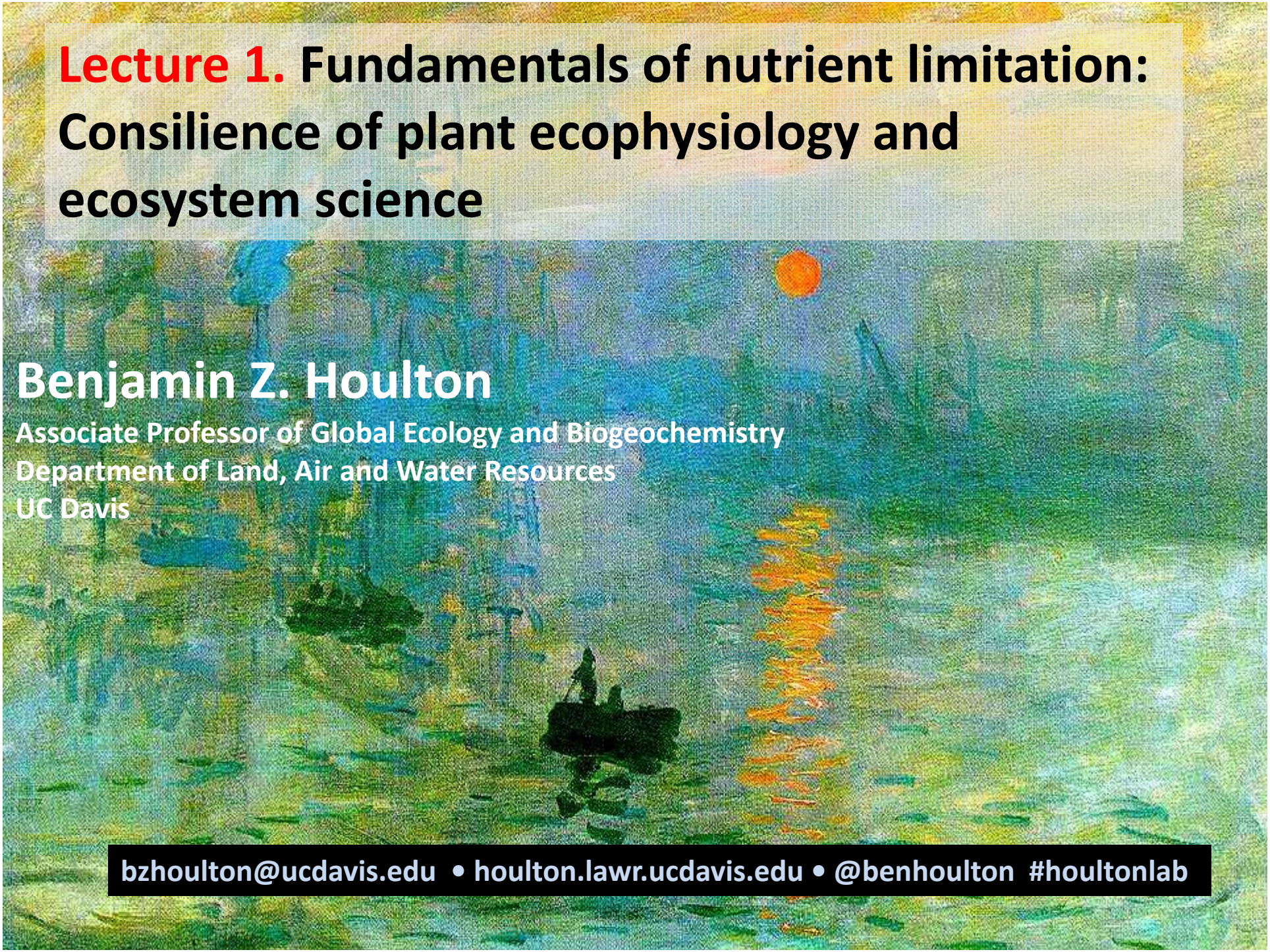
Lecture 1. Fundamentals of nutrient limitation: Consilience of plant ecophysiology and ecosystem science



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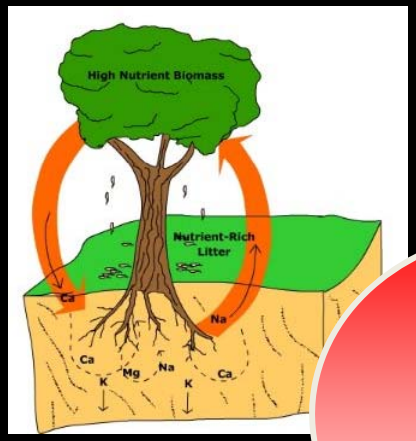
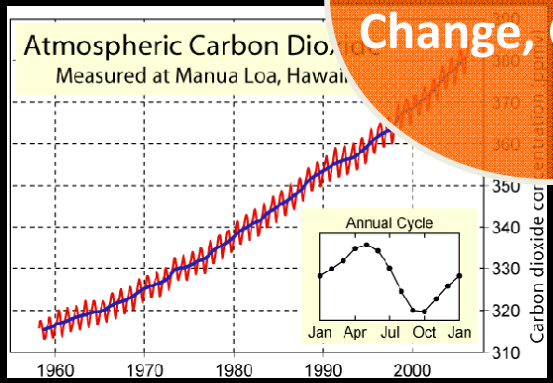


Nutrient Cycling

Human Societies Food security

Nutrient limitation

Climate Change, C Cycling



Ecosystem Functioning/ Stability

Outline

Part 1. Nutrient limitation defined

- Perspectives, theory: 3 essential concepts

Part 2. Patterns of nutrient limitation and controls

- Nitrogen limitation and controls
- Phosphorus limitation and controls
- Co-limitation, feedback and maintenance

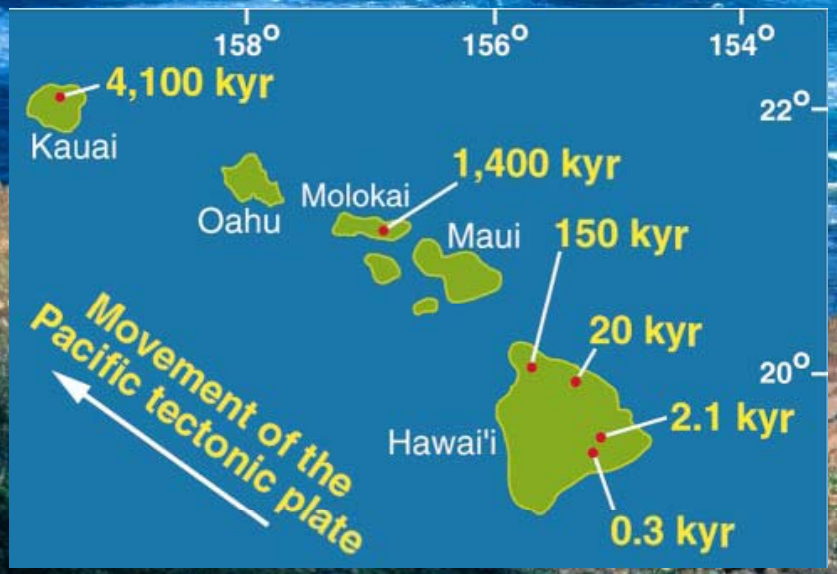
Part 1. Nutrient limitation defined

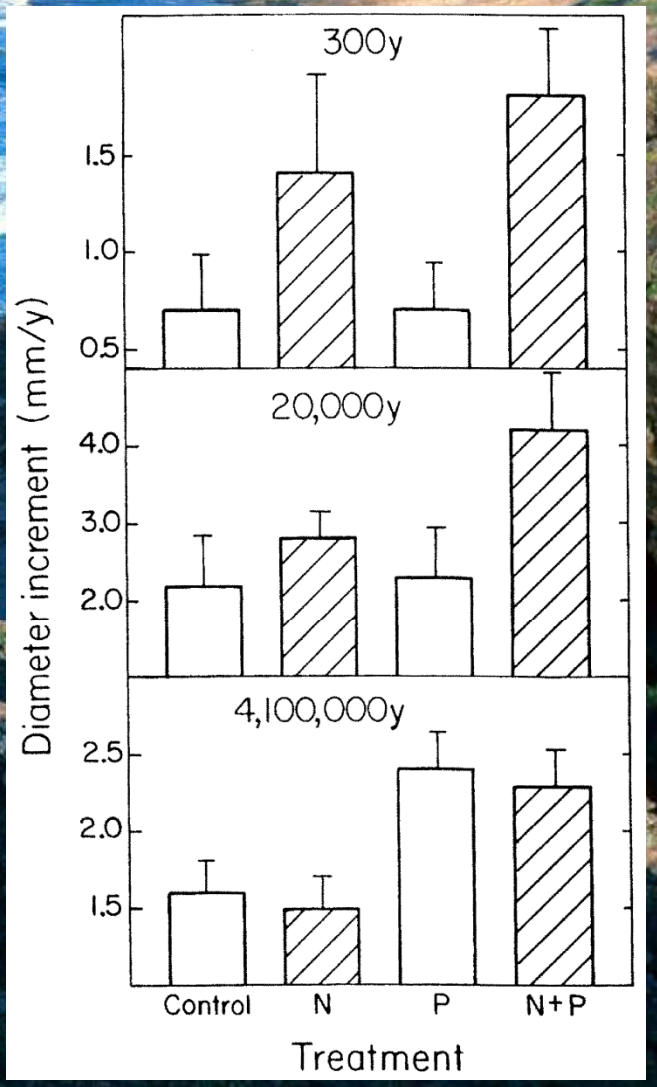
General Definition (direct assessment):

Nutrient limitation occurs when meaningful additions of an essential element in biologically available forms cause an increase in the rate of a biological process (such as primary productivity) and/or in the size of an important ecosystem compartment (such as biomass).

(after Vitousek et al. 2010)

For example…





Vitousek and Farrington, 1997

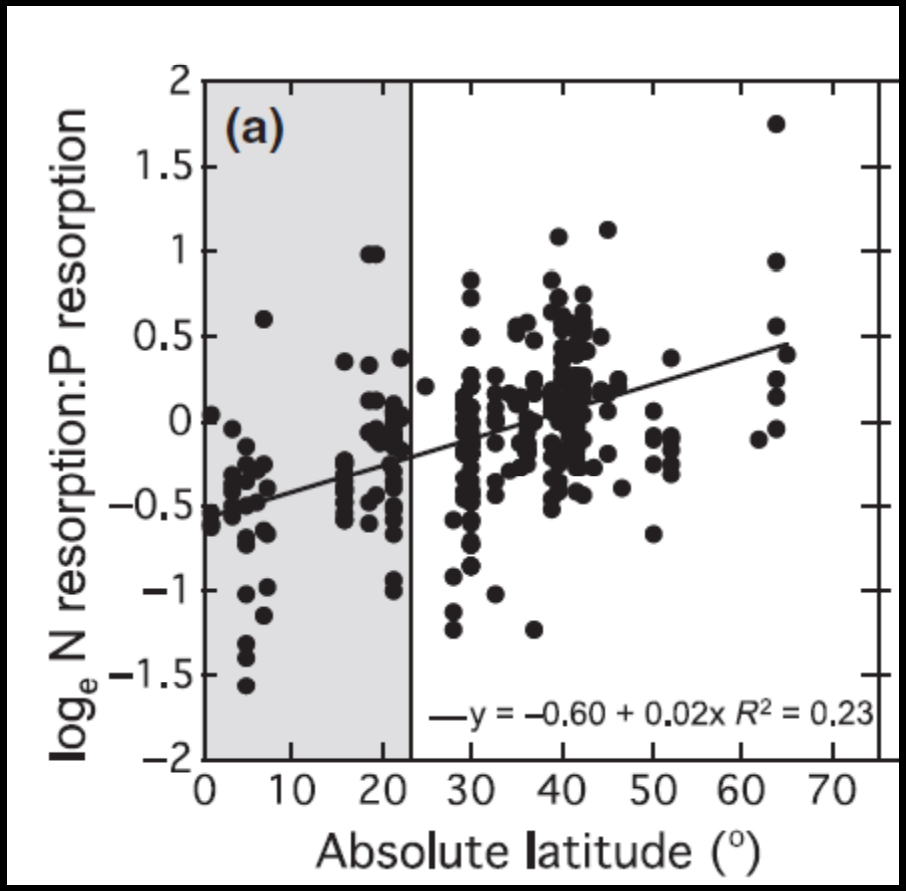
Indirect assessments

1. Nutrient availability in soil (Powers 1980)

2. Plant investments in acquiring particular nutrients (Harrison and Helliwell 1979)

3. Tissue concentrations or ratios of elements (van den Driessche 1974, Koerselman and Meuleman 1996).

For example…



Resorption

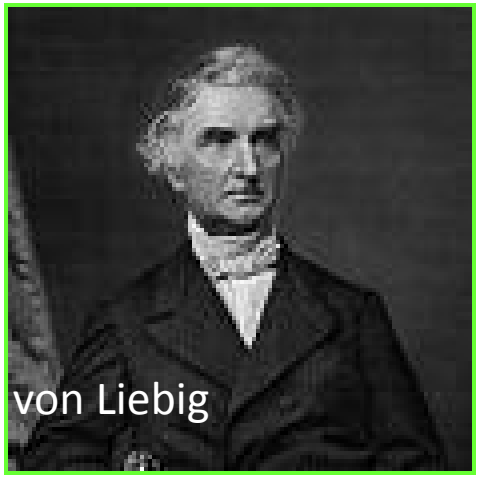
Leaf fall

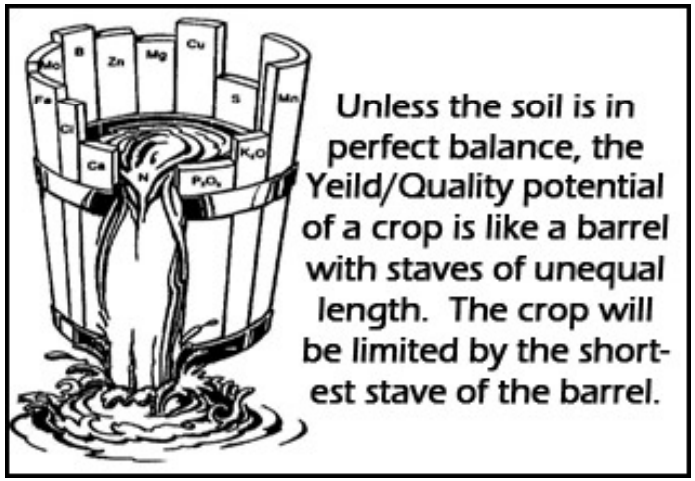
Reed et al., New Phytologist, 2012

Concept A. Single Liebig

The "law of the minimum“: the environment is unlikely to provide resources in the precise proportions required, at any given site a plant should be limited by the single resource in lowest supply relative to need. A plant should increase growth in response to addition of its one limiting resource until it becomes limited by some other resource.

After Gleeson and Tilman, 1995

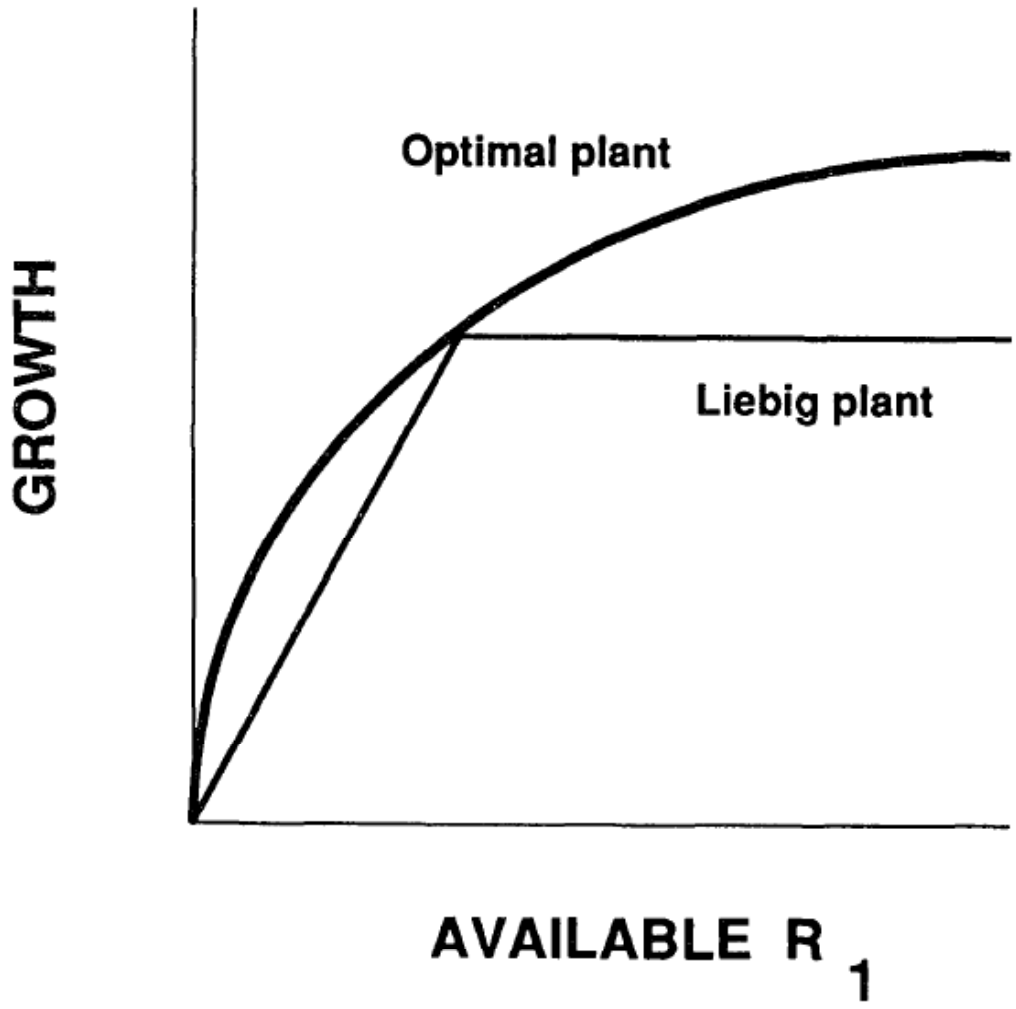

von Liebig



Concept B. Optimization theory

Optimization theory: plants should vary in physiology and morphology so as to avoid excess foraging for a non-limiting resource and to maximize effort expended in the acquisition of a limiting resource.

After Gleeson and Tilman, 1995



Gleeson and Tilman, 1995

Concept C. Multiple Resource Limitation (MRL)

Multiple resource limitation (MRL), which occurs when the addition of any one of several resources causes an increase in production and/or biomass.

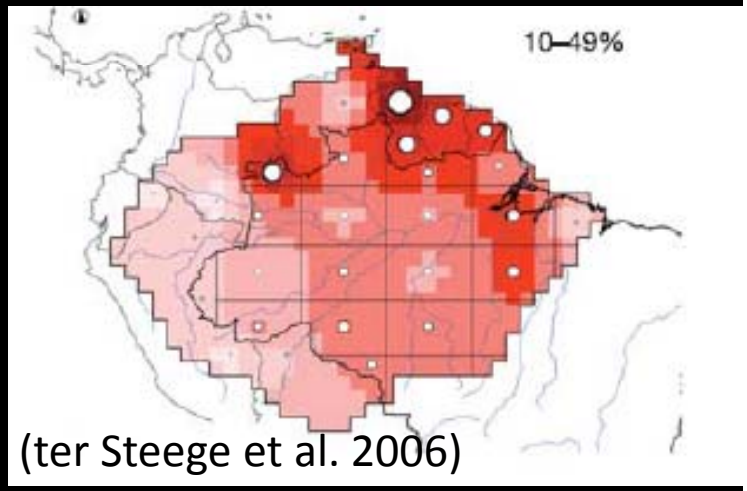
Three general pathways:

a. Physiological processes within plants – e.g., Root/shoot adjustments
b. Positive interactions in resource supply – e.g., N stimulates P mineralization
c. Limitation of different species or functional groups within an ecosystem by different resources – e.g., N fixers P limited, non-fixers N limited

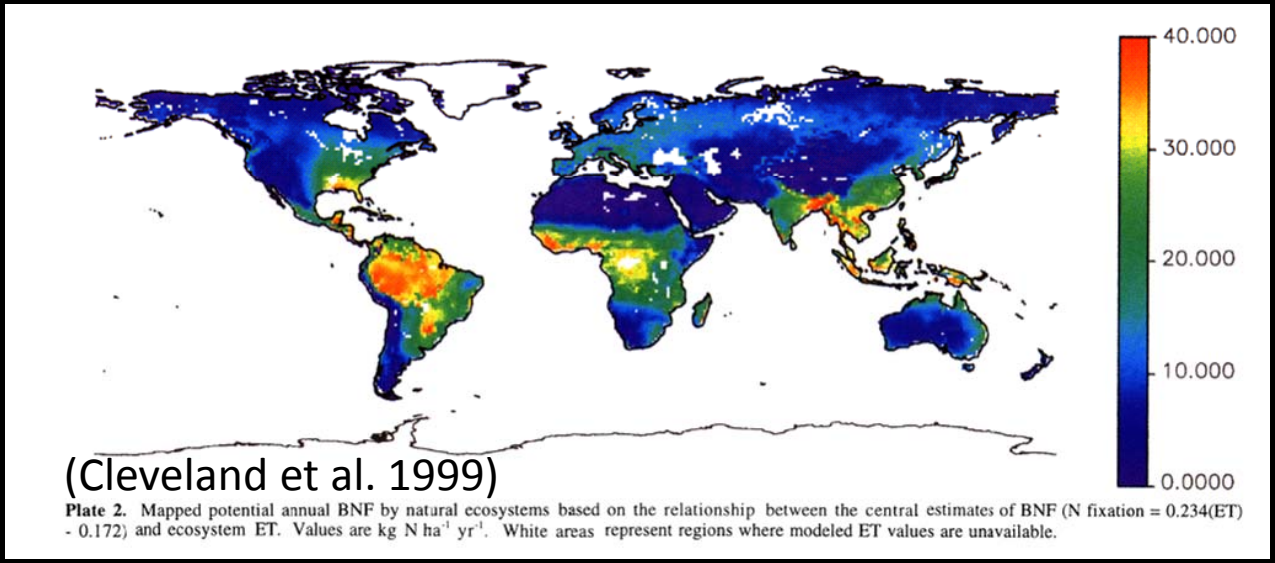
after Vitousek et al. 2010; see Bloom et al. 1985

Case study: The Problem of N fixation

Biome	Woody Legumes
Mature Boreal Forest	Absent
Mature Temperate Forest	Absent
Lowland Tropical Forest	10 – 49%
Savanna	6 – 56%

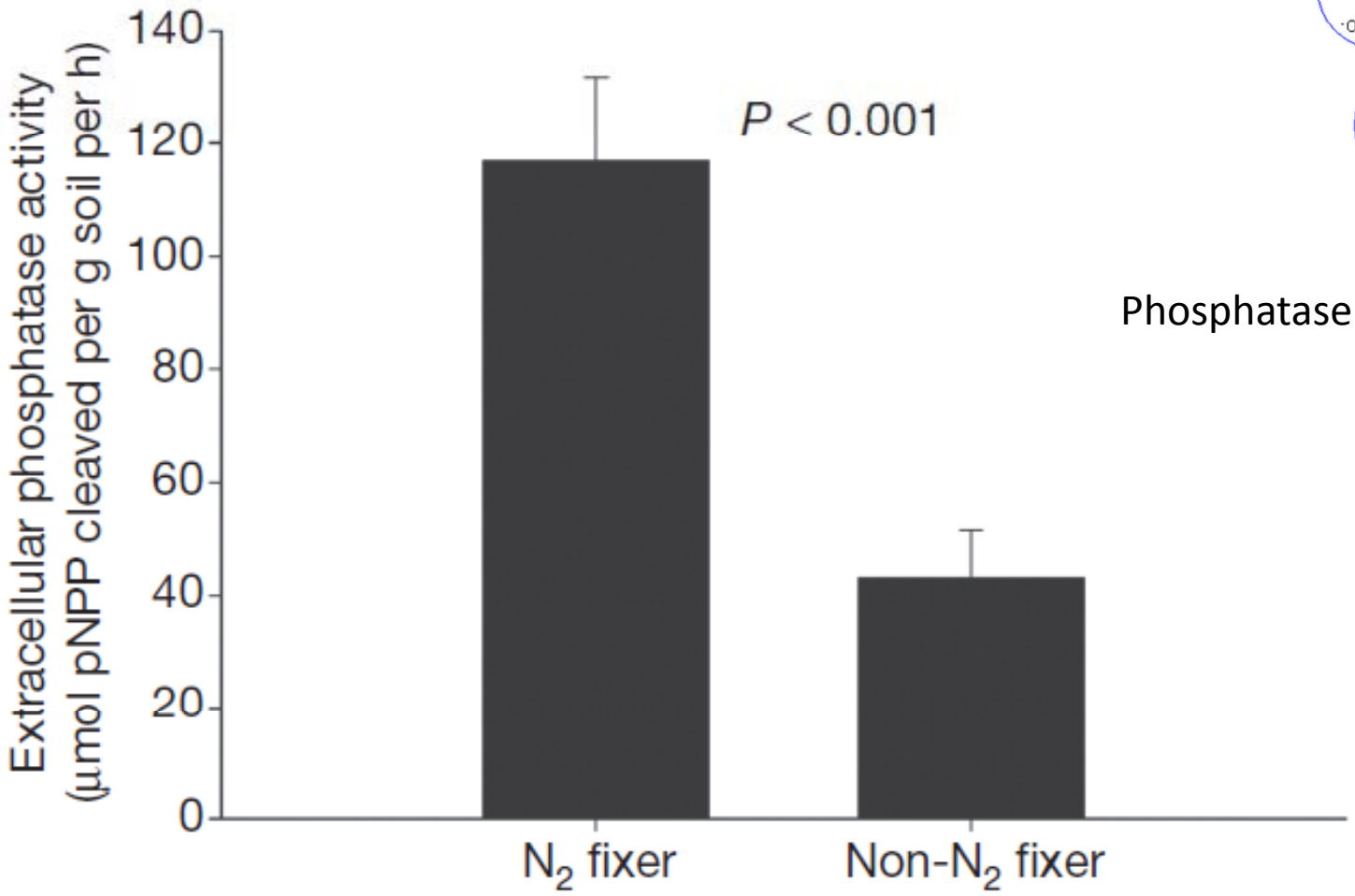


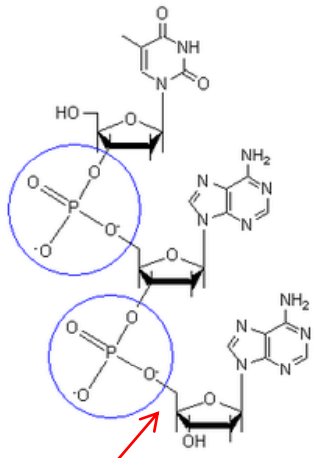
(ter Steege et al. 2006)



(Cleveland et al. 1999)

Plate 2. Mapped potential annual BNF by natural ecosystems based on the relationship between the central estimates of BNF (N fixation = 0.234(ET) - 0.172) and ecosystem ET. Values are kg N ha^{-1} yr^{-1}. White areas represent regions where modeled ET values are unavailable.

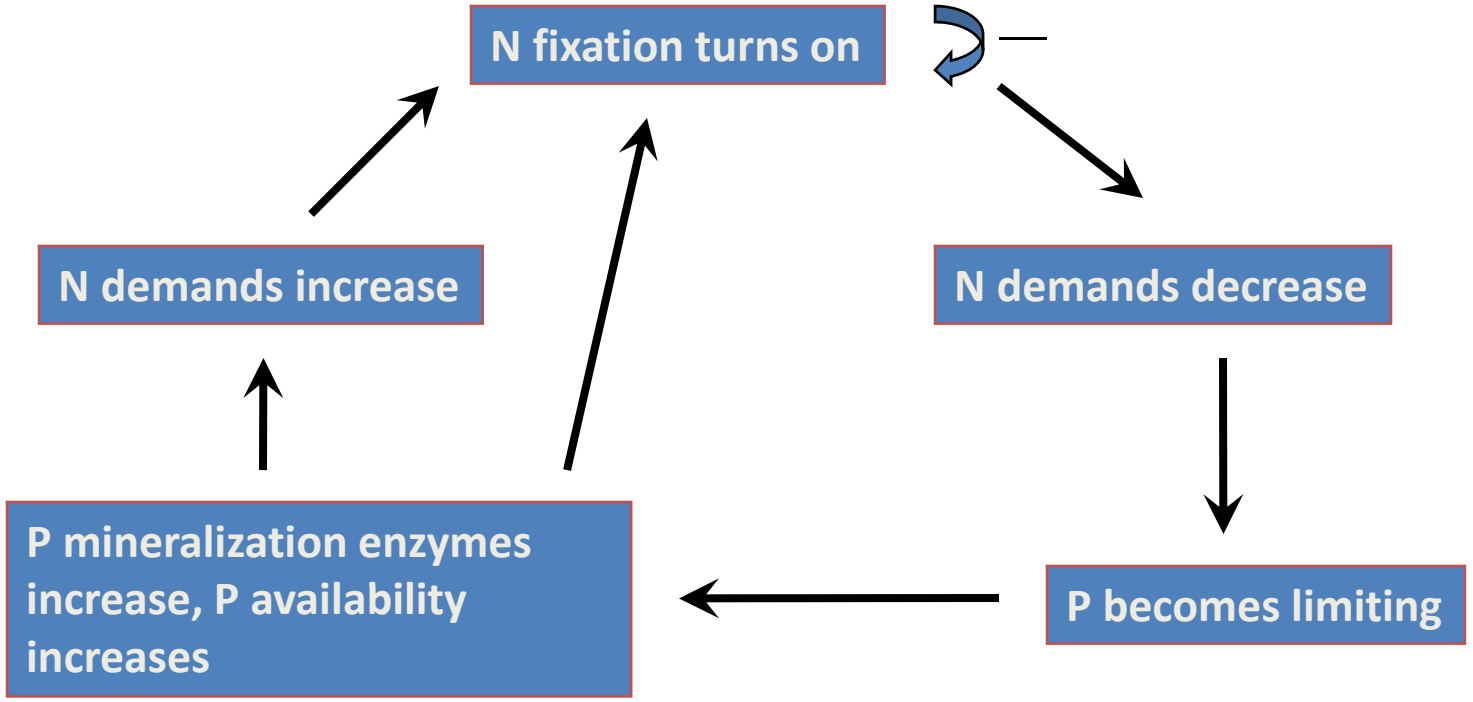


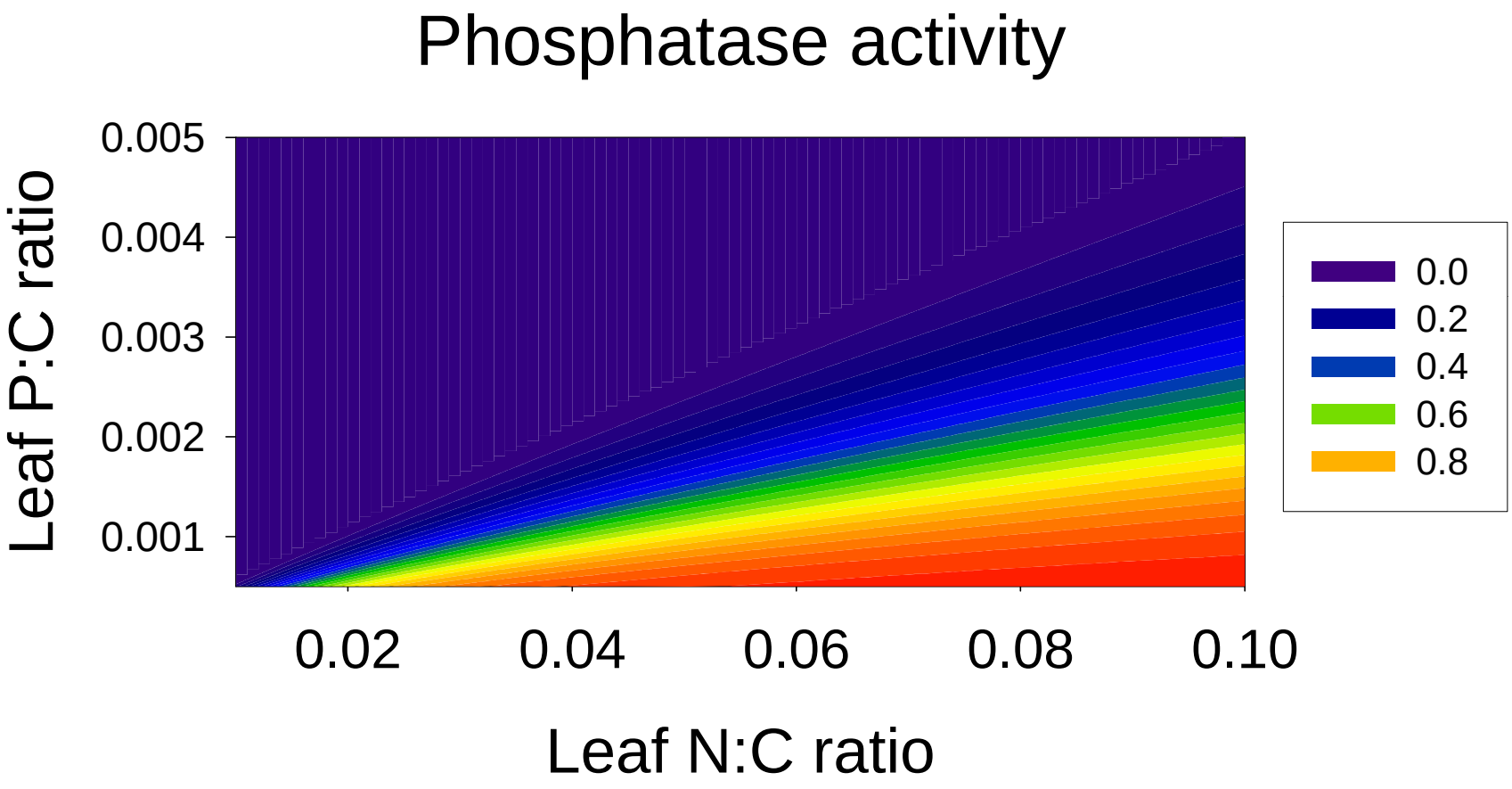


Phosphatase enzyme

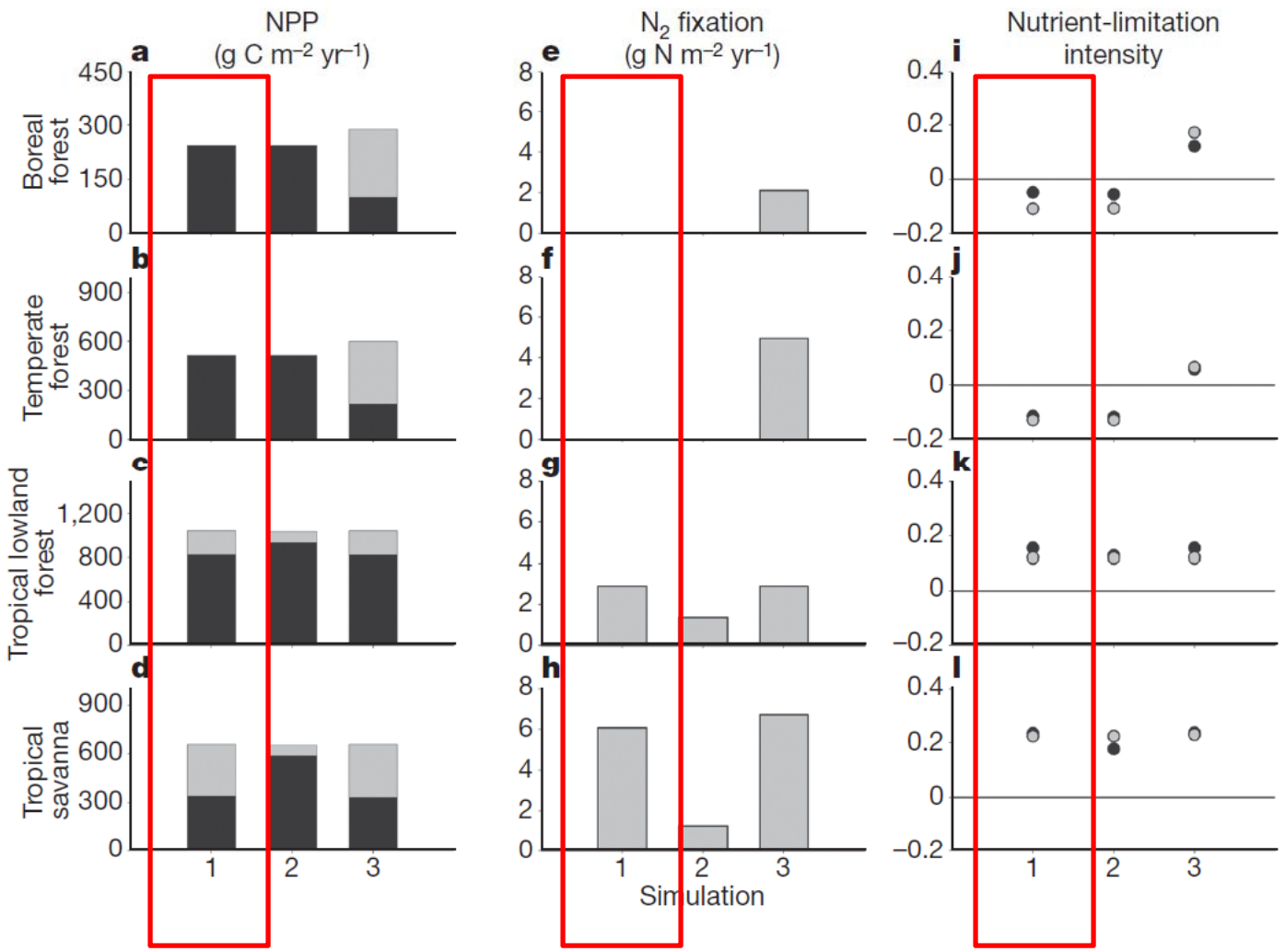
Houlton et al. Nature 2008

Proposed feedback between N fixation, N limitation, P limitation, and biochemical P mineralization



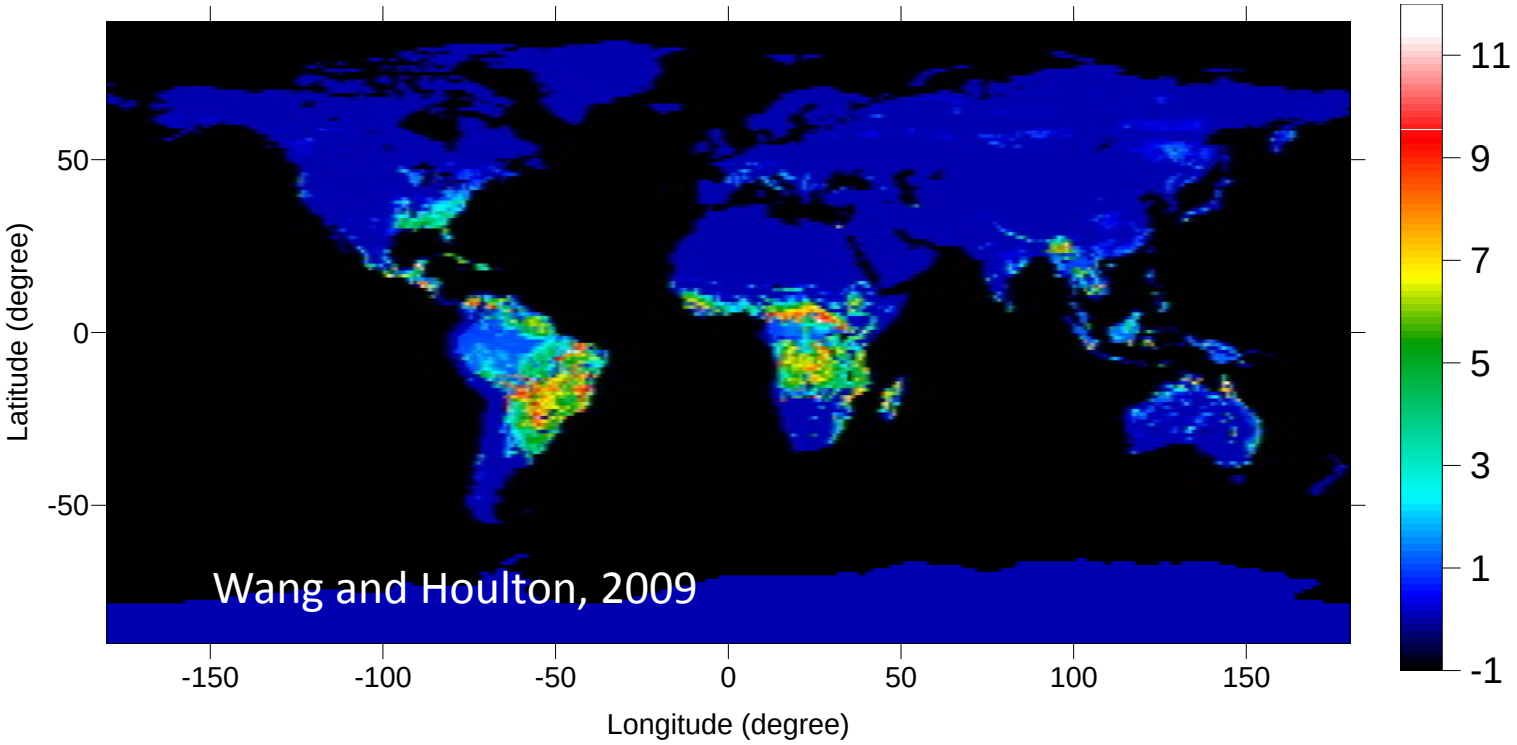


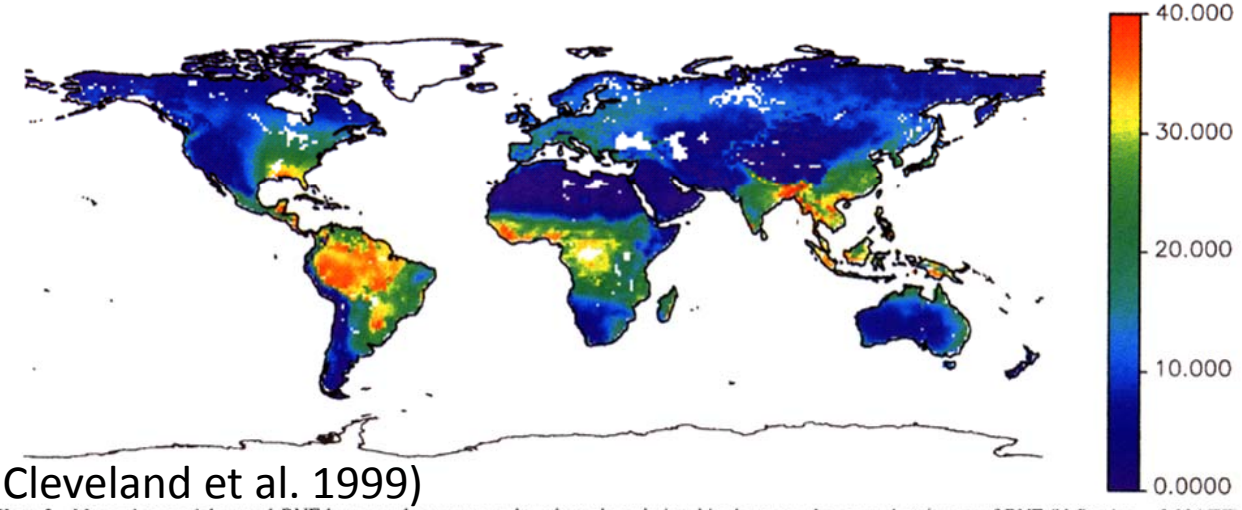
Wang, Houlton, Field, GBC, 2007



Simulation 1 = phosphatase plus energetic constraint on N fixation

Houlton et al. Nature 2008





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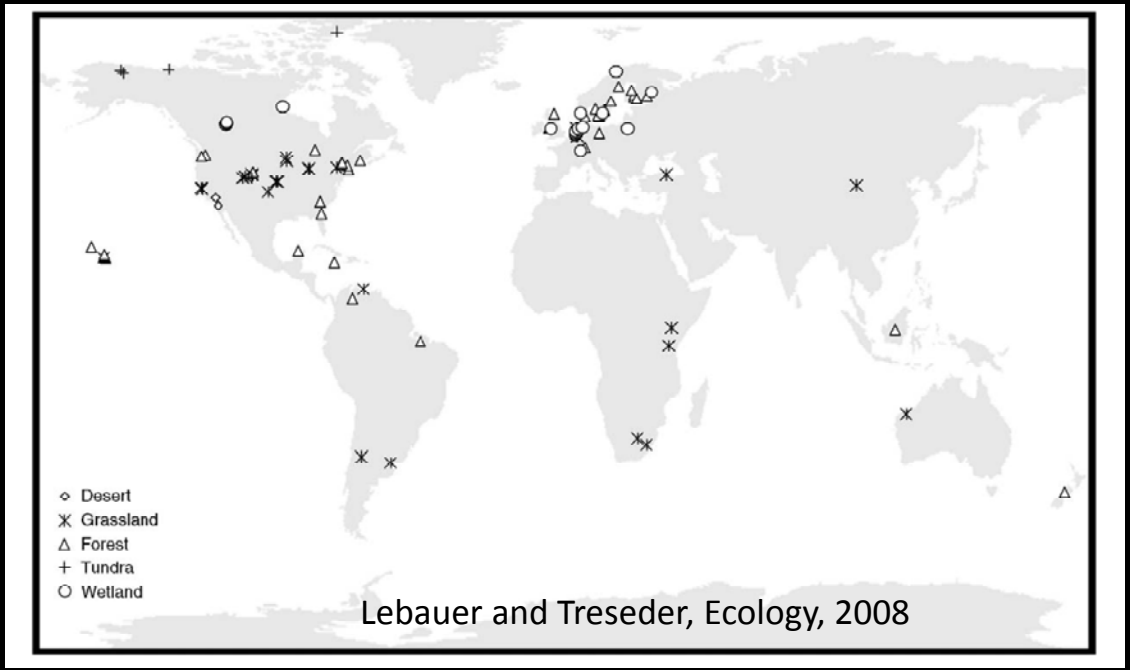
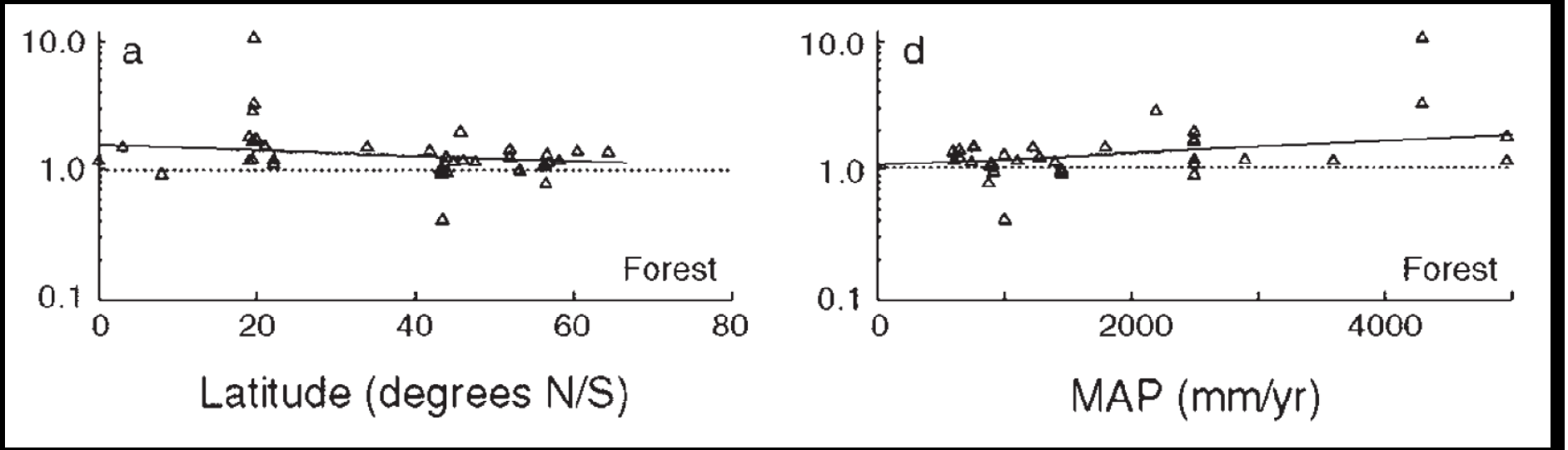
Part II. Patterns of nutrient limitation and controls

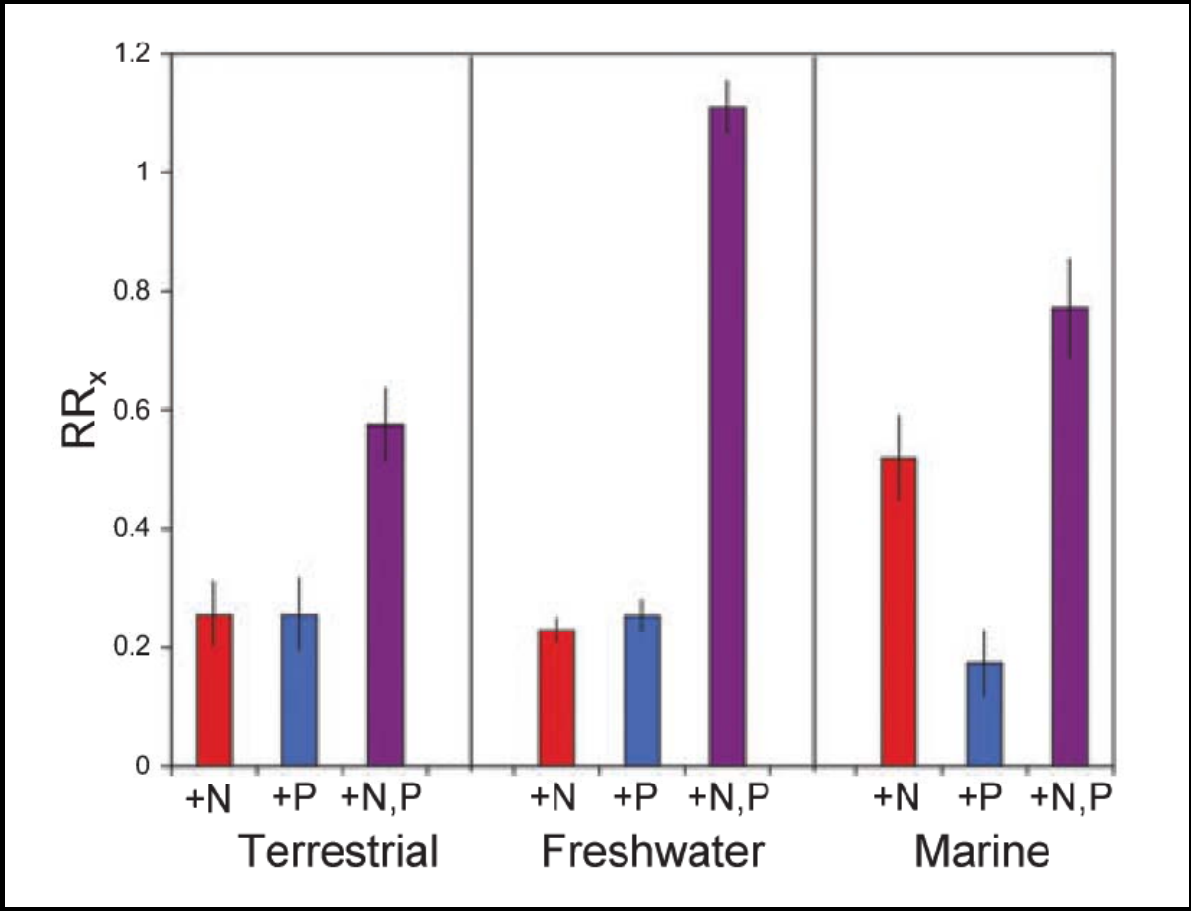
Nitrogen limitation is widespread



Lebauer and Treseder, Ecology, 2008



…but so is P…



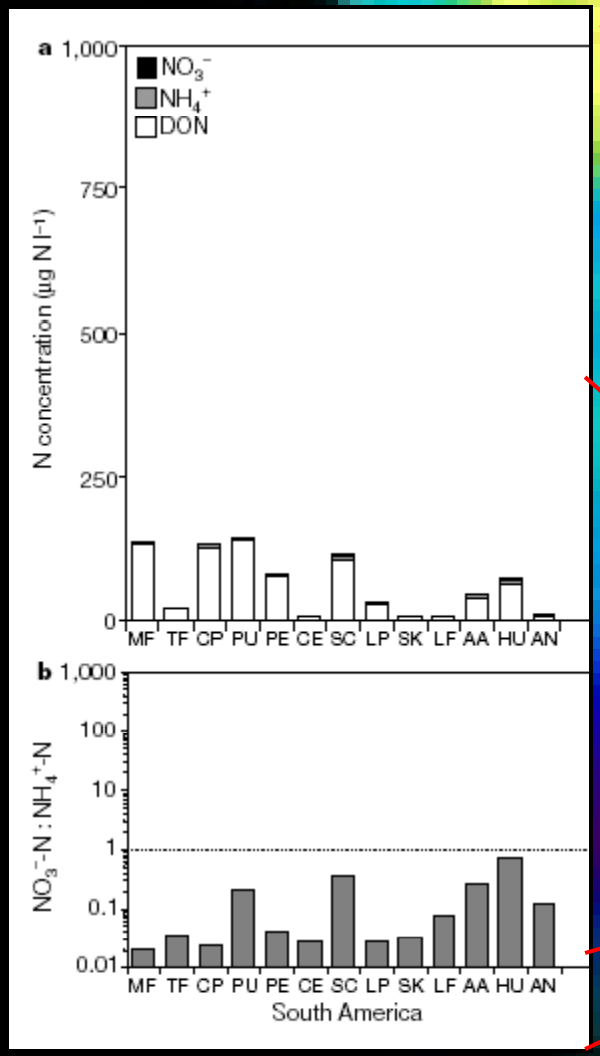
Elser et al., Ecology Letters, 2008

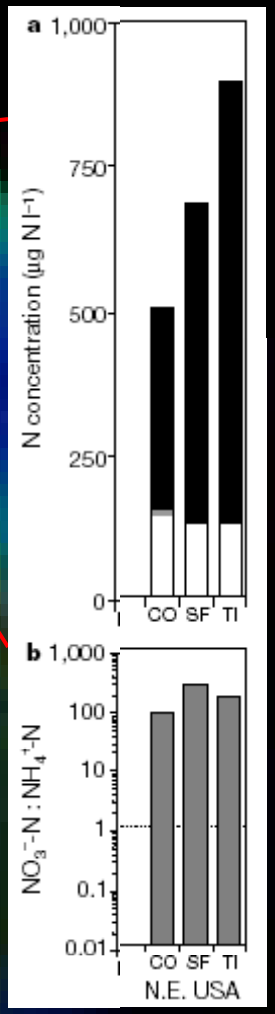
Ecosystem-scale mechanisms of N limitation

Pathway	Mechanism	Timescale
Demand-independent losses	losses of combined N that organisms cannot prevent, including leaching of DON, post- disturbance losses, some gaseous pathways	decades to centuries; depends on loss pathway
Constraints to biological N fixation	biological N fixation is slow or absent even when N is limiting; could be due to energetic costs, differential grazing, demands for P, Mo, or other essential elements	decades to centuries
Transactional	slow release of N from complex organic into soluble forms, relative to the supply of other resources	years to centuries
Sink driven	sequestration of available N in an accumulating pool within ecosystems	decades to millenia

after Vitousek et al. 2010

Availability independent losses of N and the imprint of humans on the global N cycle

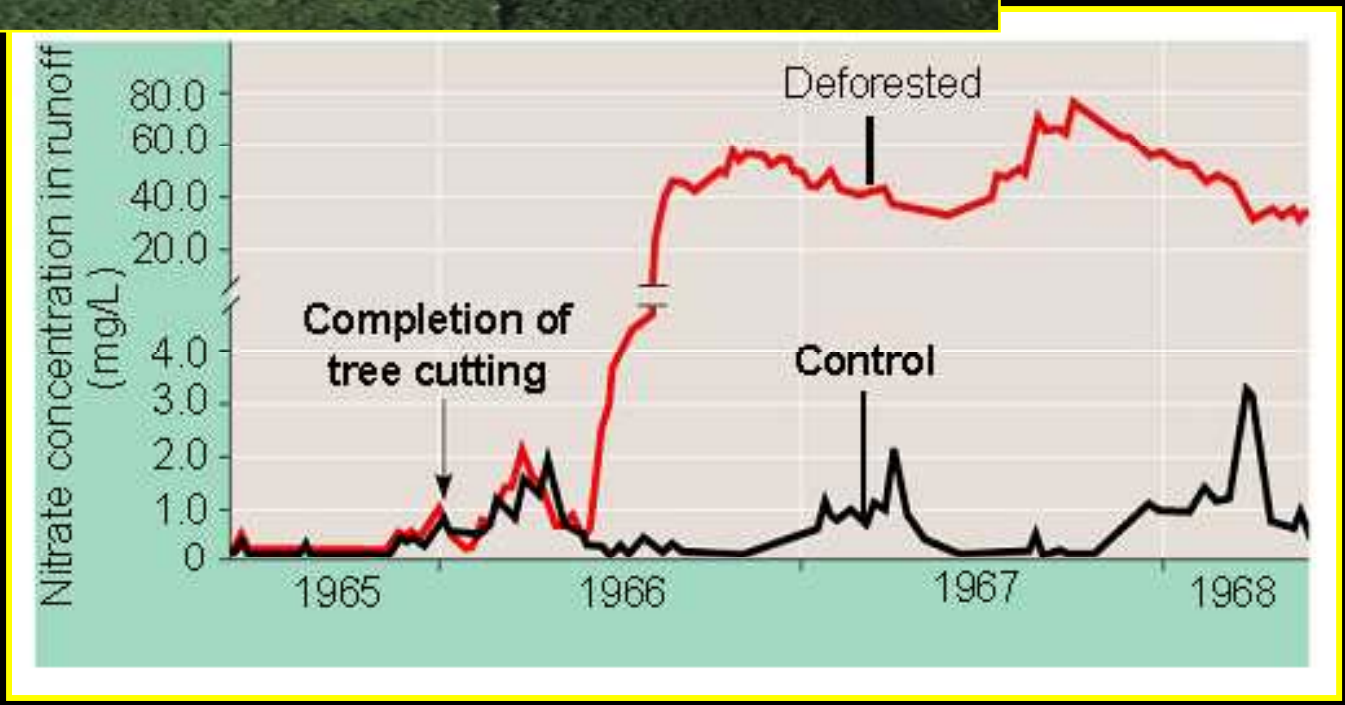




Modified from Perakis and Hedin, Nature,2002

Case Study: HBEF

Likens and Bormann, 1995



Natural vs. Anthropogenic Disturbance

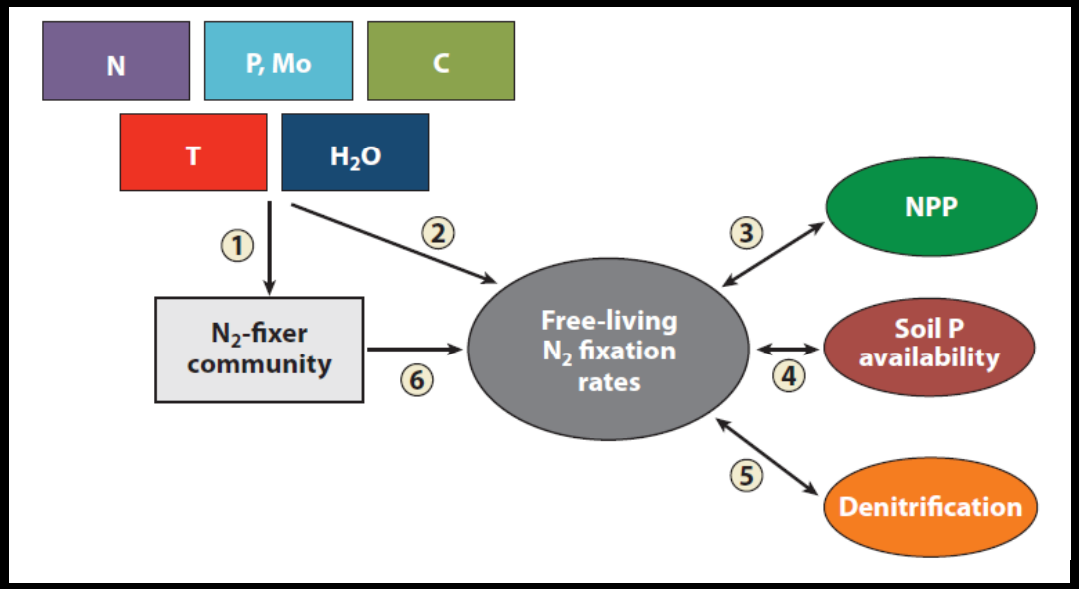
Table 6. Nitrate (NO_3^-) Losses (mol/ha y) Observed for Disturbances to Temperate Broadleaf Forest Ecosystems

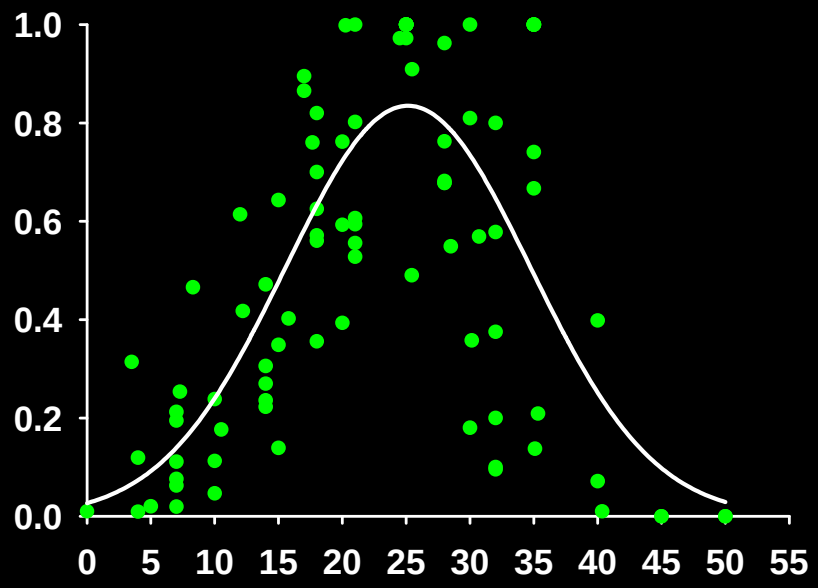
	Agent of Disturbance						
		Natural			Anthropogenic		
				Clear-Cut			
Stream Flux	Soil Freezing[a]	Insect Defoliation[b]	Ice Storm[c]	Commercial[d]	Experimental[d]	Strip-Cut[e]	Whole-Tree Harvest[e]
NO_3^-	100–450	70–350	349–522	4100	10,000	1200	2000

[a] *Mitchell and others 1996.*
[b] *Eshleman and others 1998.*
[d] *Likens and others 1978.*
[e] *Pardo and others 1995.*
[c] *Hubbard Brook Experimental Forest watershed 1 longitudinal gradient (this study).*

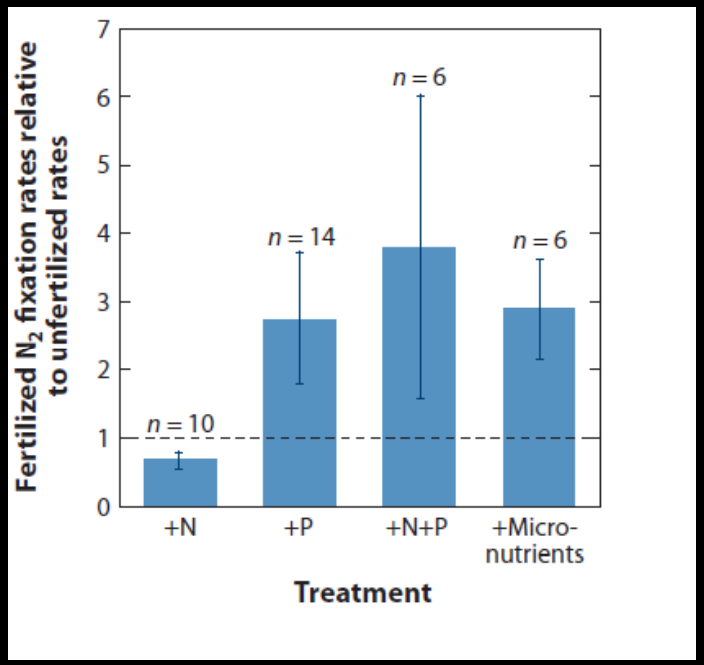
Houlton et al., Ecosystems, 2003

Constraints to N_2 fixation





Houlton et al., Nature, 2008



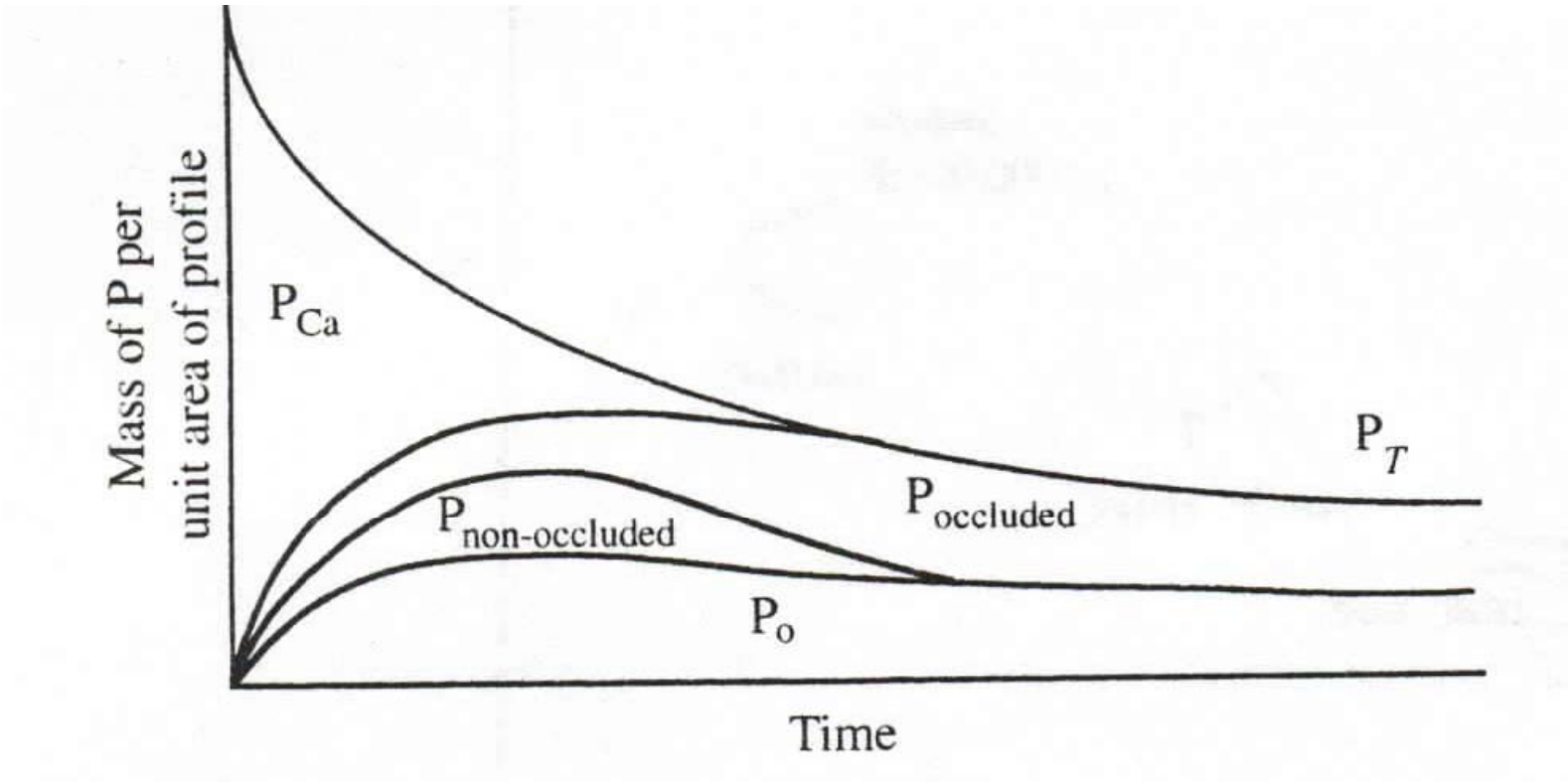
Reed et al., Eco Mon., 2012

Ecosystem-scale mechanisms of P limitation

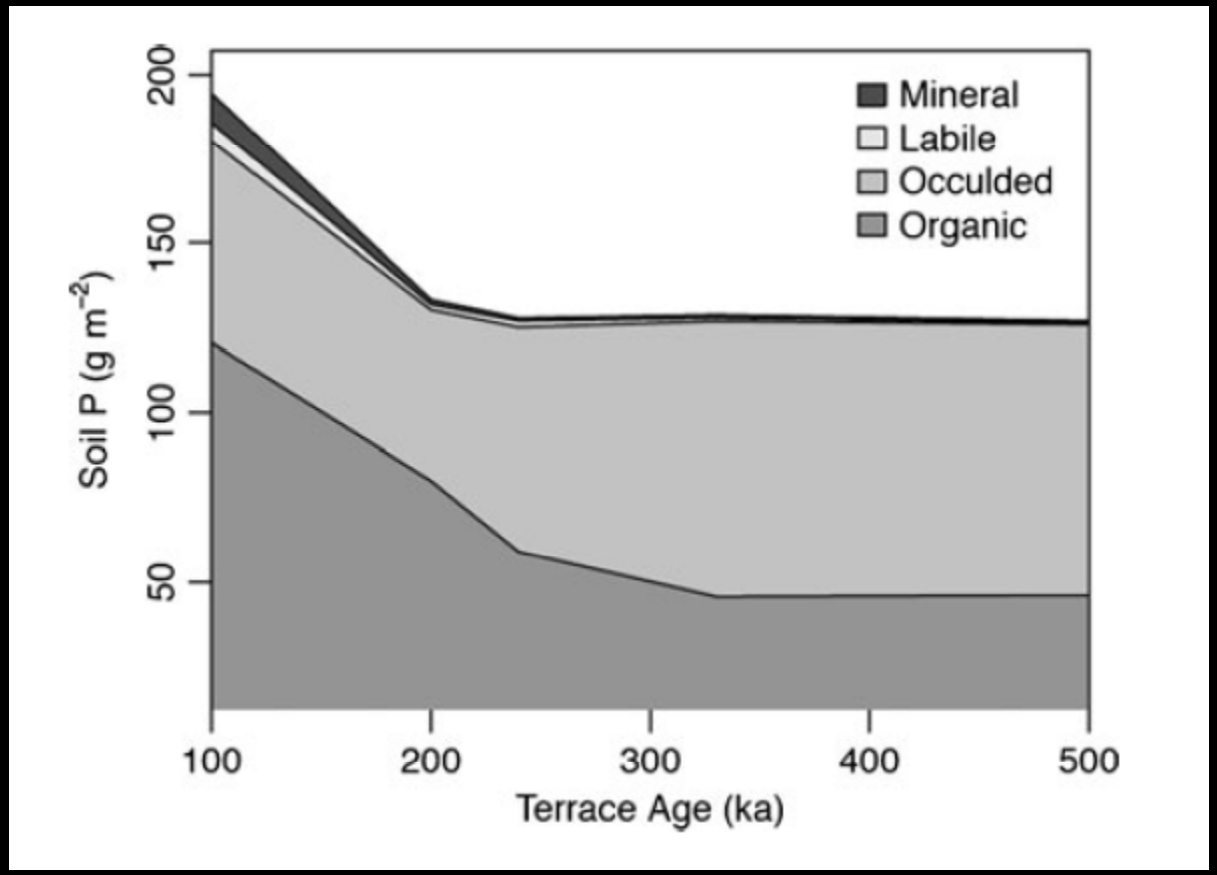
Pathway	Mechanism	Timescale
Depletion driven	loss of inorganic and dissolved organic P via leaching; exhaustion of primary minerals in soil	millions of years
Soil barrier	formation of soil layers that physically prevent/inhibit access by roots to potentially available P	hundreds to tens of thousands of years
Transactional	slow release of P from mineral forms, relative to the supply of other resources	decades to centuries
Low-P parent material	low inputs of P via weathering due to low concentrations of P in rock	all; develops quickly and persists
Sink driven	sequestration of available P in an accumulating pool within ecosystems	decades to millenia
Anthropogenic	enhanced supply of other resources (especially N) causes P limitation	years to decades

Vitousek et al. 2010

Depletion-driven P limitation: "The Walker & Syers model"



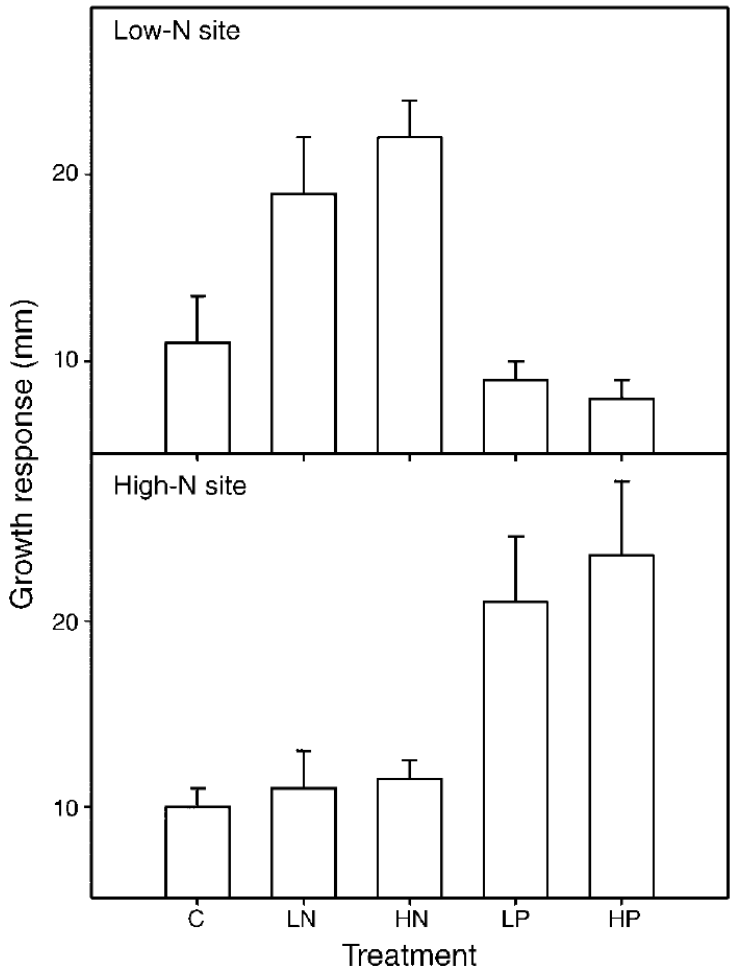
Case Study: Ecological Staircase



		T1	T2	T3	T4	T5
N:P	*P. muricata*	5.96	7.52	11.4	11.2	13.3

Izquierdo, Houlton, and van Huysen, Plant and Soil, 2013

Anthropogenic P limitation

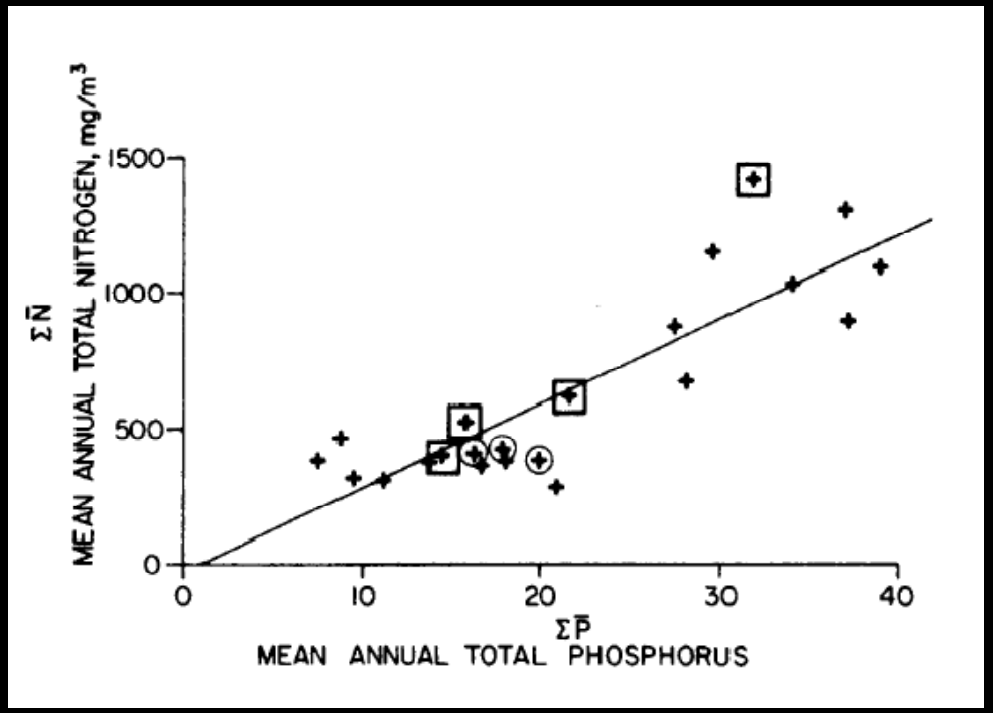


Vitousek et al. 2010

Nutrient cycling interactions and synergy

- P by N interaction in lakes, etc
- Phosphatase enzymes: N by P interactions on land

Increased P availability → (+) N_2 fixation ← (+) Decreased N availability

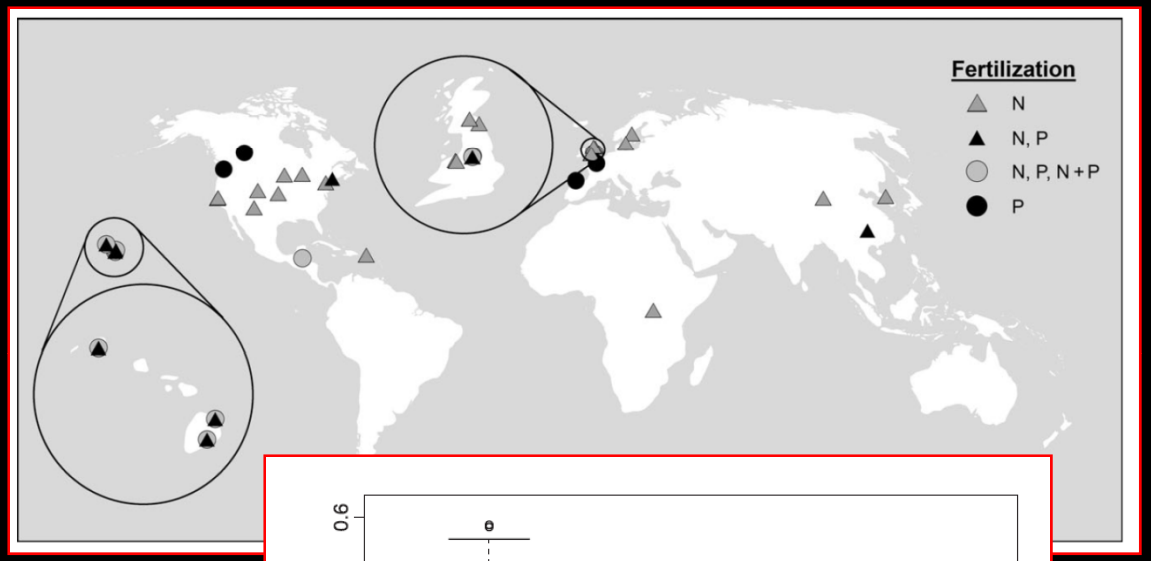


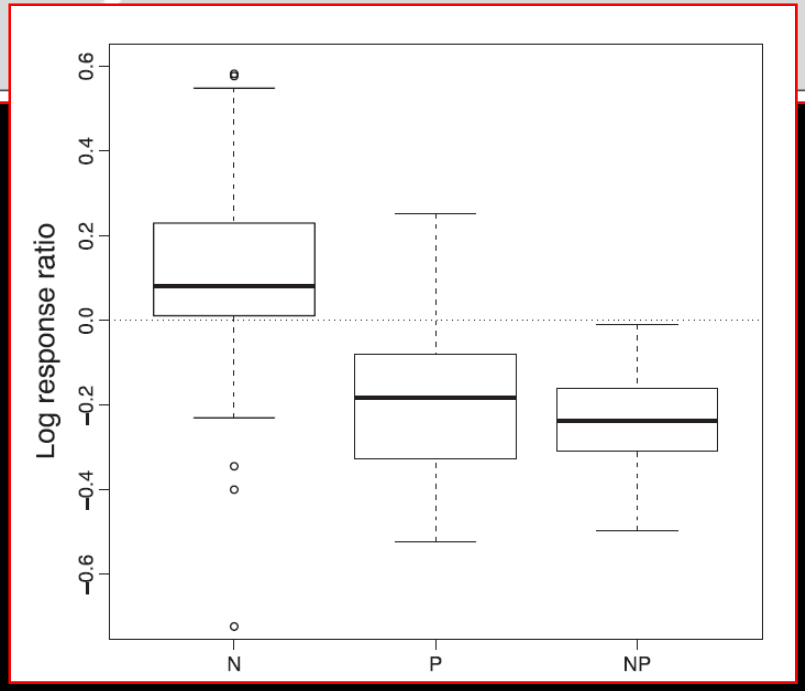
Schindler, Science, 1977

Phosphatase: N by P interaction

- Class of enzymes that cleave ester-bonded P making it available for uptake.

-Global meta-analysis data show an increase in plant and microbial phosphatase with added N, a decrease with added P.





Marklein and Houlton, New Phytologist, 2012

Summary

- Nutrient limitation is widespread, observed directly and indirectly.
- Three concepts: Single “Liebig”; Optimization; Multiple Resource Limitation
- Ultimately, mass-balance determines limitation by N and P
- Synergies can (and do) alter patterns of N and P co-limitation