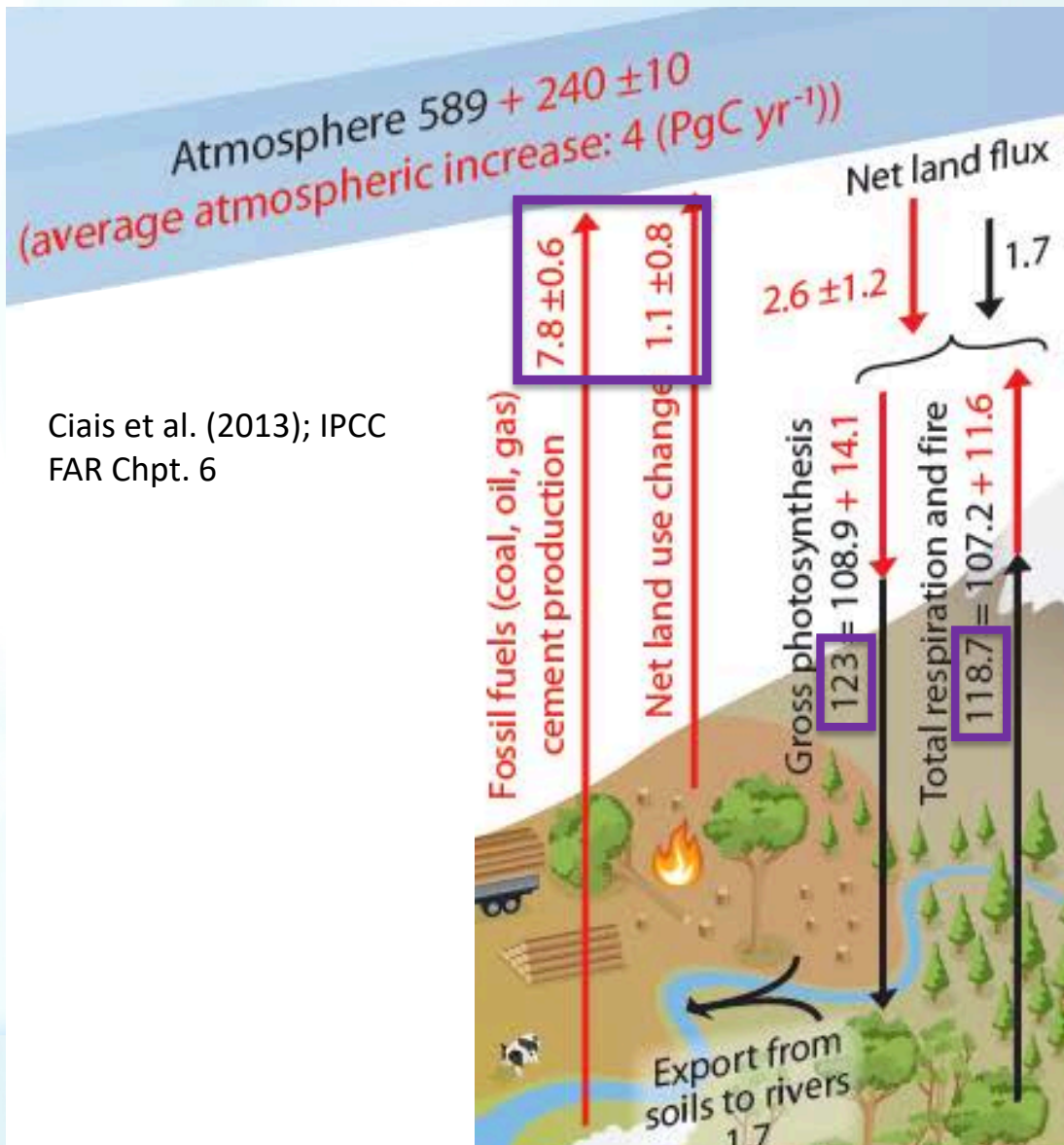
- Gross terrestrial CO_2 fluxes are ~10 times as large as current anthropogenic emissions
- Relatively small biases in land fluxes have large implications on atmospheric CO_2 burden

Land Models Must Represent a Wide Variety of Terrestrial Systems and Processes

- Above ground variability and heterogeneity

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Land Models Must Represent a Wide Variety of Terrestrial Systems and Processes

- Belowground variability and heterogeneity

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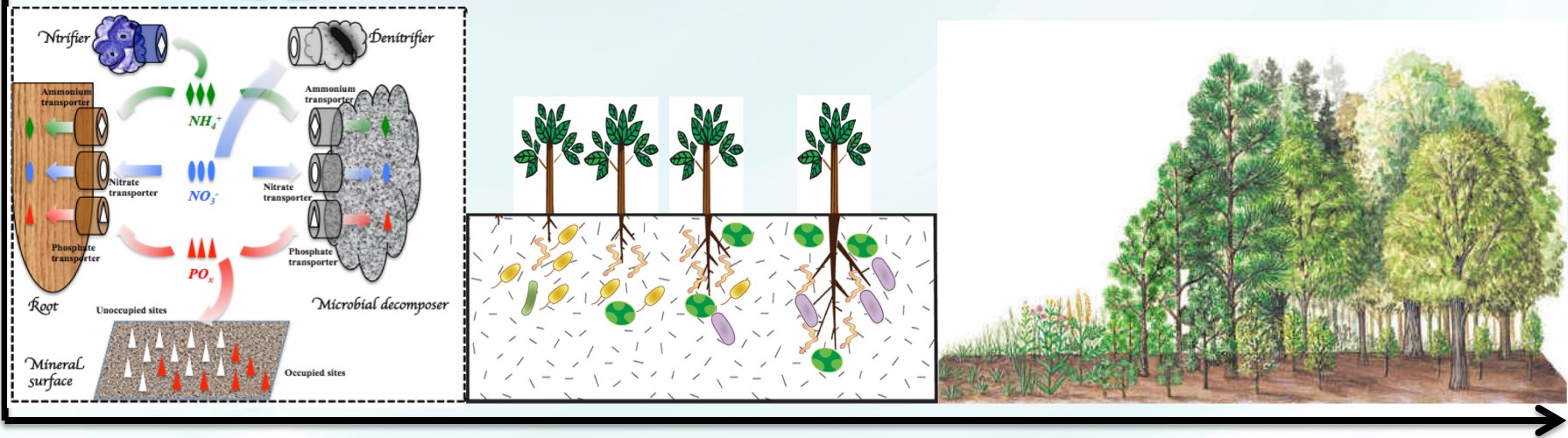
ENERGY OF
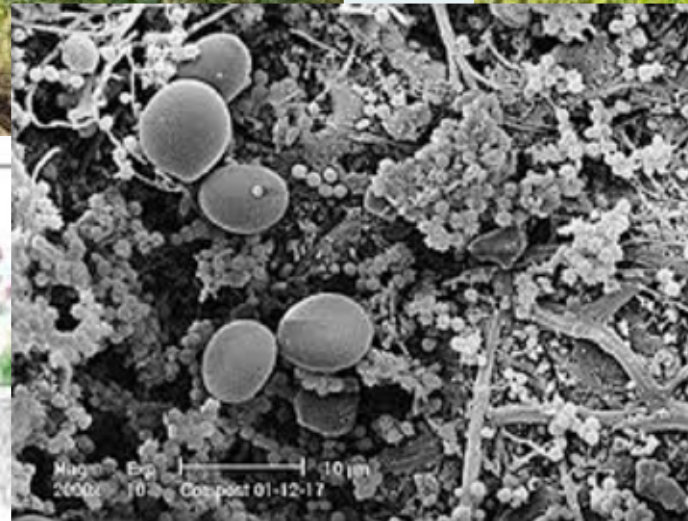
Time Scales

Direct Competition

Plant Allocation & Microbial Diversity

Successional Dynamics

Hours   Week   Month   Year   Decade   Time Scale

- How are nutrient controls important to terrestrial responses to increasing CO_2?
  - Photosynthesis (carboxylation, ATP)
  - Microbial turnover, N fixation, mycorrhizal associations
  - Allocation (e.g., investment for P acquisition)
  - N losses (e.g., N_2O, leaching)
- Observational constraints
  - Free Air Carbon Enrichment (FACE) studies
  - Fertilization experiments

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Fertilization Experiments

- Many experimental studies have investigated role of N and P on plant growth

- E.g., LeBauer and Tresseder (2008) meta-analysis of 126 experiments:

Fig. 1. Global distribution of studies included in the meta-analysis, by biome.

Grouping	n	R
Overall	126	1.29
Biome	7	
Temperate forest	22	1.19
Tropical forest	16	1.60
Excluding young Hawaiian soils	8	1.20
Young Hawaiian soils	8	2.13
Tundra	10	1.35
Tropical grassland	6	1.26
Desert	3	1.11
Temperate grassland	32	1.53
Wetland	36	1.16

Fertilization Experiments

- Elser et al. (2007) performed a meta-analysis of 173 terrestrial experiments

Elser et al., 2007 EL

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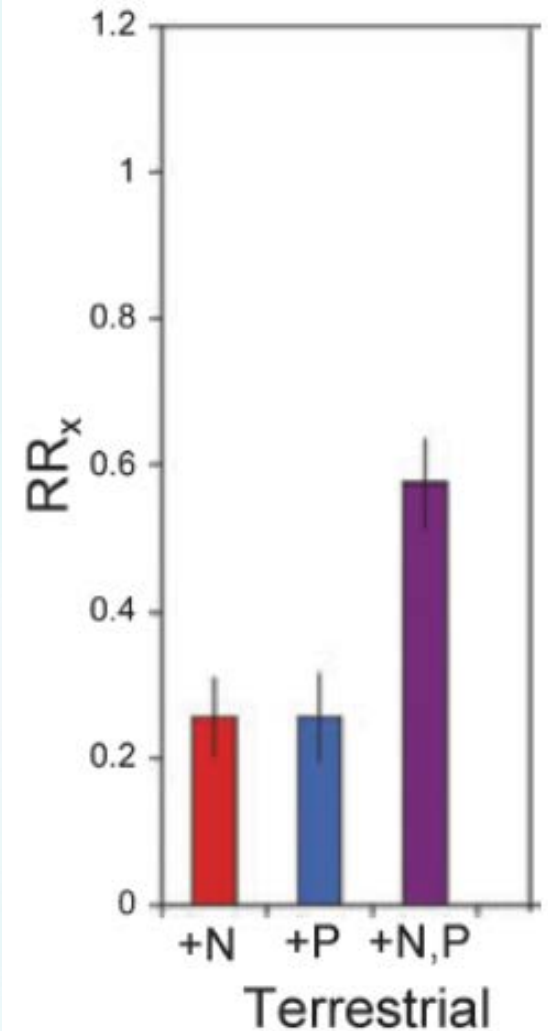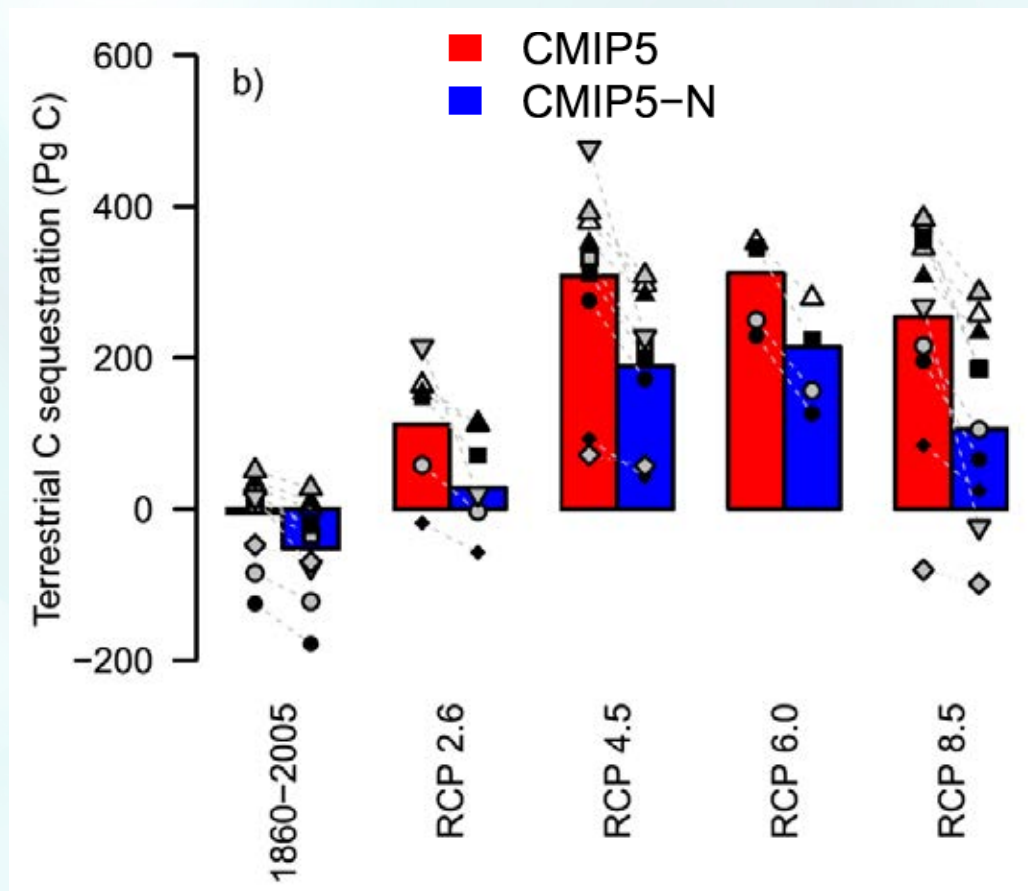
Effects on Global C cycle

- Hungate et al. (2003) used IPCC TAR simulation to estimate N required for additional C stored to 2100
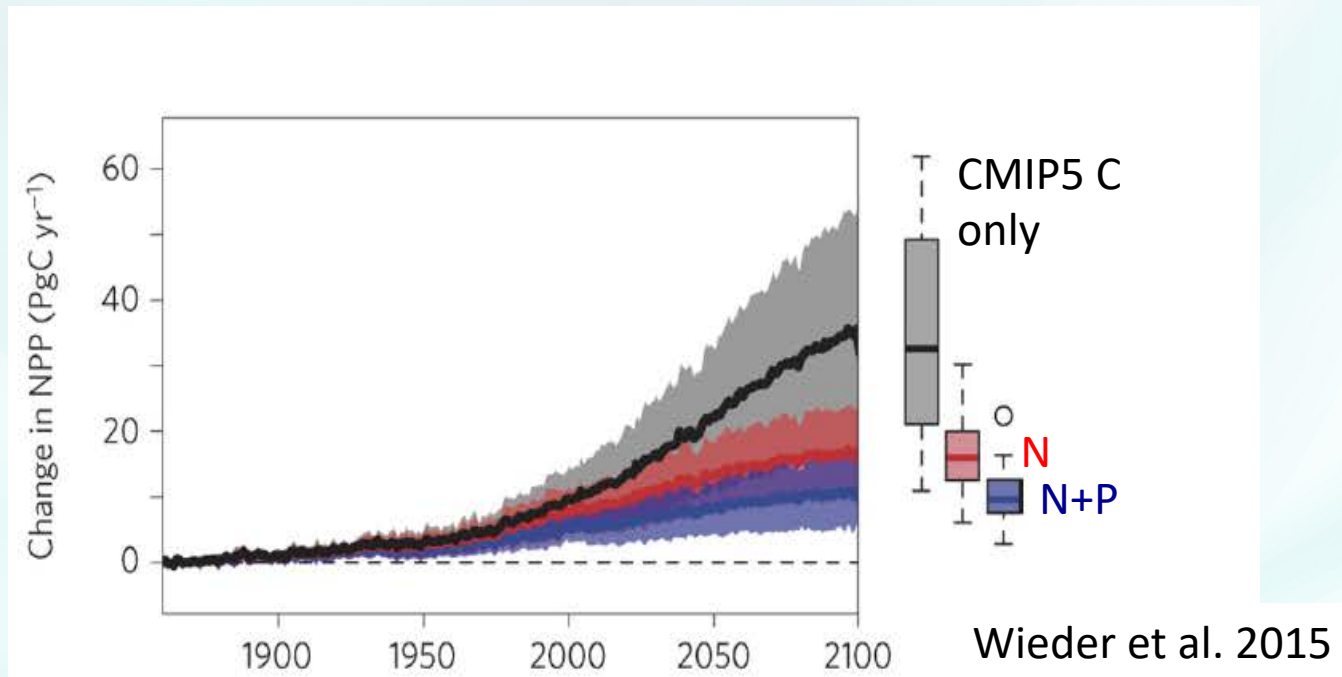 - Far out-stripped available N
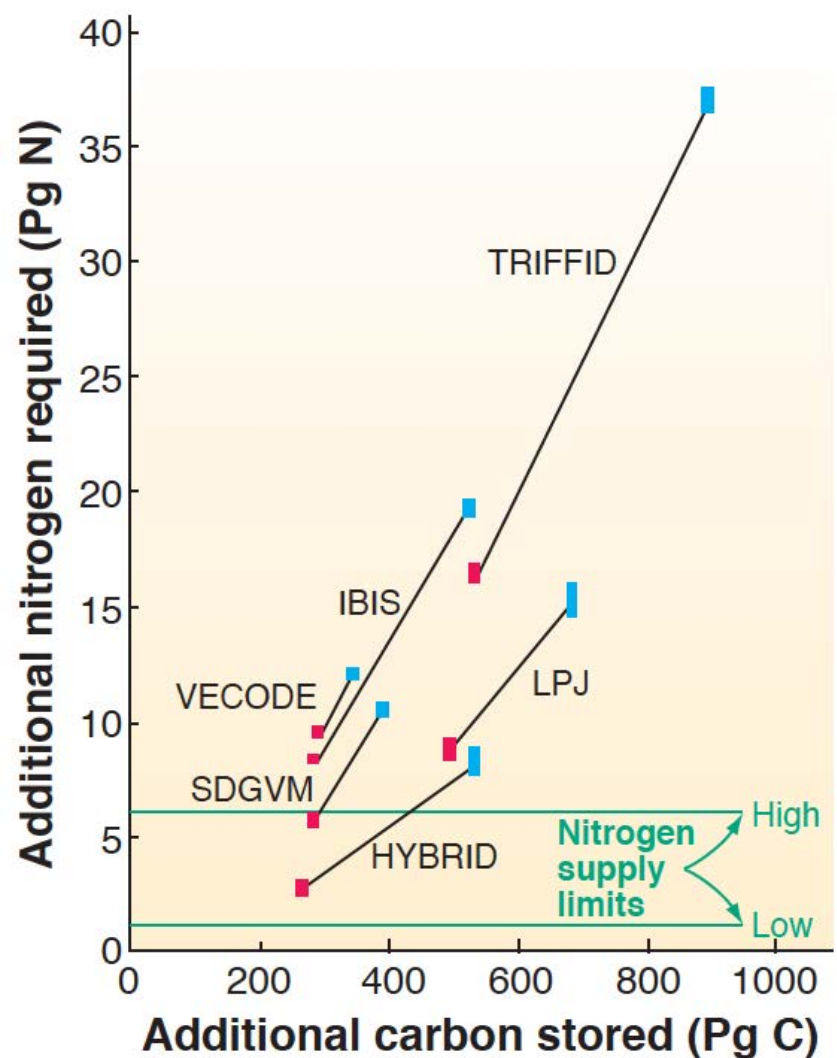
Effects on Global C cycle
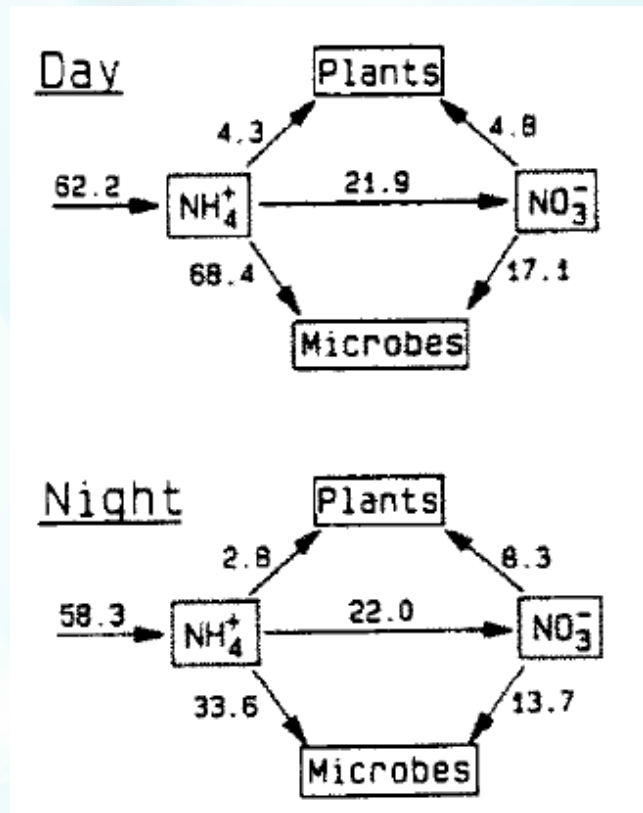

Zaehle et al. 2015

Effects on Global C cycle

- Wieder et al. (2015) estimated N and N+P limitations on CMIP5 estimated changes in NPP over 21st Century
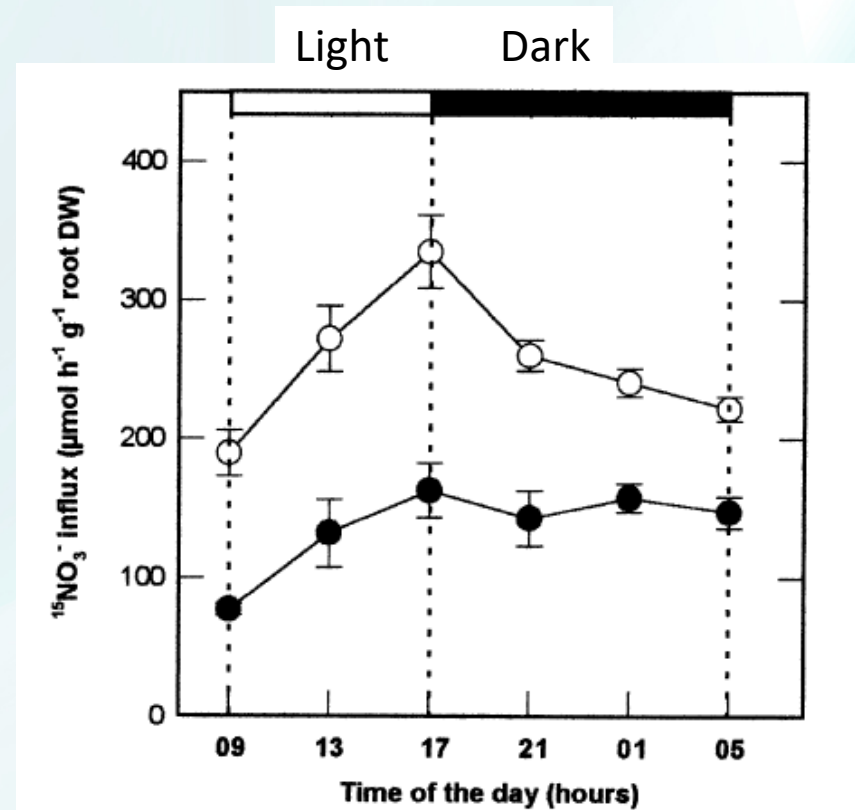

Wieder et al. 2015

Nighttime and Non-Growing Season Nutrient Uptake Observations

Nighttime Uptake Observations

Schimel et al. (1999)

Lejay et al. (1999)

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Nighttime Uptake Observations


Dark   Light
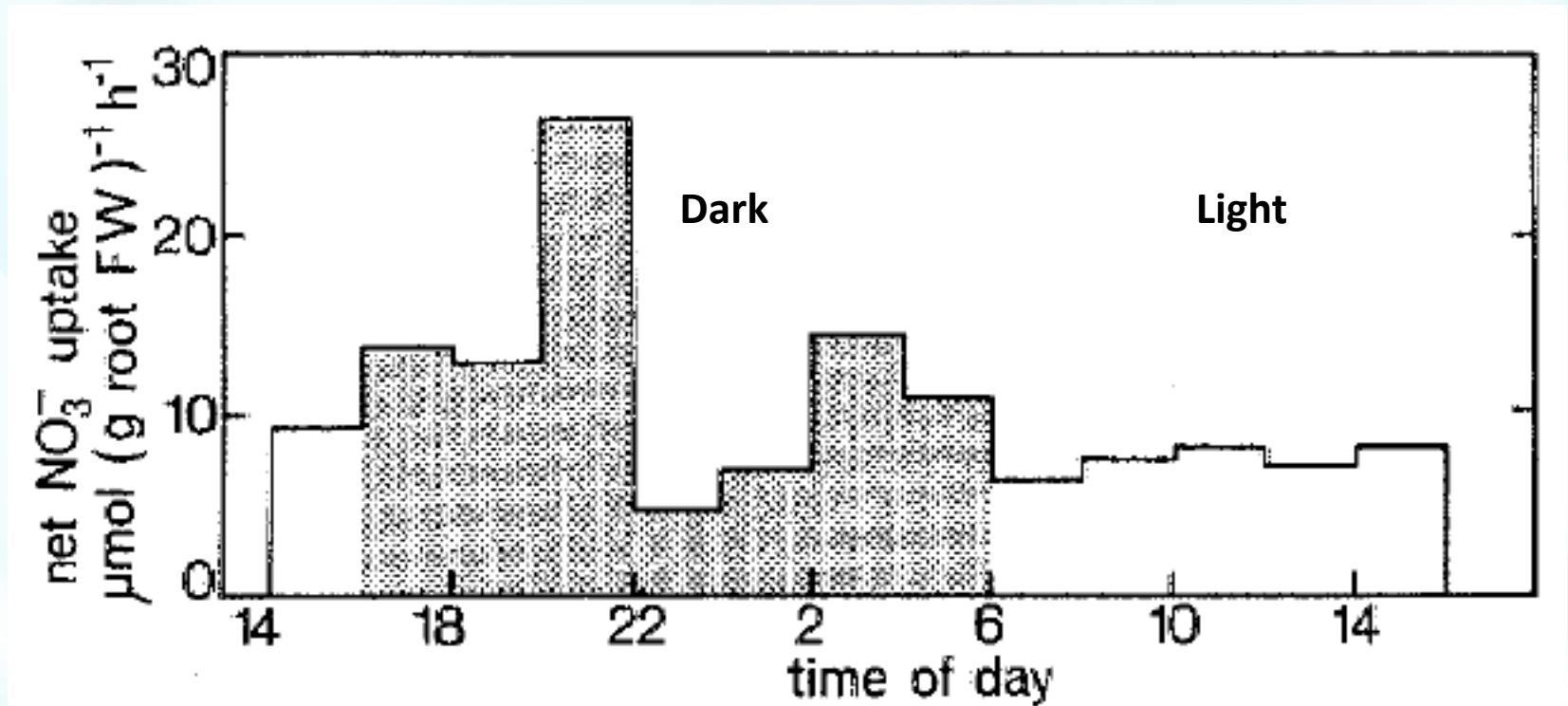
Steingrover et al. (1980)

Nighttime Uptake Observations

- We identified ~20 isotope-labeling studies of nighttime nutrient uptake

  – All indicate nighttime uptake **accounts for ~30 to 60% of total uptake**

- No studies contradict this finding

Non-Growing Season Uptake Observations

- Up to 90% of tundra vascular plant biomass is belowground, and root production is often delayed compared to aboveground (Iversen et al. 2015; Blume-Werry et al. 2016)

Blume-Werry et al. (2016)
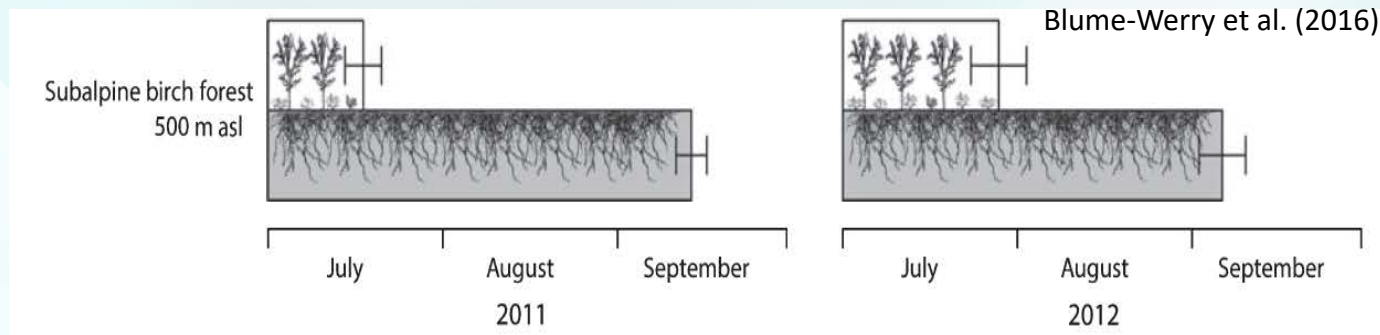
- Root infrastructure exists, and can be active, all year

Non-Growing Season Uptake Observations

- Observational studies demonstrate that plants acquire soil nutrients well past plant senescence
- E.g., Keuper et al. (2017)
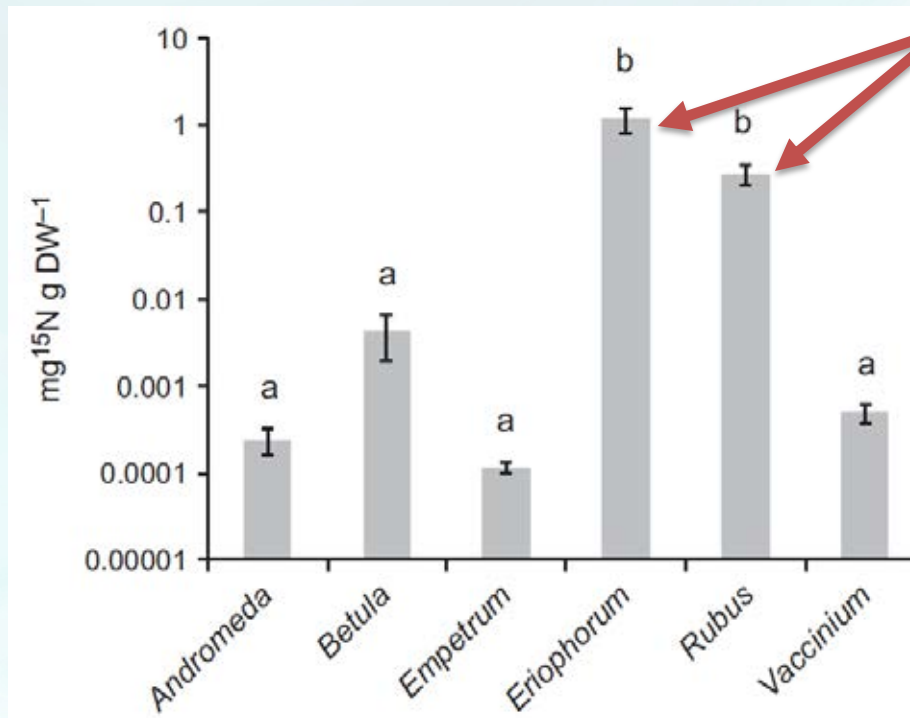
Over the winter, deep-rooted plants acquire ^{15}N injected at PF boundary

Non-Growing Season Uptake Observations

- E.g., at the NGEE-Arctic Barrow polygonal tundra site

ccsi.ornl.gov

Day of Year

Riley et al. in prep.
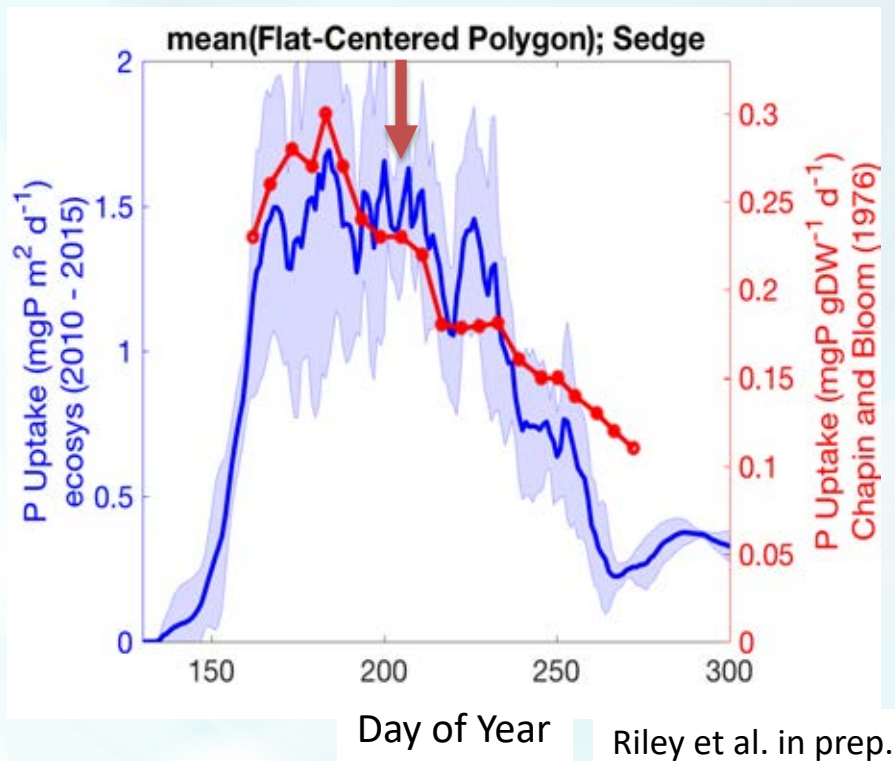
Grant et al. 2017a,b

Non-Growing Season Uptake Observations

- We identified ~10 isotope-labeling studies of non-growing season nutrient uptake

  - All indicate non-growing season uptake **accounts for ~10 to 50% of annual uptake**

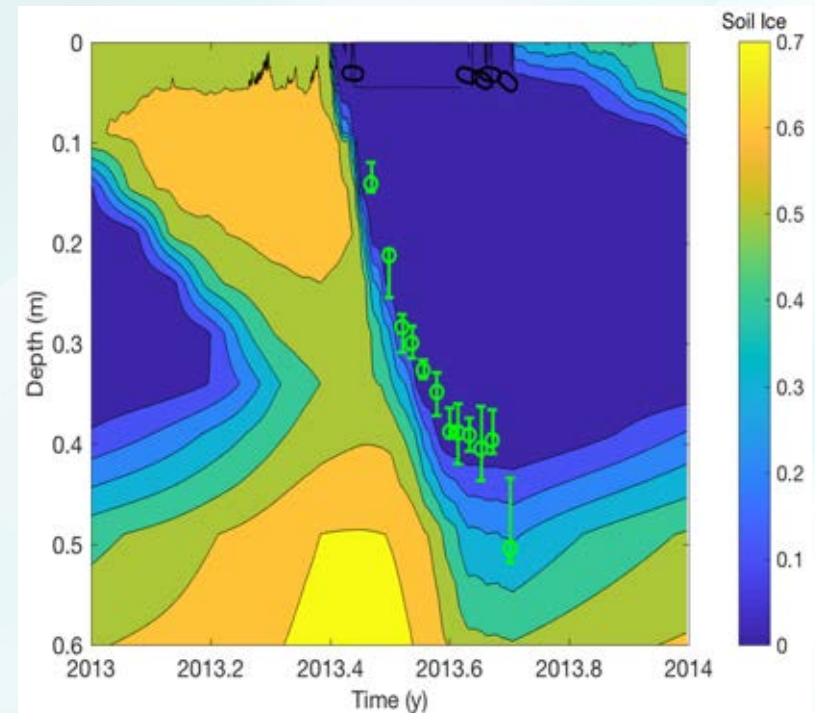- No studies contradict this finding

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Competitive Interactions
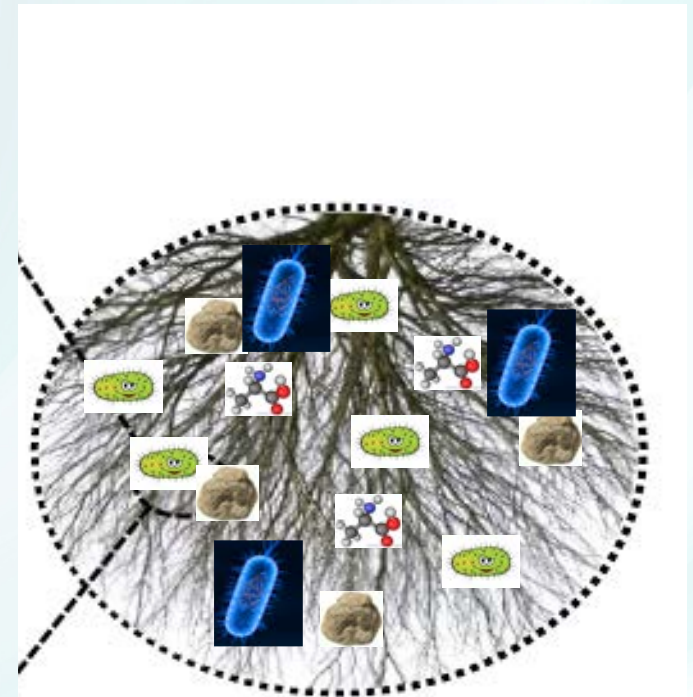
Zhu et al. 2017

Competitive Interactions
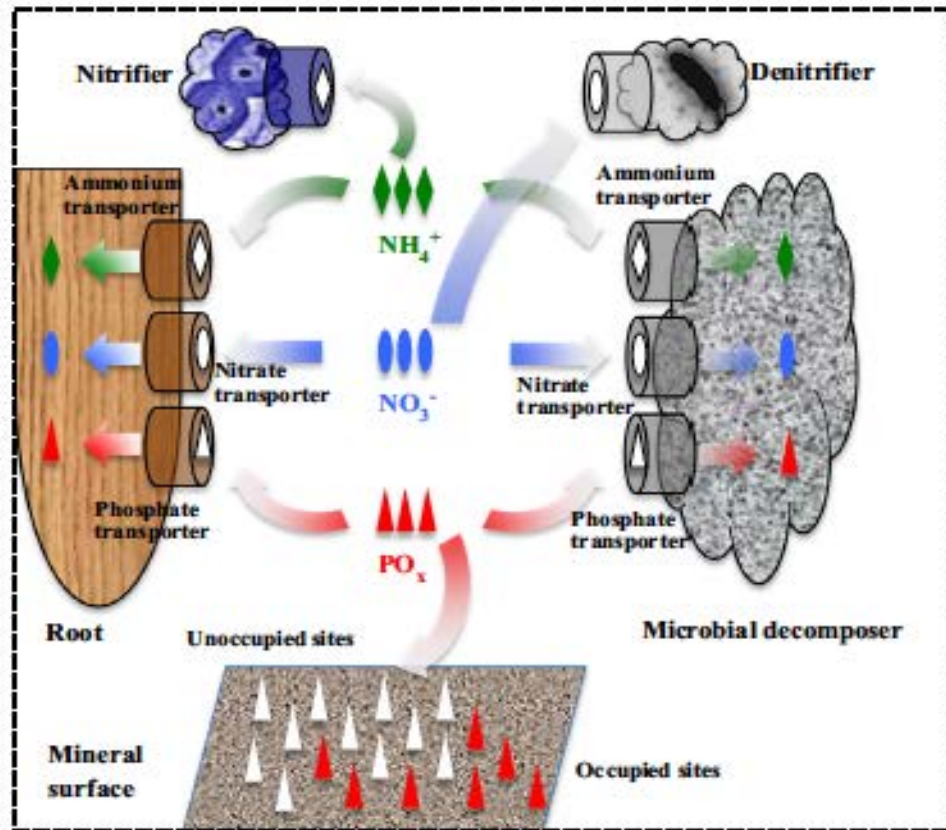
Zhu et al. 2017

Traditional Approach to Represent Nutrient Competition in Models

- We reviewed 12 nutrient-enabled CMIP6 land models

- All represent nutrient competition with the "Relative Demand" concept:

  – Root and soil microbe competition resolved based on non-nutrient-constrained demand

  – Acquisition scaled by relative demand of all competitors

  – Simplifies interactions and is relatively easy to implement

- But, instantaneous Relative Demand approach precludes non-growing season and nighttime plant nutrient uptake

New Methods to Model Nutrient Competition

Single Substrate, Single Enzyme Kinetics

L. A NOTE ON THE KINETICS
OF ENZYME ACTION.

By GEORGE EDWARD BRIGGS
AND JOHN BURDON SANDERSON HALDANE.

(*From the Botanical and Biochemical Laboratories, Cambridge.*)

(*Received March 9th, 1925.*)

Developed to explain the Michaelis-Menten (1913) observed dynamics

$$S + E \overset{k_1^+}{\underset{k_1^-}{\leftrightarrow}} C \overset{k_2^+}{\rightarrow} P + E$$
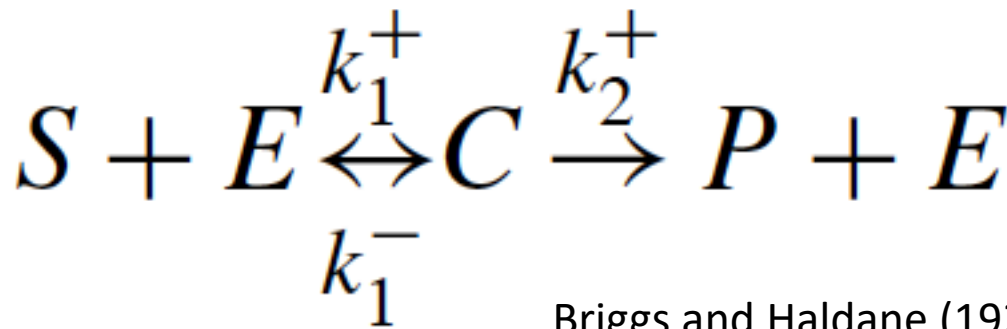
Briggs and Haldane (1925)

Goal is not to represent each enzymatic reaction on the planet, but to find theoretically consistent functional-form representations

Single Substrate, Single Enzyme Kinetics

Applying the Quasi Steady-State Approximation for a single substrate and enzyme gives the Michaelis-Menten kinetics (1913):

$$v = \frac{V_{max} S}{K_S + S}$$

Single Substrate, Single Enzyme Kinetics

- Studies have found discrepancies between Michaelis-Menten kinetics and observations
  - Cha and Cha (1965); Williams (1973); Suzuki et al. (1989); Maggi and Riley (2009)
- So, a number of modifications have been proposed (e.g., Cha and Cha (1965)):

$$v = \frac{V_{\max} S_{\mathrm{T}}}{K_{\mathrm{S}} + E_{\mathrm{T}} + S_{\mathrm{T}}}$$

The Equilibrium Chemistry Approximation

- We extended these ideas with the more general problem of multiple substrates and "consumers":

$$S_i + E_j \overset{k^+_{ij,1}}{\underset{k^-_{ij,1}}{\leftrightarrow}} C_{ij} \overset{k^+_{ij,2}}{\rightarrow} E_j + P_{ij}$$
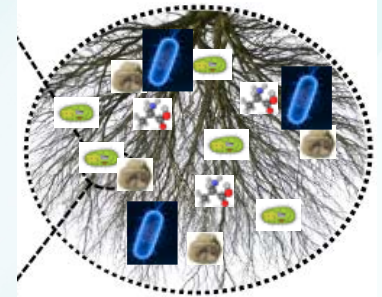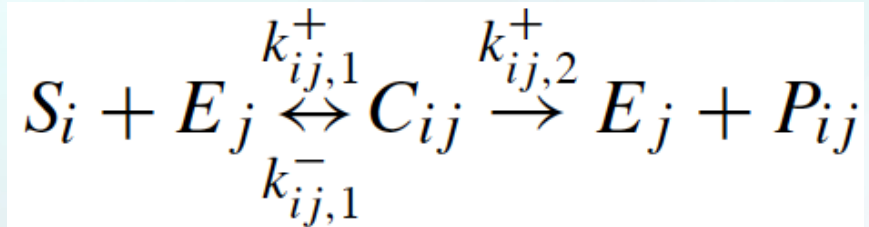
- Assuming:
  - QSS
  - No binding between C_{ij}

- A first order approximation is the ECA:

$$\tilde{C}_{ij} = \frac{S_{i,\mathrm{T}} E_{j,\mathrm{T}}}{K_{\mathrm{S},ij}\left(1 + \sum_{k=1}^{k=I} \frac{S_{k,\mathrm{T}}}{\tilde{K}_{\mathrm{S},kj}} + \sum_{k=1}^{k=J} \frac{E_{k,\mathrm{T}}}{\tilde{K}_{\mathrm{S},ik}}\right)}$$

(Tang and Riley 2013)

ECA

$$\tilde{C}_{ij} = \frac{S_{i,\mathrm{T}} E_{j,\mathrm{T}}}{K_{\mathrm{S},ij}\left(1 + \sum_{k=1}^{k=I} \frac{S_{k,\mathrm{T}}}{\tilde{K}_{\mathrm{S},kj}} + \sum_{k=1}^{k=J} \frac{E_{k,\mathrm{T}}}{\tilde{K}_{\mathrm{S},ik}}\right)}$$

Method facilitates inclusion of an arbitrary number of sorption, inhibitory mechanisms, diffusion limitations, and microbial traits

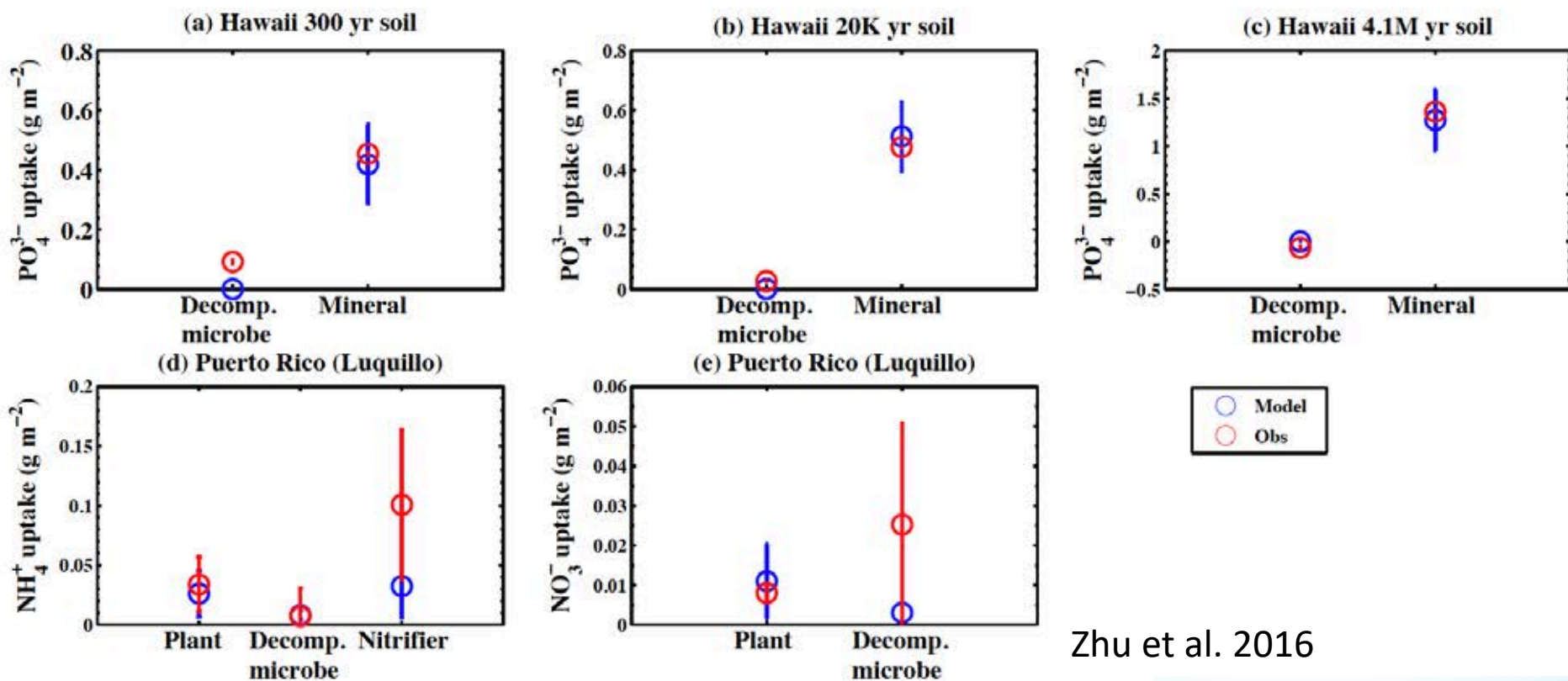$$\tilde{K}_{\mathrm{S},ij} = \frac{K_{\mathrm{S},ij}}{\sum_{k=1}^{k=L} \frac{I_{k,\mathrm{T}}}{K_{I,ijk}} + 1}$$

$$\tilde{K}_{\mathrm{S},ij} = K_{\mathrm{S},ij}\left(1 + \frac{V_{\mathrm{max},ij}}{4\pi D_i r_{\mathrm{c},j} n_j K_{\mathrm{S},ij}}\right)$$

(Tang and Riley 2013; Tang 2015; Tang and Riley 2017, 2018)

Energy Exascale
Earth System Model

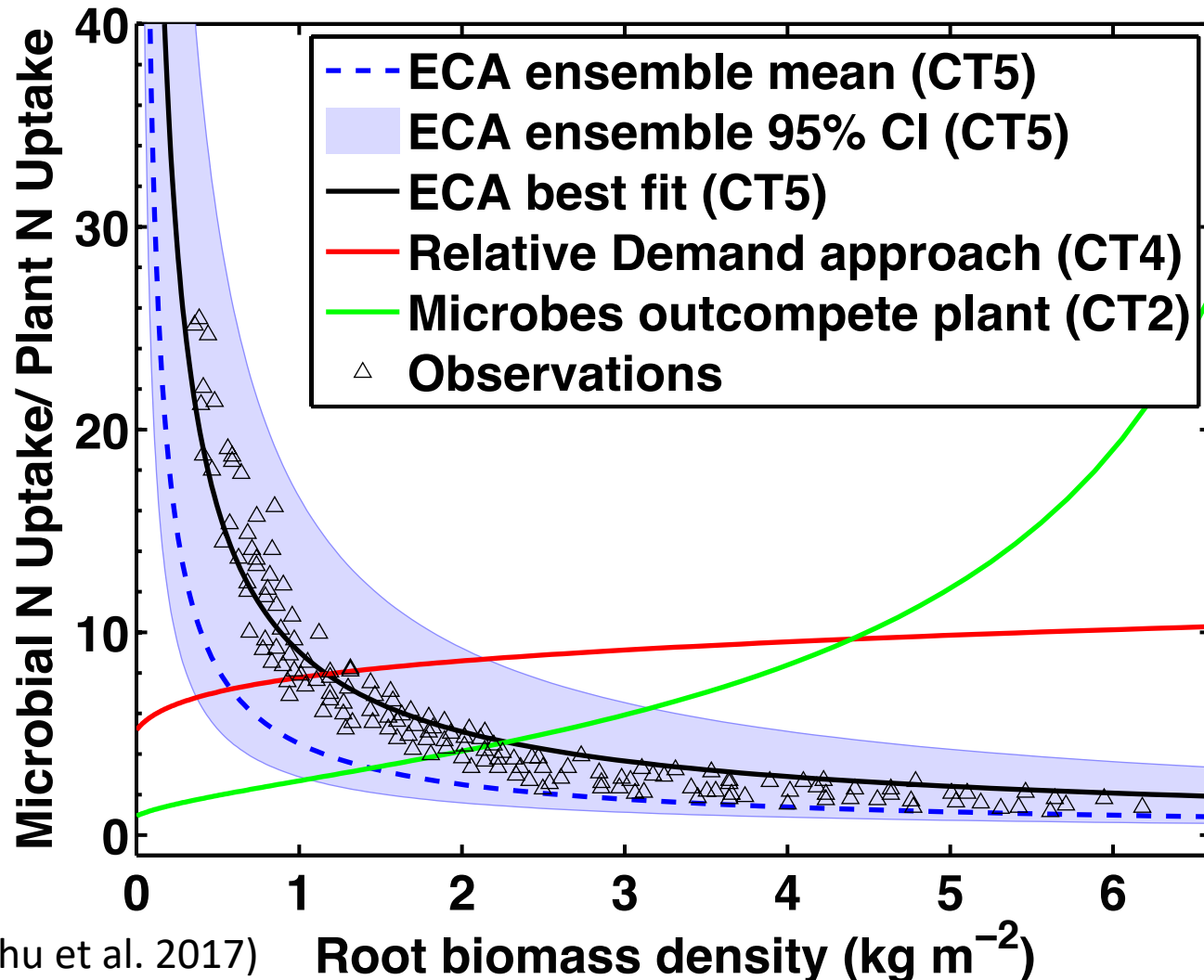U.S. DEPARTMENT OF
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ECA Application: Tropical Sites

- Soil NO_3^-, NH_4^+, PO_x competition between plants, microbes, and mineral surfaces in several tropical forests

Zhu et al. 2016

ECA Application: Soil ^{15}N tracer in an alpine meadow (Xu et al. 2011)


(Zhu et al. 2017)

- ECA approach qualitatively matches observations with parameters from other systems
  - Excellent match after calibration
- No calibration results in the other Competition Theories having the correct functional form

Energy Exascale Earth System Model

- Two other land models have also implemented the ECA concept for nutrient competition
  - ED2 (Medvigy et al. (in review))
  - ORCHIDEE (Huang et al. 2018)

ELMv1-ECA

- ECA kinetics for nutrient competition
- Dynamic plant allocation responds to resources and stress
- Dynamic plant stoichiometry based on a large meta-analysis
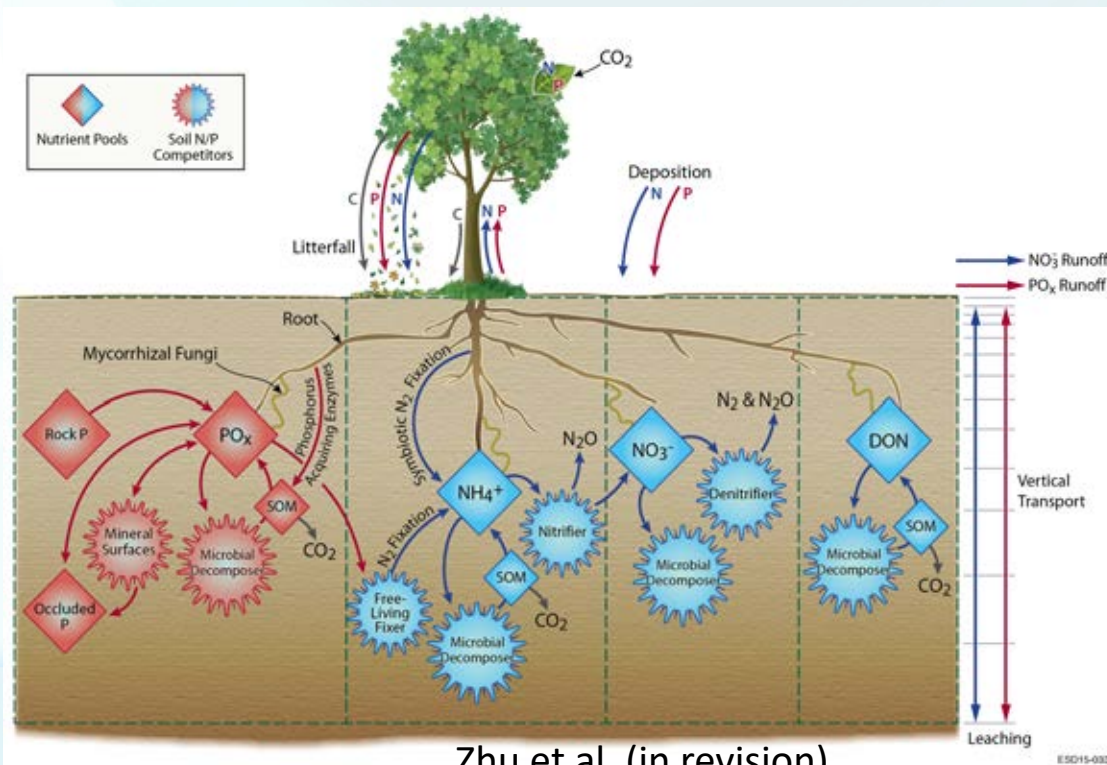

Zhu et al. (in revision)

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Nighttime Nutrient Uptake

- For example, at the grassland site measured by Schimel et al. (1989)
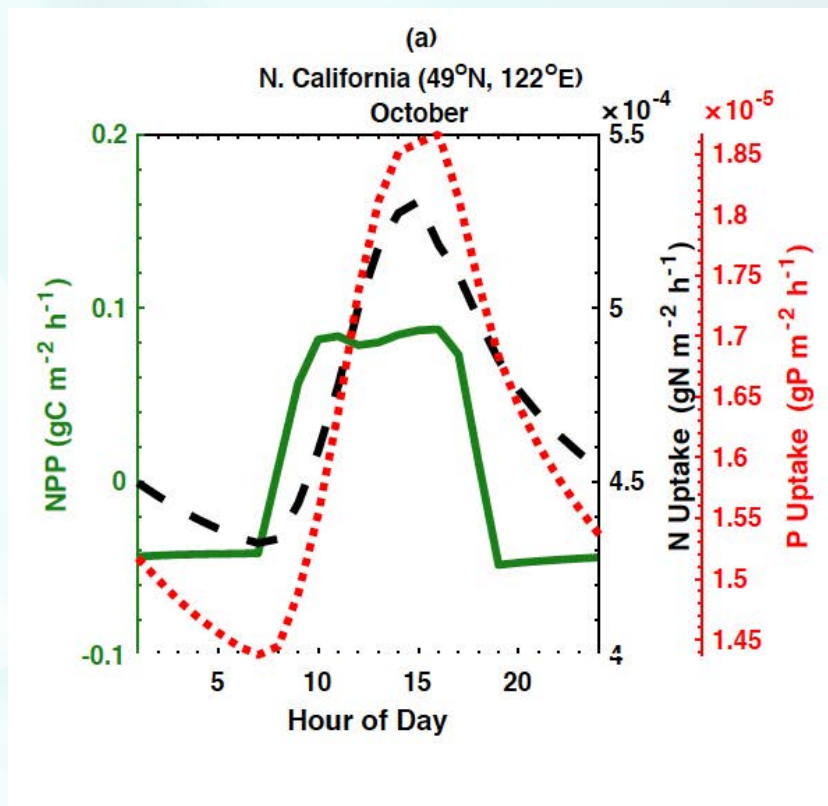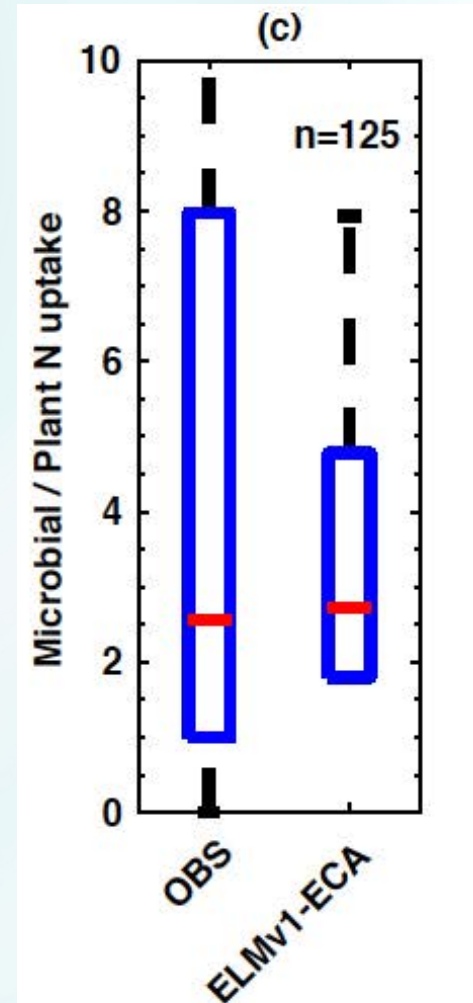

Riley et al. (2018)
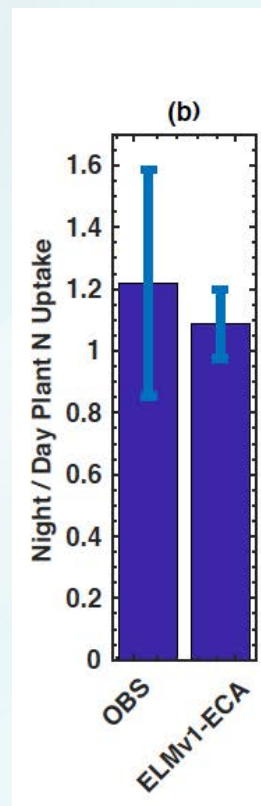
Short-Term N Uptake Evaluation

- We also evaluated the model against observed ratios of microbial to plant nitrogen uptake from 123 short-term isotopic tracer studies from 23 sites.

Riley et al. (2018)

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ELMv1-ECA Performance

- GPP Bias

0.67   0.75   0.78

(d) CLM4.0 bias   (f) CLM4.5 bias   (b) ELMv1-ECA-CNP bias

Gross Primary Productivity bias ($g\,m^{-2}\,d^{-1}$)
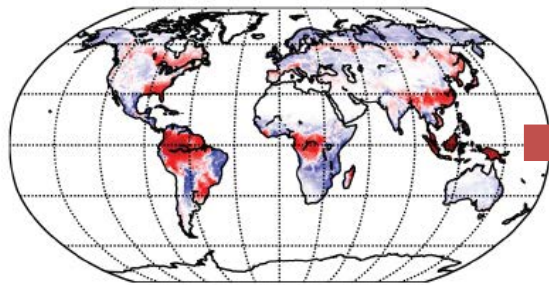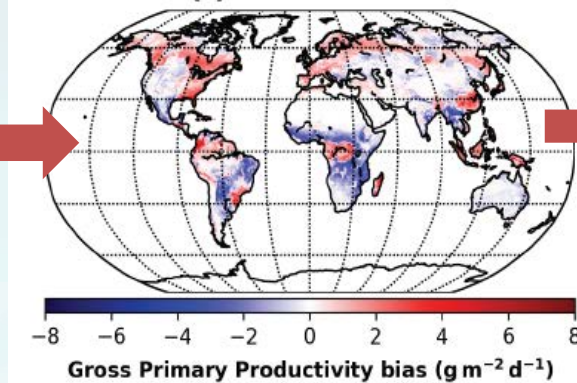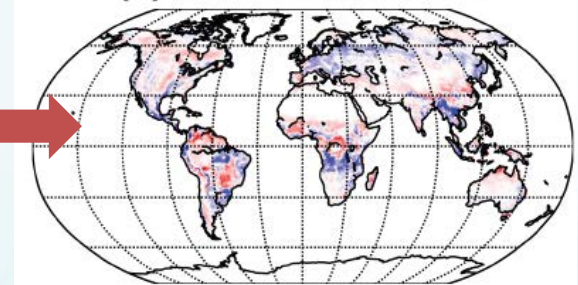
Zhu et al. (2018)

ELMv1-ECA Performance

- Plant biomass Bias

0.45   0.48   0.74
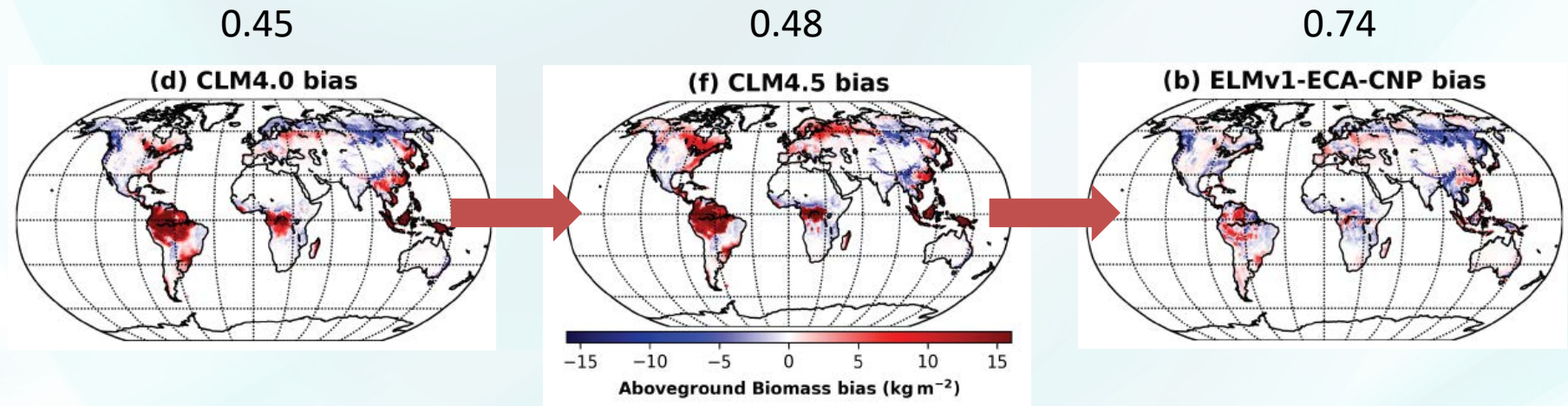
Zhu et al. (2018)

ELMv1-ECA Performance

- Comparison based on Houghton et al. (2015); Zhu and Riley (2015) Nature Climate Change
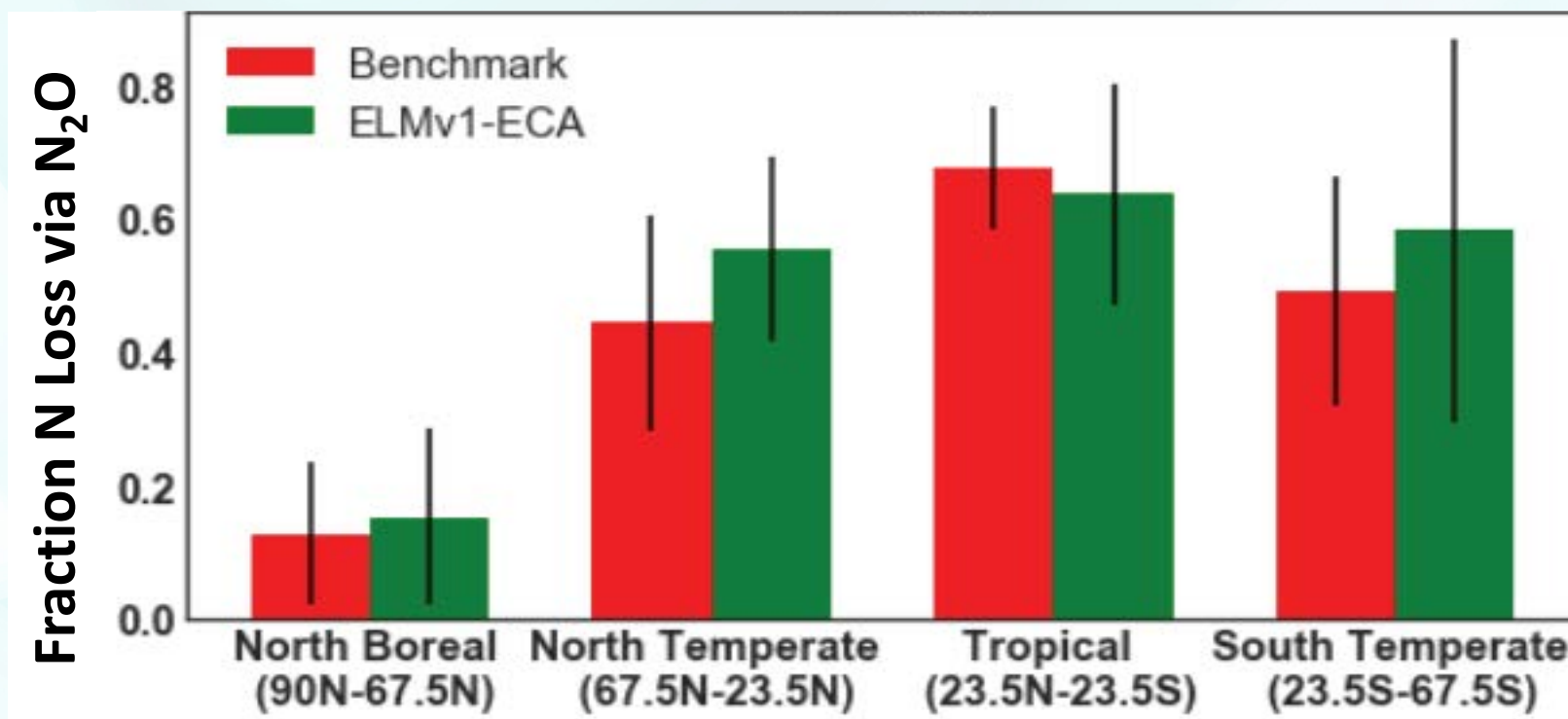
Zhu et al. (2018)

PIP Nutrient Dynamics

- ELMv1-ECA predicted large fractions of annual N and P uptake occurs during photosynthesis-inactive periods
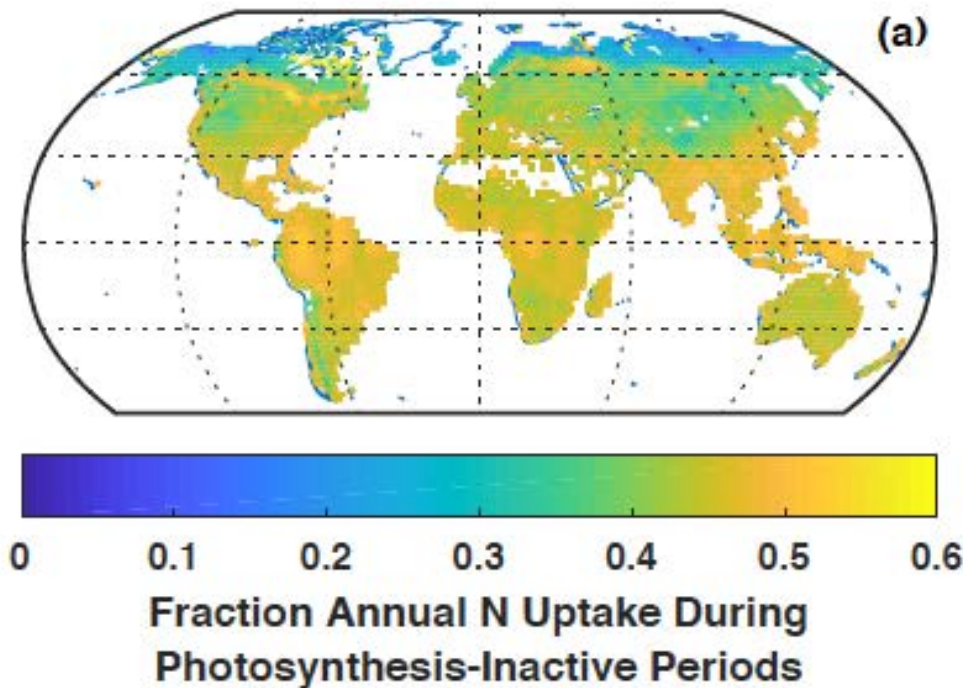
Fraction Annual N Uptake During Photosynthesis-Inactive Periods

PIP Nutrient Dynamics

- ELMv1-ECA predicts large fractions of annual N and P uptake occurs during photosynthesis-inactive periods

(a)

Non-growing Season

Nighttime

Fraction Annual N Uptake During Photosynthesis-Inactive Periods

Riley et al. (2018)

PIP Nutrient Dynamics

- ELMv1-ECA predicts large fractions of annual N and P uptake occurs during photosynthesis-inactive periods

(d) Fraction Annual P Uptake During Photosynthesis-Inactive Periods

(e) Fraction Annual P Uptake During Photosynthesis-Inactive Periods

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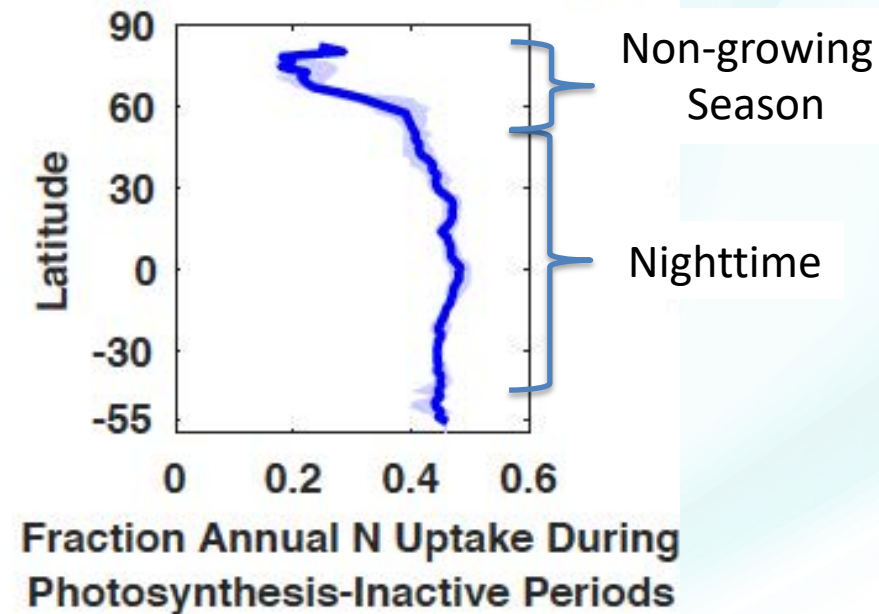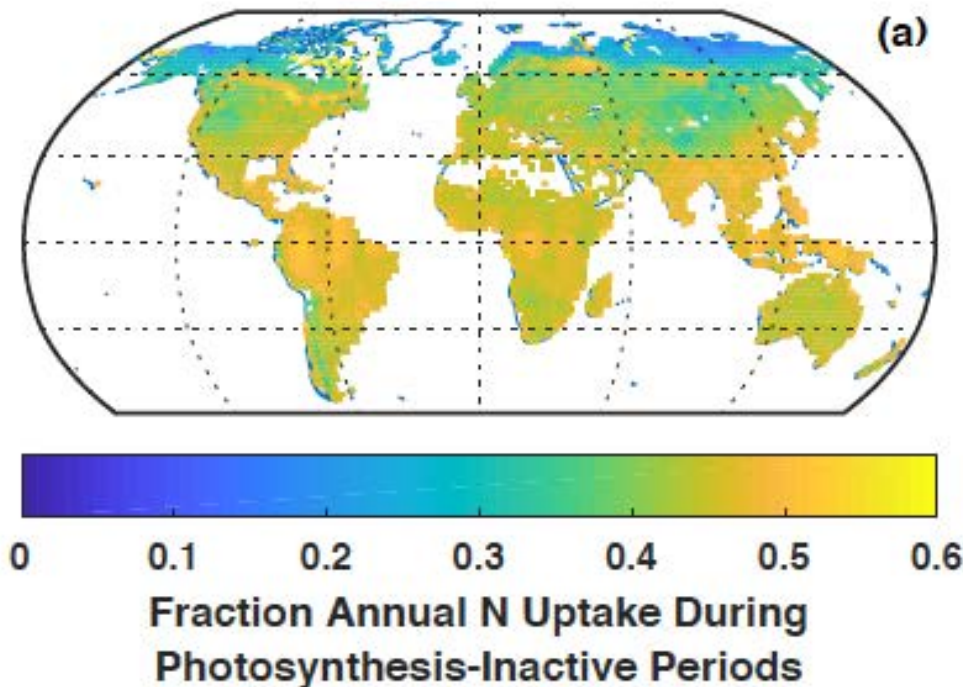U.S. DEPARTMENT OF ENERGY
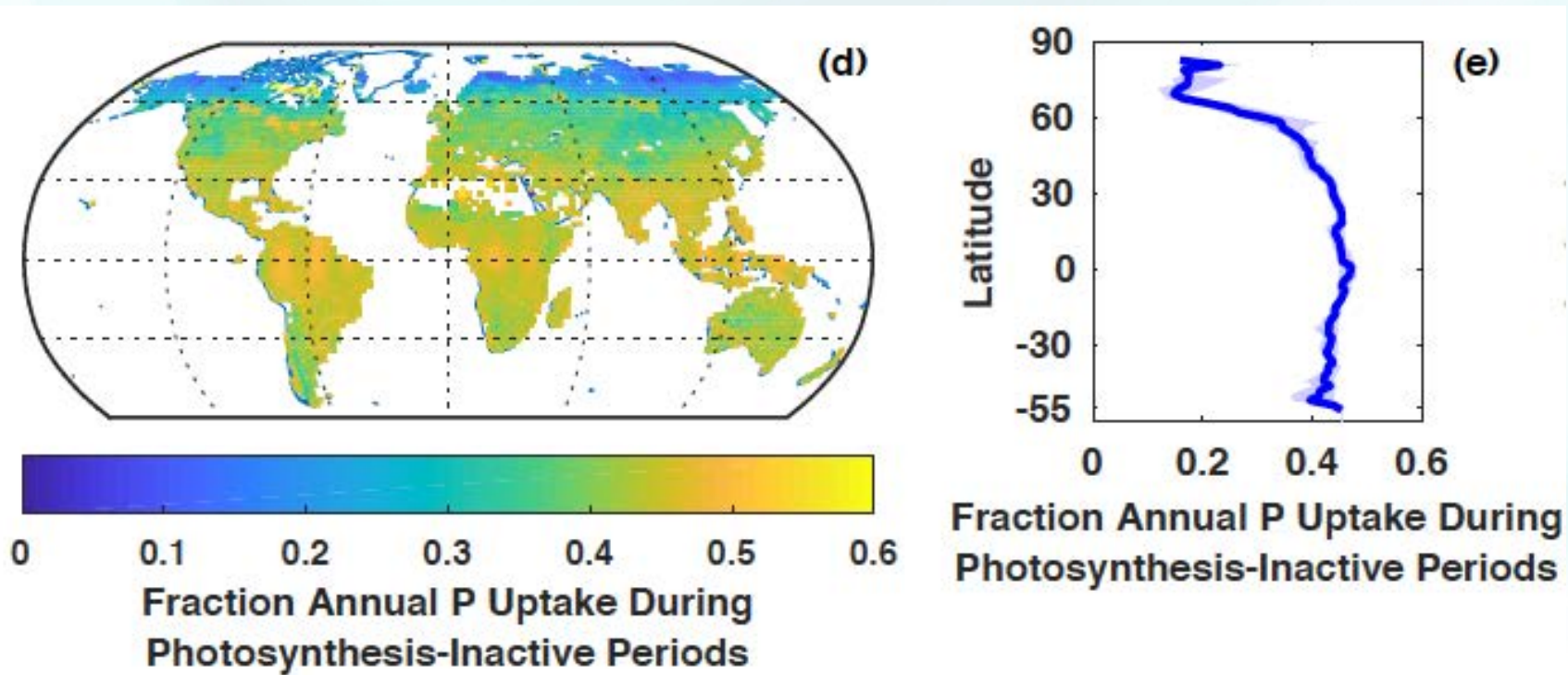
Implications of Ignoring PIP Nutrient Uptake

- Two sets of simulations
  - From baseline ELMv1-ECA model, suppress N and P uptake during PIPs for 10 years
  - Fully spinup "no-PIP nutrient uptake" model version, then allow PIP N and P uptake for 10 years
- Differences from 2 baseline simulations indicate relative magnitude of PIP nutrient uptake effects

Implications of Ignoring PIP Nutrient Uptake: Ecosystems Become N "Leakier"

(c) $\Delta(N_2O\ Emission)\ (gN\ m^{-2}\ yr^{-1})$

(d) $\Delta(N_2O\ Emission)\ (gN\ m^{-2}\ yr^{-1})$
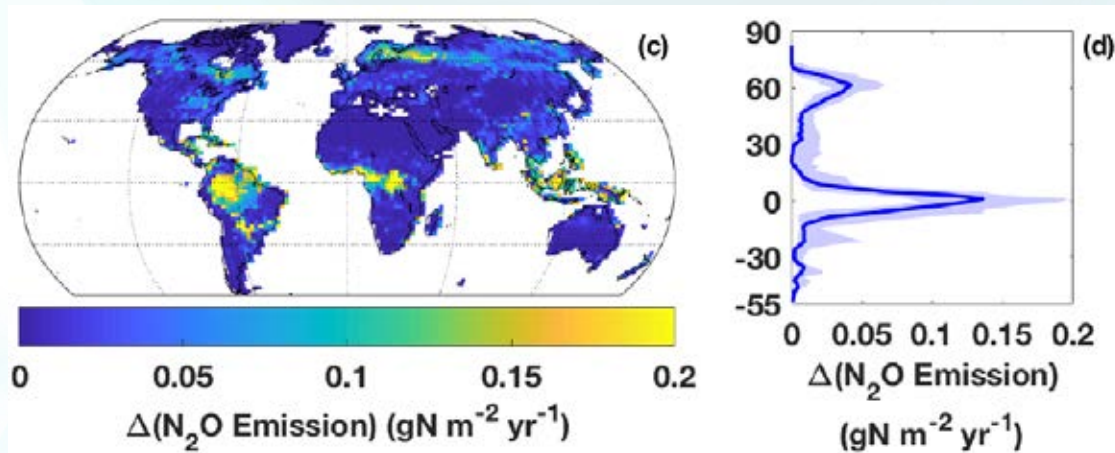
Increased losses:

- 5.7 – 7.2 TgN y^{-1} of N_2O
  - 2.4 to 3.0 Pg CO_2-equivalent y^{-1}
  - Current land C sink: 0 to 12 Pg-CO_2 y^{-1}
  - ~25% to >100% of the current land CO_2 sink

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Implications of Ignoring PIP Nutrient Uptake: Ecosystems Become N "Leakier"

(a)

(b)

Δ(N Leached) (gN m^{-2} yr^{-1})

Δ(N Leached) (gN m^{-2} yr^{-1})
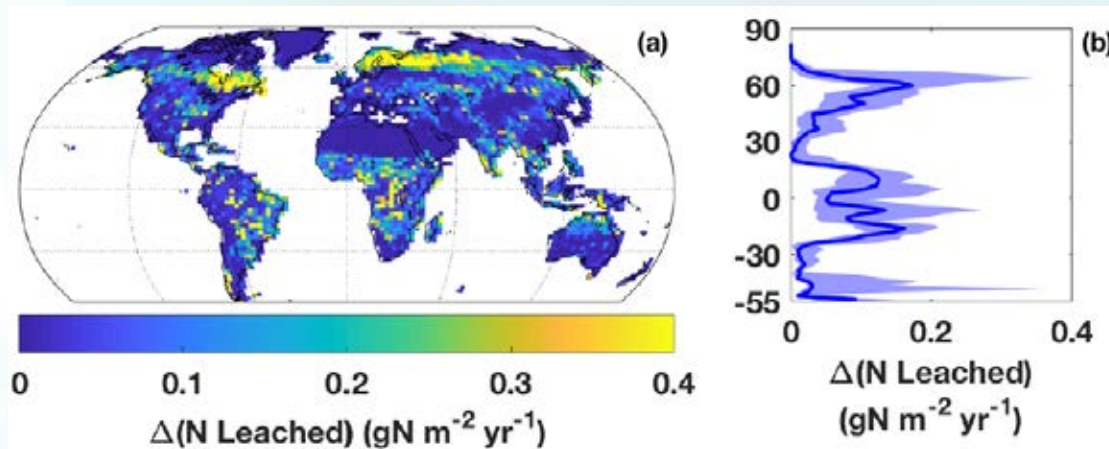
Increased losses:

- 16 - 19 TgN y^{-1} of N leached

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High-Latitude Non-Growing Season Uptake

- 5 to >50% of annual N and P uptake occurs outside of growing season

- Large variation between plant functional types

0   0.05   0.1   0.15   0.2   0.25   0.3   0.35   0.4

**Fraction Annual N Uptake During
Photosynthesis-Inactive Periods**
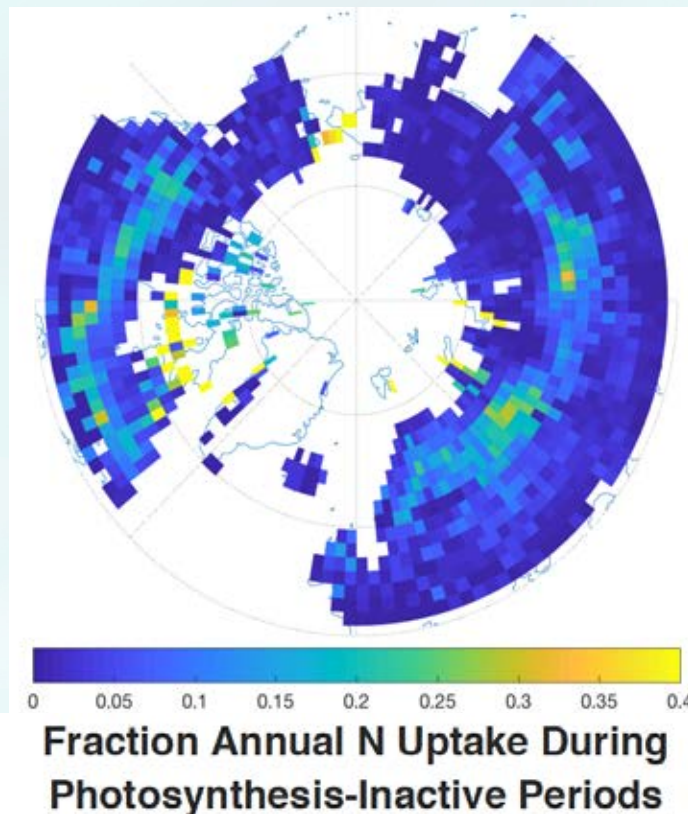
Summary

- Photosynthesis-Inactive Period (nighttime and non-growing season) nutrient uptake accounts for 20-60% of annual uptake

    - ~45% NPP-weighted global average

- Ignoring this process, as is done in all CMIP6 models reviewed and ELMv1-CTC (i.e., those using a Relative Demand approach), leads to:

    - Biased 'leaky' terrestrial ecosystems: N leaching (16 - 19 TgN y^{-1}) and N_2O emissions (5.7 – 7.2 TgN y^{-1})

    - This N_2O emission bias has a GWP equivalent of ~25% to >100% of the current terrestrial CO_2 sink

    - Potentially large effects on modeled terrestrial C exchanges with the atmosphere

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ELM Papers Cited

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- Zhu, Q., Riley, W. J., and Tang, J. Y.: A new theory of plant and microbe nutrient competition resolves inconsistencies between observations and models, Ecol Appl, DOI:10.1002/eap.1490, 2017.

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