Addressing questions about ecosystem nutrition: main concepts and pitfalls

Laurent Augusto

SPP 1685: New Approaches to Ecosystem Nutrition - Phosphorus and Beyond

Addressing questions about ecosystem nutrition: main concepts and pitfalls

(a personal point of view)

Laurent Augusto
Lab: Interactions Soil-Plant-Atmosphere (ISPA)
Team: Nutrition, Contamination, Ecosystems (NiCE)

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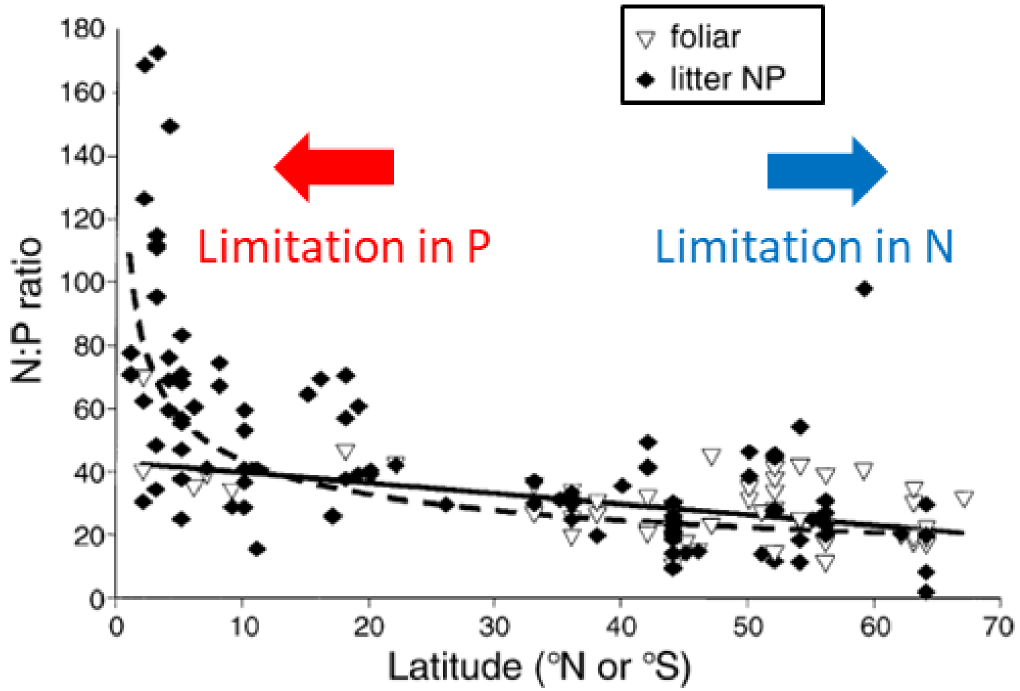
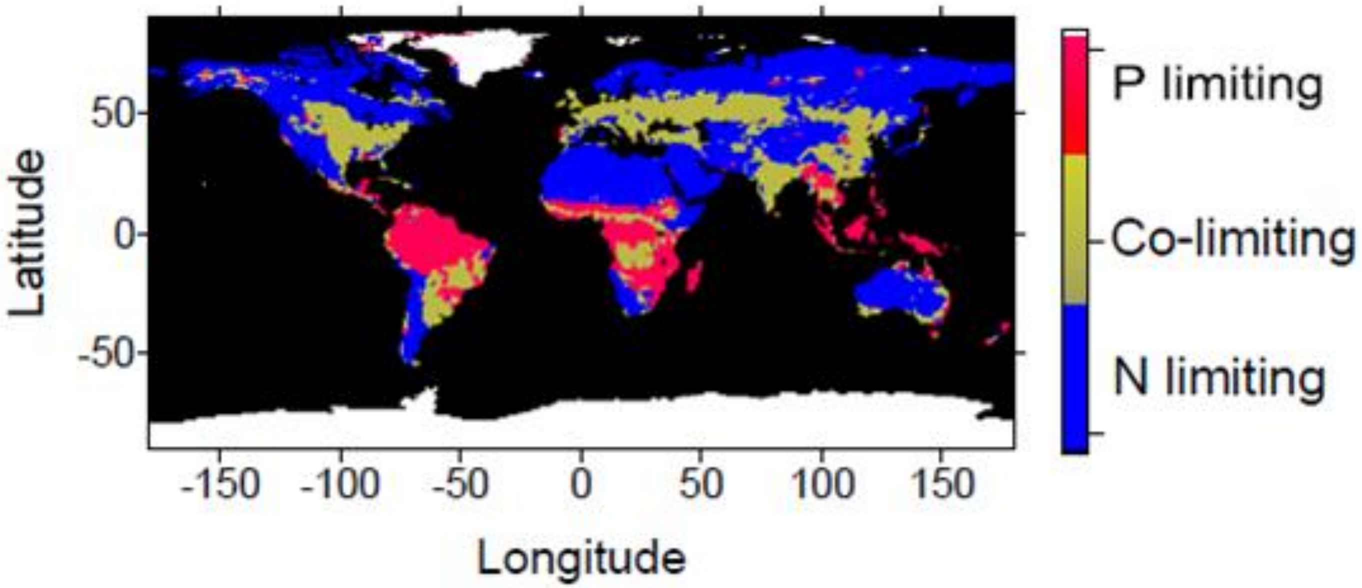
Why worrying about plant nutrition?
The world is simple:
"Tropical ecosystems are phosphorus limited whereas boreal ecosystems are nitrogen-limited"

Empirical approach



McGroddy et al. (2004, Ecology, 85, 2390-2401)

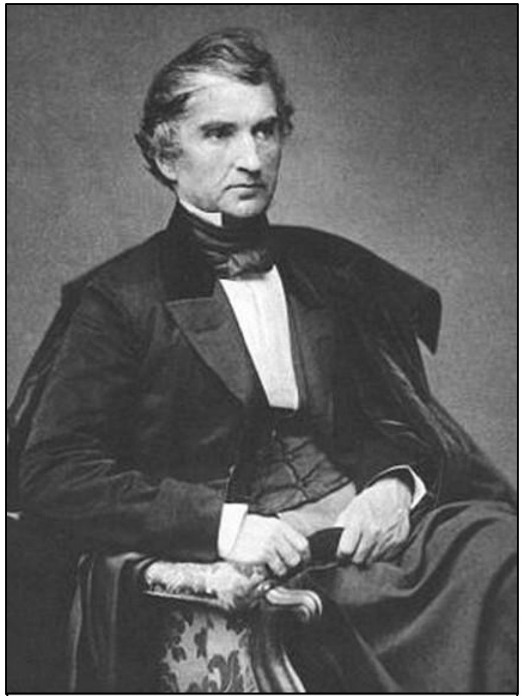
Modelling approach



Wang et al. (2010, Biogeosciences, 7, 2261-2282)

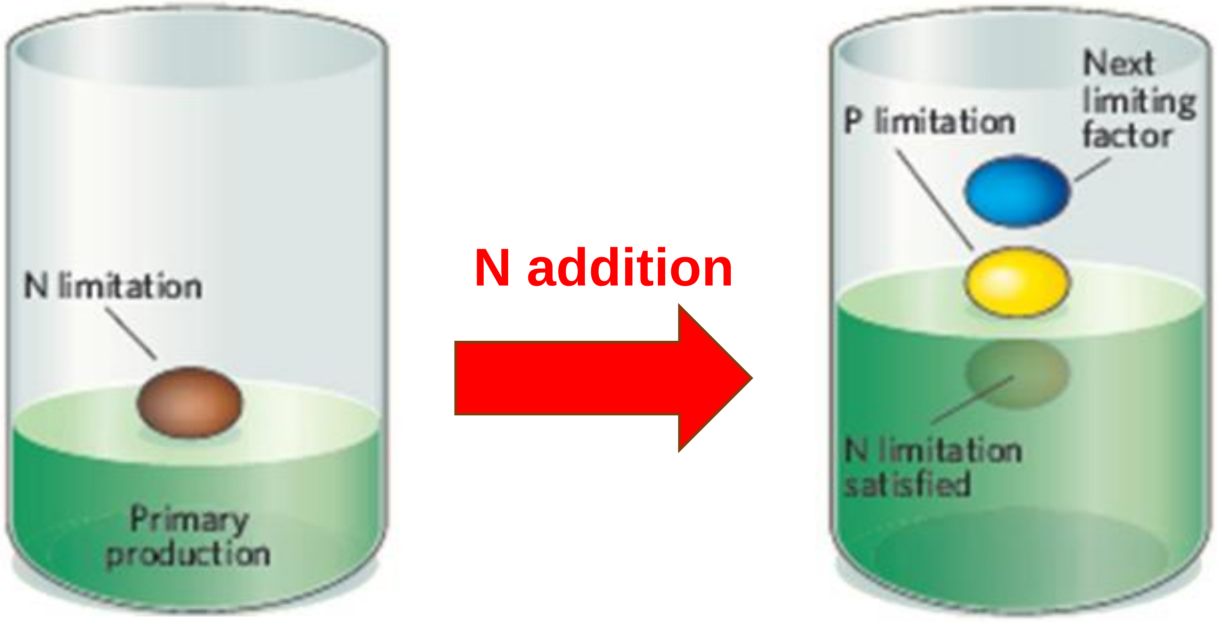
Why worrying about plant nutrition?
The world is simple:
“Plant growth is driven by the resource in lowest availability”
[taking into account the stoichiometry of plants need]

⇔ Liebig’s law of the minimum



Justus Freiherr von Liebig (1803-1873)

Source: Wikimedia



Davidson & Howarth (2007, Nature, 449, 1000-1001)

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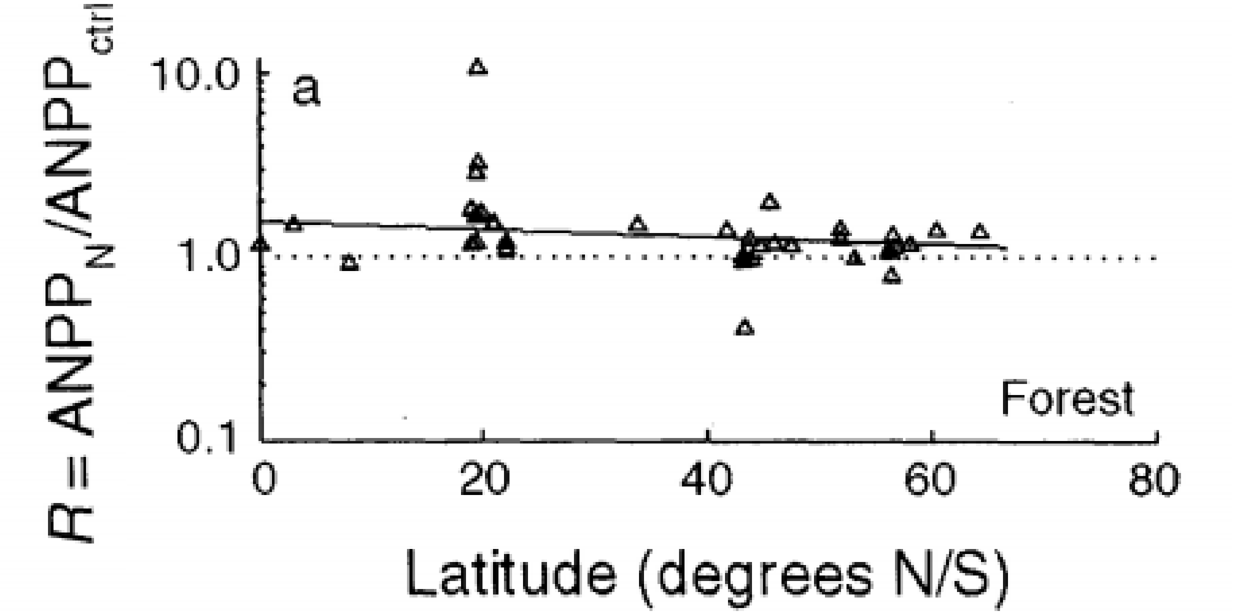
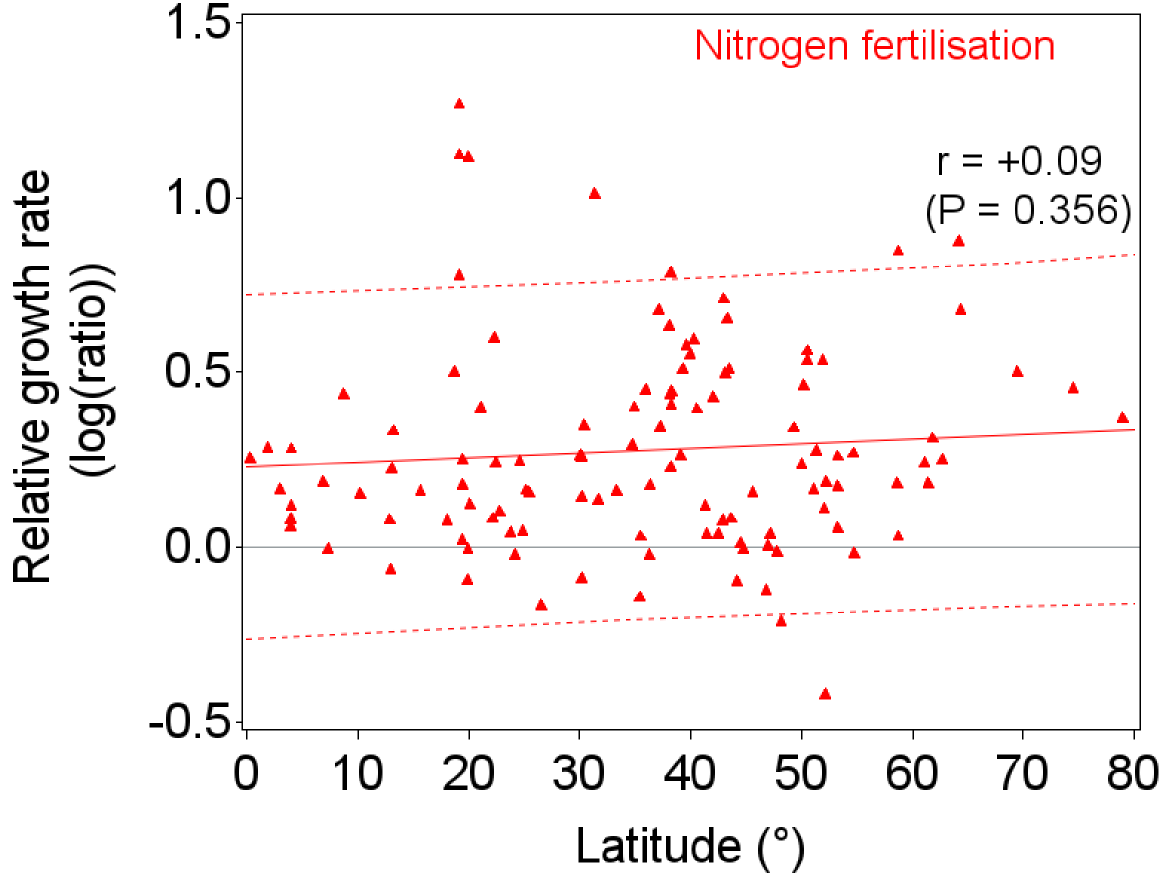
Of course, reality is more complicated: Plant's response to N-addition is widespread, and not particularly prominent at high latitudes

Elser et al. (2007, Ecology Letters, 10, 1135-1142)



LeBauer & Treseder (2008, Ecology, 89, 371-379)



Augusto et al. (2017, Global Change Biology, 23, 3808-3824)

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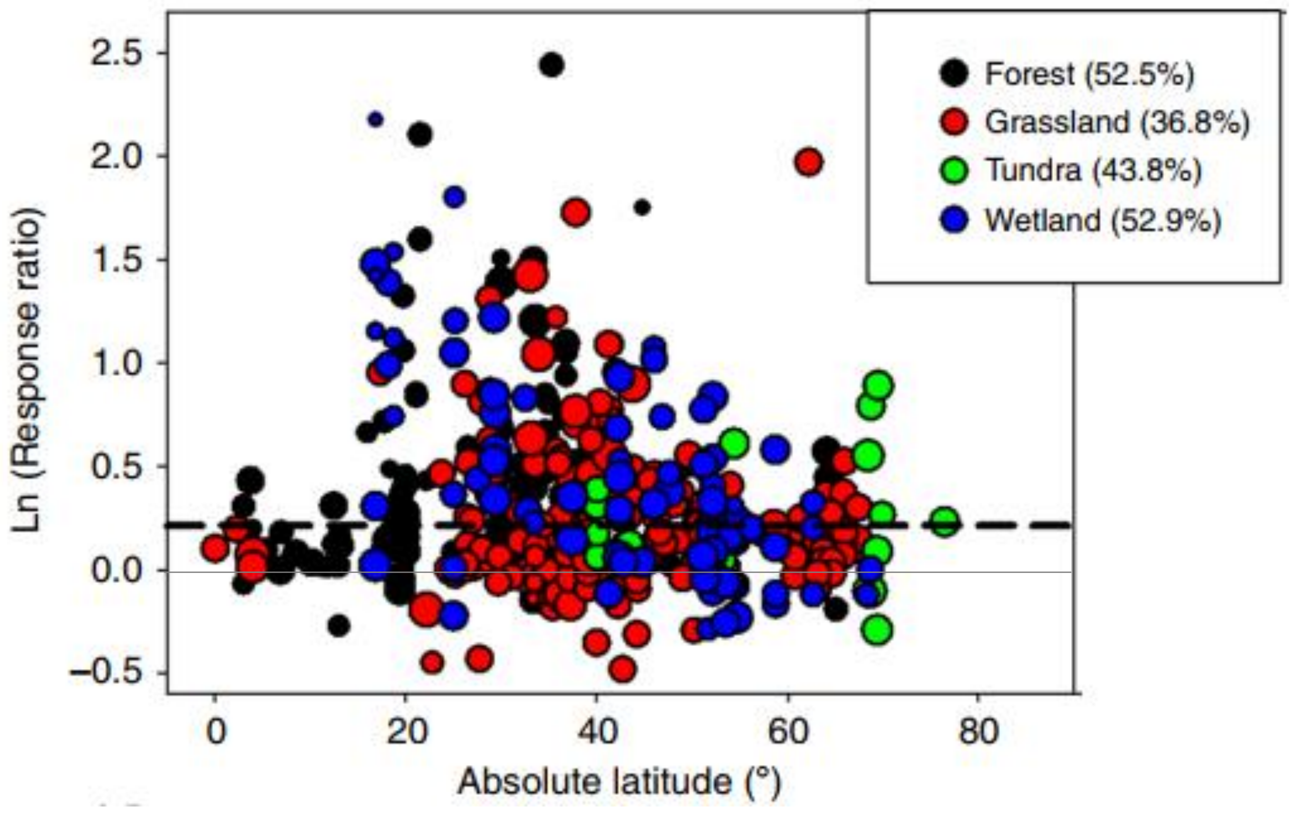
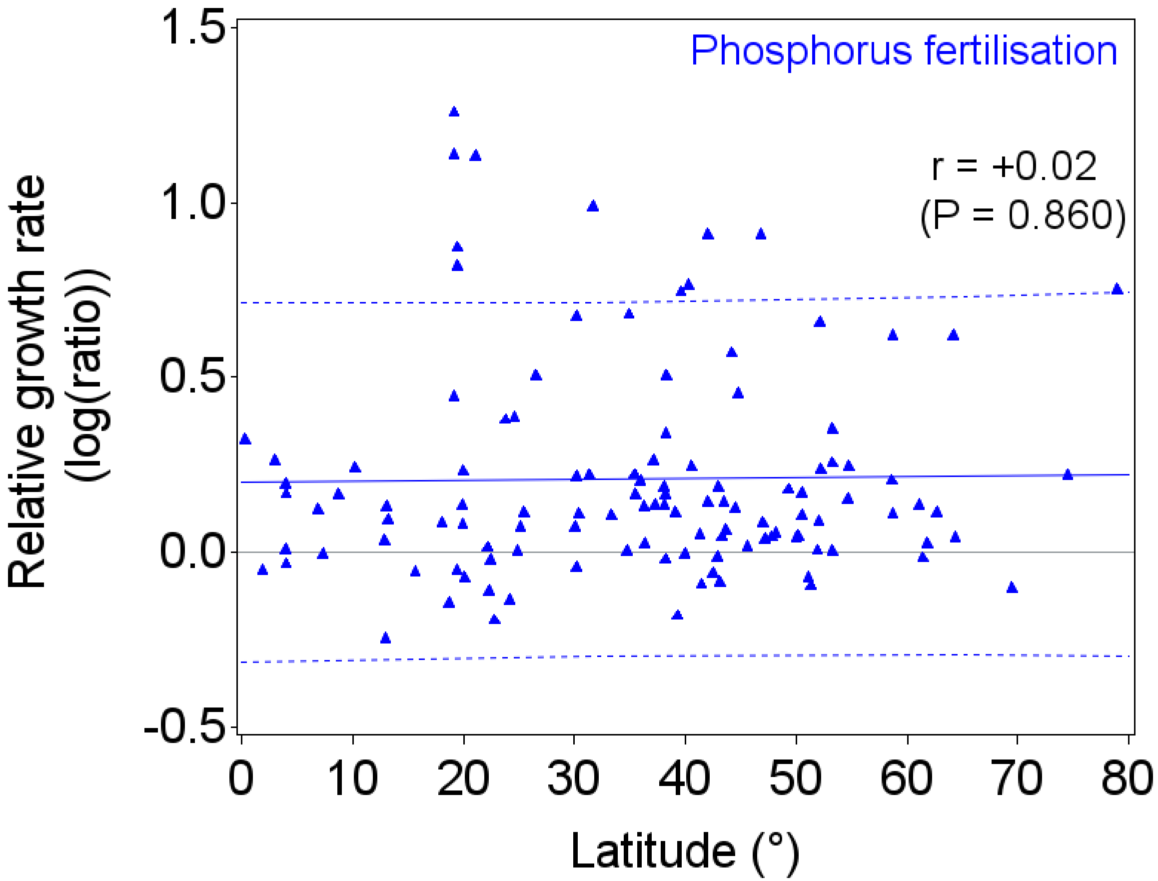
The same applies to phosphorus: Plant's response to P-addition is widespread, and not particularly prominent at low latitudes

Elser et al. (2007, Ecology Letters, 10, 1135-1142)



Hou et al. (2020, Nature Communications, 11, 637, 1-9)



Augusto et al. (2017, Global Change Biology, 23, 3808-3824)

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Not only nitrogen or phosphorus are limiting

- Potassium
  (Jordan, 1985; Tripler et al. 2006; Lloyd et al., 2015; Sardans & Penuelas, 2015; Yavitt et al., 2011)
- Calcium
  (Vitousek & Sanford, 1986; Naples & Fisk, 2010; Baribault, Kobe, & Finley, 2012)
- …
- Micronutrients *(Fay et al., 2015; White et al., 2012)*

nature plants LETTERS
PUBLISHED: 6 JULY 2015 | ARTICLE NUMBER: 15080 | DOI: 10.1038/NPLANTS.2015.80

Grassland productivity limited by multiple nutrients

Philip A. Fay *et al.**

Nutrient limitations are more synergetic than sequential:

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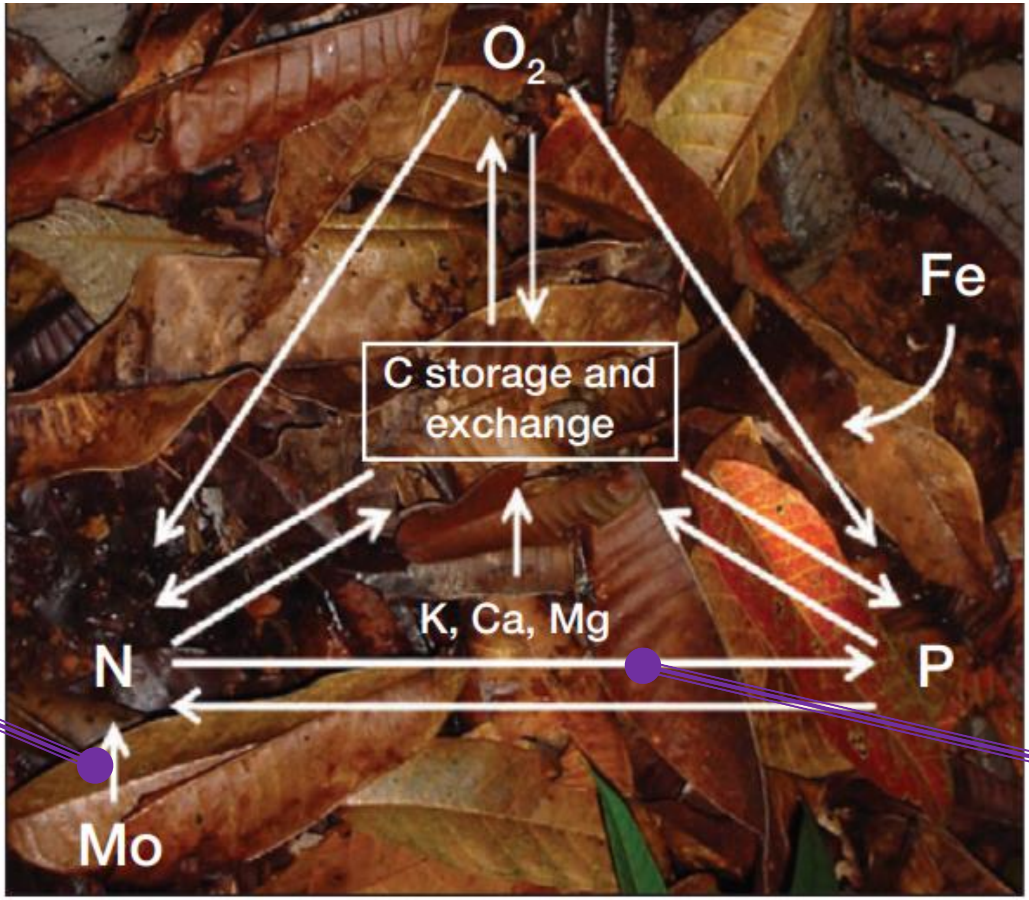


Control of N biological fixation

Production of phosphatases

COUPLED BIOGEOCHEMICAL CYCLES

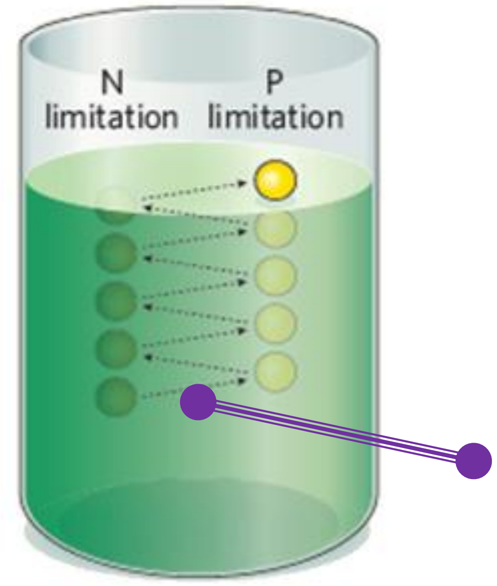
Multi-element regulation of the tropical forest carbon cycle

Front Ecol Environ 2011; 9(1): 9–17,

Alan R Townsend[1*], Cory C Cleveland[2], Benjamin Z Houlton[3], Caroline B Alden[4], and James WC White[5]

Many ecosystems may tend to a dynamic N-P colimitation:

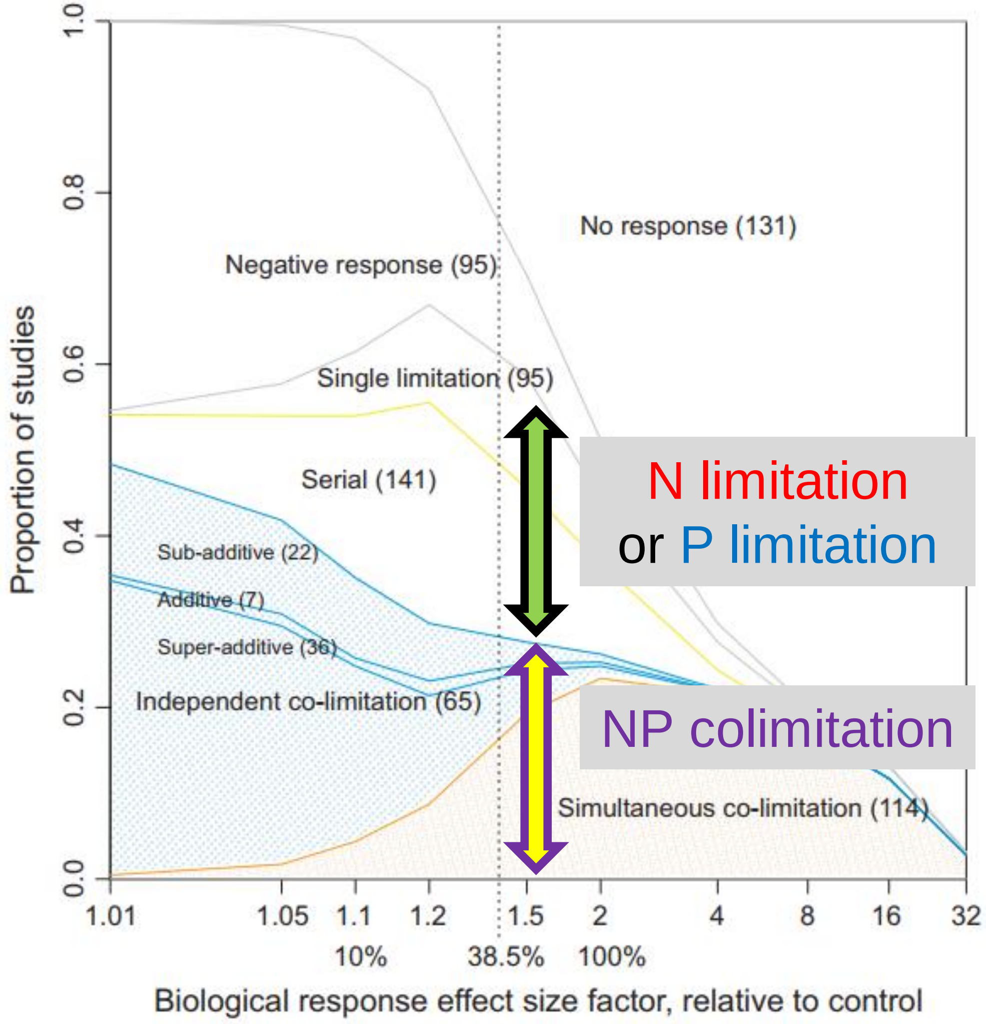
*Adapted from
Davidson & Howarth (2007, Nature, 449, 1000-1001)*



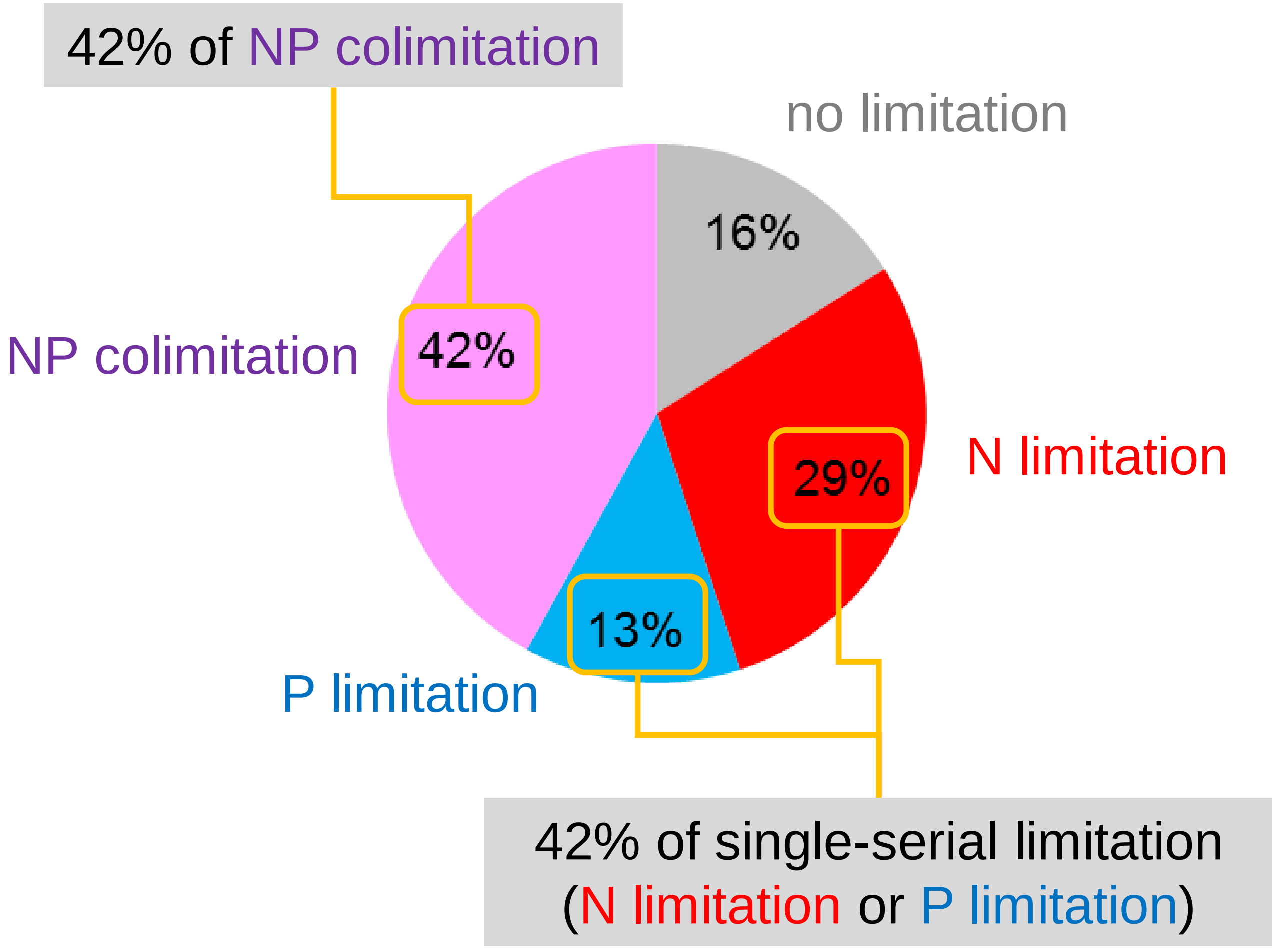
- Selective mining activity
(extra enzymes, organic acids, ligands, …)
- Biological nitrogen fixation
- Plasticity of plant composition
…

Bloom et al. (1986, ARES, 16, 363-392)

At the global scale, single-serial limitation (N limitation or P limitation) co-dominates with NP colimitation



Harpole et al. (2011, Ecology Letters, 14, 852–862)



Augusto et al. (2017, Global Change Biology, 23, 3808-3824)

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First set of conclusions in a nutshell:

- Nutrient limitations are widespread
- Both single-nutrient limitation, NP colimitation and multiple nutrient regulation exist

So what?

How to assess ecosystem nutrition?

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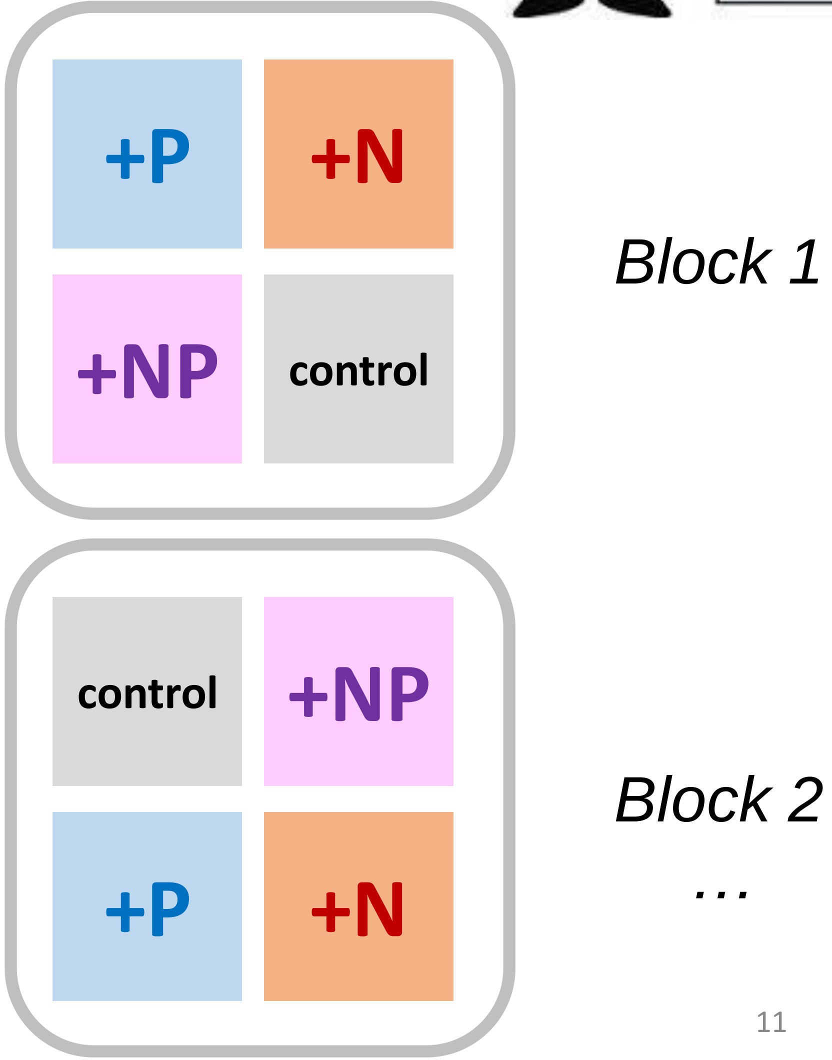
Add nutrients and assess the consequences (i.e. fertilisation experiments)



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Fertilising forests: not a trivial method

- ✓ Enables to control the factors
- ✓ Fairly straight forward to interpret

but

Trial setup

- ± Occupies large areas
- ± Difficult to install in heterogeneous areas (mountains, high biodiversity, …)

Response

- ± Dose effect (Hou et al., 2021, Ecology Letters)
- ± Effect may vary over time (Fay *et al.*, 2015, Nature Plants)
- ✗ May depend on plant age and on plant species

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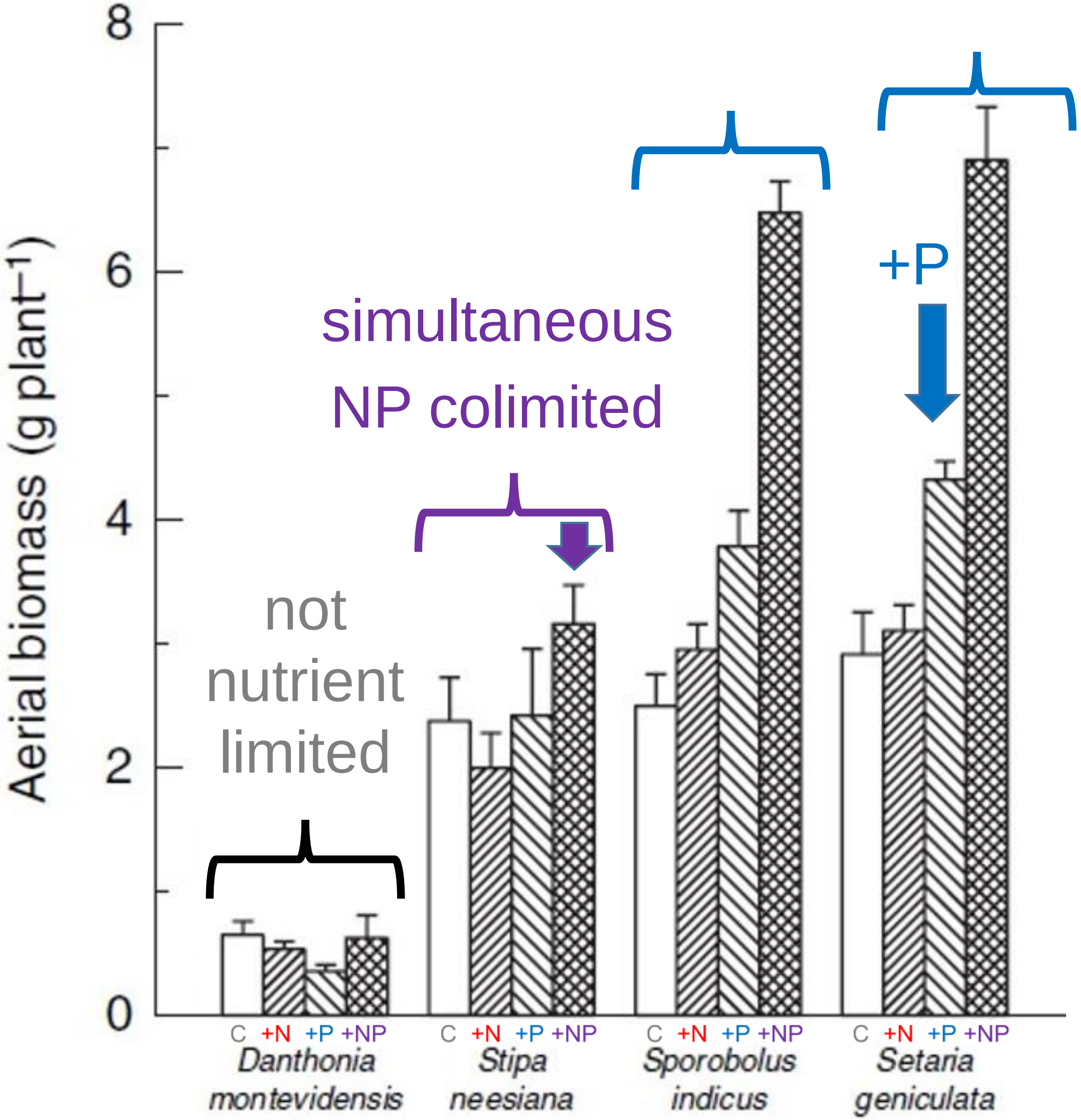
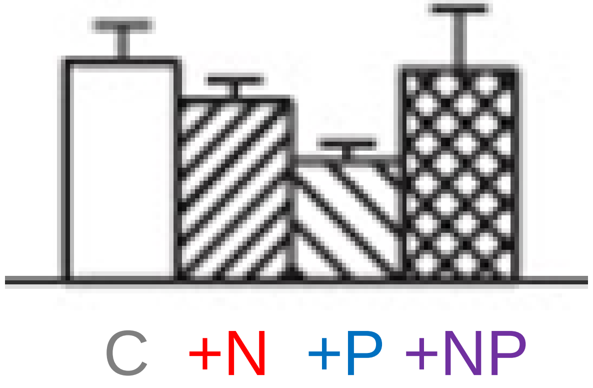
May depend on plant species

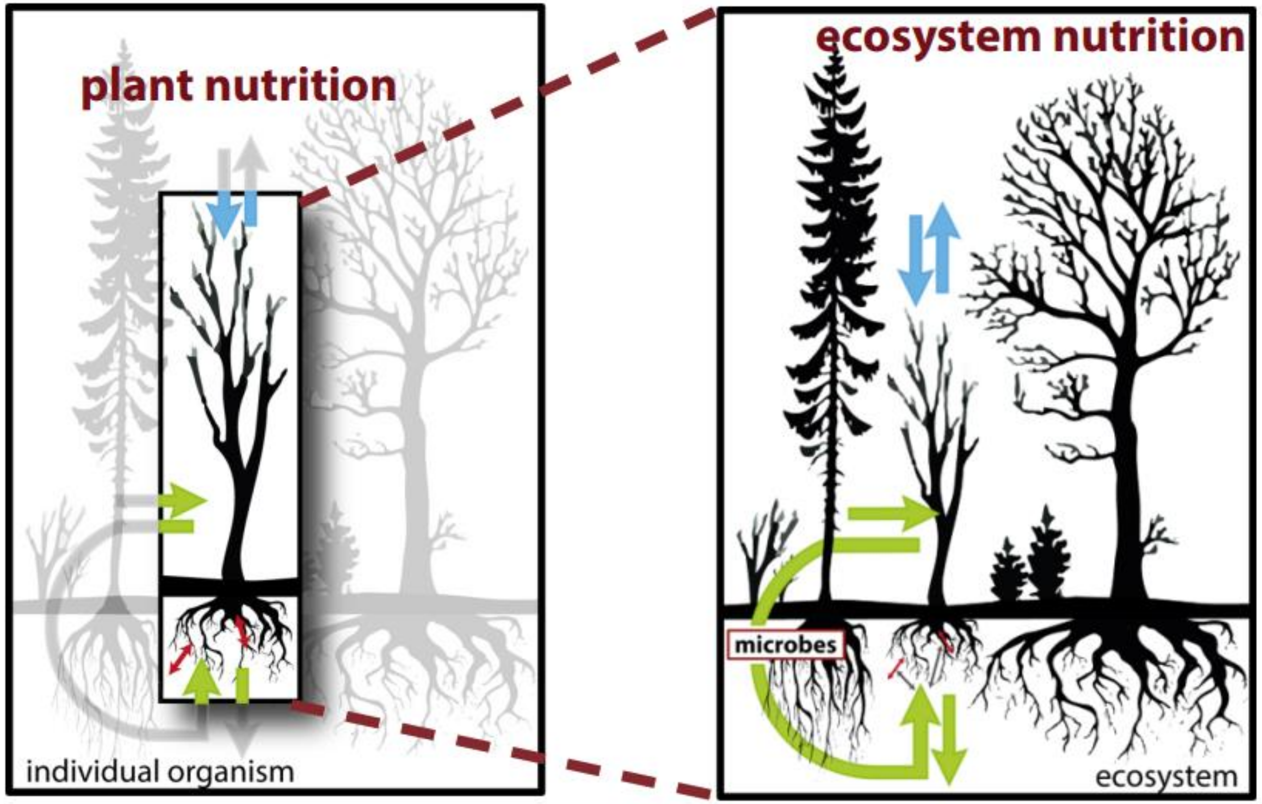


serial limitations (P, then N)



Rubio et al. (2010, Grass and Forage Science, 65, 102-109)

Plant nutrition ≠ Ecosystem nutrition



(SPP 1685)

Pervasive phosphorus limitation of tree species but not communities in tropical forests

Benjamin L. Turner[1], Tania Brenes-Arguedas[1] & Richard Condit[1]

Nature, 2018, 555, 367-370

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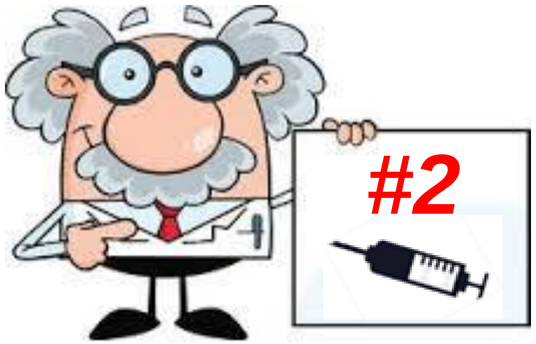
Assess the nutrient composition of plant foliage



https://cdnsciencepub.com

Sampling of green foliage

Chemical analyses

Compare with reference values

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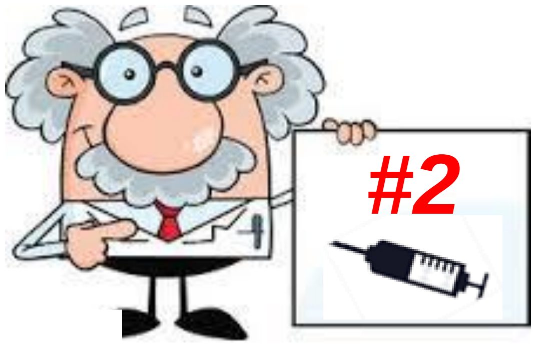

AUGUSTO LAURENT Né le 11/02/1972
Dossier n° **1802270444**
Prélevé le 27/02/18 à 07:43:04
Enregistré le 27/02/18 à 07:39:45
Édité le 27/02/18 à 17:05:50

HÉMATOLOGIE

Sang total

Chemical analyses — Reference values

Measured values — *Range of "normal" values*

NUMÉRATION GLOBULAIRE

Leucocytes *Impédance électrique*	**4,2**	*G/L*	*VR 4,0 - 11,0*
Hématies *Impédance électrique*	**4,58**	*T/L*	*VR 4,6 - 6,2*
Hémoglobine *Photométrie*	**13,7**	*g/dl*	*VR 13,0 - 18,0*
Hématocrite	**41,1**	*%*	*VR 37,0-50,0*
V.G.M.	**89,8**	*fl*	*VR 79,0- 97,0*
T.C.M.H.	**30,0**	*pg*	*VR 27,0-32,0*
C.C.M.H.	**33,4**	*g/dl*	*VR 31,0-36,0*
I.D.R.	**14,3**	*%*	*VR 12,3-17,0*

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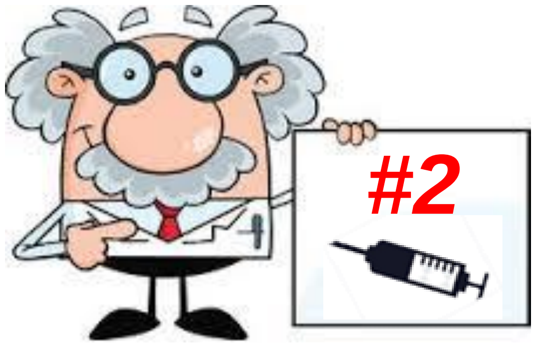
Analysing foliage: not a trivial method



- ✔ Fairly easy and cost-effective method
- ✔ Straight forward to interpret

but

Constraints

- ± Only during the vegetative period
- ± Composition varies over time
- ± Composition varies over tree life
- ✖ Reliable reference values only for common species

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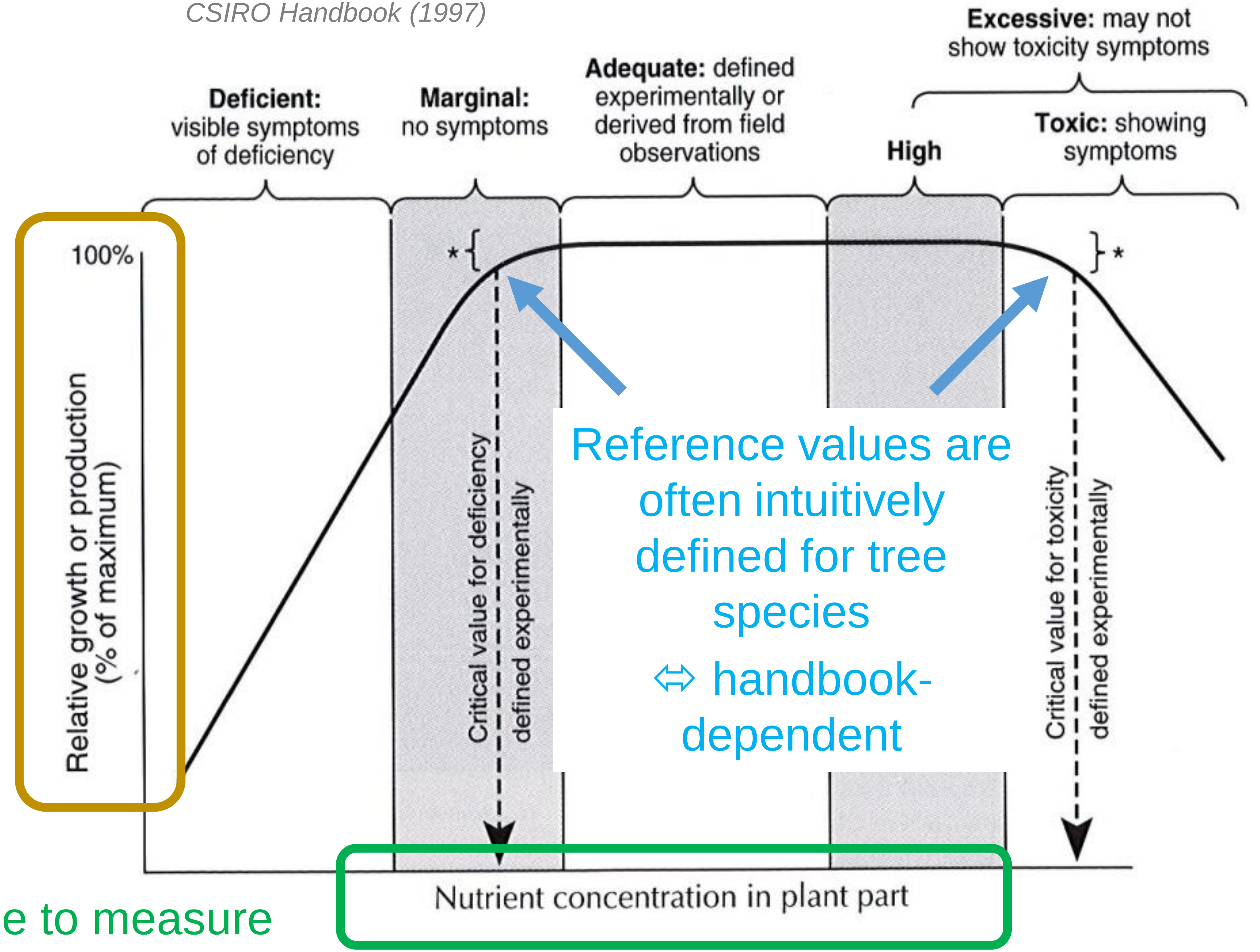
CSIRO Handbook (1997)

Very difficult to measure for mature trees growing *in natura*



Very simple to measure

Defining reliable reference values is possible for intensively studied species (meaning a lot of data). For instance Norway spruce, Scots pine, European Beech…

ORIGINAL PAPER

Comparison of new foliar nutrient thresholds derived from van den Burg's literature compilation with established central European references

Karl Heinz Mellert · Axel Göttlein

Eur. J. For. Res., 2018, 555, 367-370

Things are different for other tree species…

van den Burg J (1990) Foliar analysis for determination of tree nutrient status—A compilation of literature data; 2. Literature 1985–1989. ,,de Dorschkamp“ Institute for Forestry and Urban Ecology, Wageningen, Niederlande

> 600 pages of hand-written tables for thousands of values!

4. Visual deficiency symptoms:
   a. observed
   b. threshhold value or threshold range

6. Intermediate (adequate, normal, sufficiency)

7. Optimum range

Pinus pinaster

1	2	3	4 a	4 b	5	6	7	8	9 a	9 b	10
Pinus pinaster Ait. (syn. Pinus maritima Mill.)	N	seedlings in pot trial	0.75–0.90	ca 1.0	1.1–1.3	1.3–1.5	1.5–1.8				Nakos (1980)
		" " " "	0.75–0.90		1.1	1.52	1.52 – 2.0				Nakos (1980)
		young plantations				1.22–1.37					Guinaudeau et al. (1963)
		young stands		0.78	1.02	1.15					Alexandris (1976)
		" "		0.4–0.9		0.9–1.4					...ay et al. (1968)
		—				1.2–1.5					...onneau (1973)*
		—			<0.9	0.9–1.2	>1.2				Reboisement (1971)
		adult stands			0.84–0.94		>1.2				Bonneau et al. (1972)
	P	seedlings in pot trial	0.09–0.10			0.10–0.26					Nakos (1980)
		" " " "	0.05–0.09	0.10		0.10–0.14					Nakos (1980)
		young plantations			0.07–0.09	0.12–0.14					Guinaudeau et al. (1963)
		young stands				0.09					Alexandris (1976)
		" "		0.05		0.11					...s et al. (1968)
		—				0.10–0.11					...onneau (1973)
		—			<0.09	0.09–0.13	>0.13				Reboisement (1971)
		adult stands			0.06–0.07	0.09–0.10					Bonneau et al. (1972)

≈ 0.9–1.5 %-N

≈ 0.09–0.13 %-P

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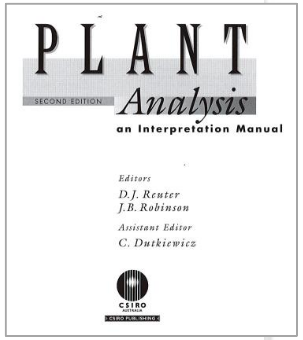


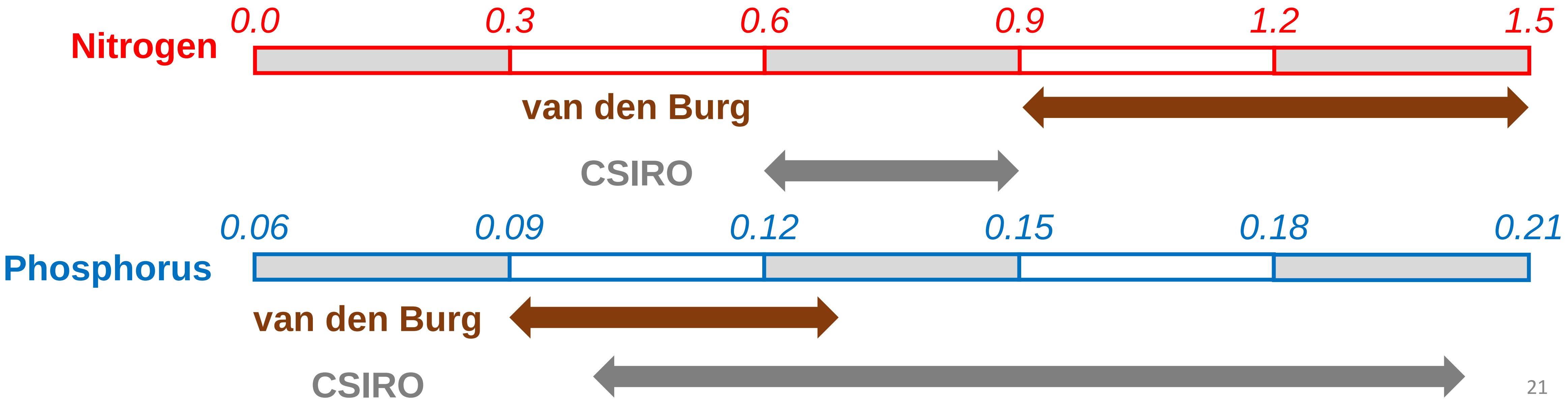
CSIRO Handbook (1997)

PINUS PINASTER (Maritime Pine)

Nutrient	Growth Stage	Plant part	How established	Concentration range					Country	Ref
				Deficient	Marginal	Adequate	High	Toxic		
N(%)	Mat	YMF	F	0.39-0.6		0.6-0.9				20 83 112
P(%)	Mat	YMF	F	<0.054-0.56>	0.06-0.08	<0.10-0.20>				20 83 112 138

0.6–0.9 %-N

0.10–0.20 %-P



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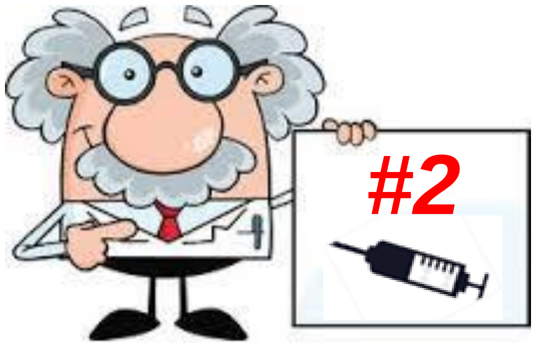
Analysing foliage: not a trivial method



- OK for comparing different trees of the same species
- In any case, interpret with caution!

Other methods related to foliage:

- - Nutrient ratio (Güsewell, 2004, New phytol., 164, 243-266)
- but N/P = 12 = 12/1 = 24/2 = 6/0.5
- - Nutrient resorption (Achat *et al.*, 2018, Ecol. Monog., 88, 408-428)
- but not so accurate to detect small differences

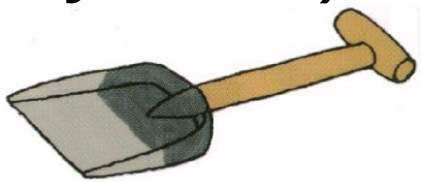
<u>Second set of conclusions</u> in a nutshell:

Cons for using plant metrics in nutrition studies:

- Plant response is highly species-dependent
- Plant homeostasis makes data often tricky to interpret

Pros:

- “Real” response of the vegetation
- Integrates spatial variability (soil exploration by roots)



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Make holes everywhere in the soil

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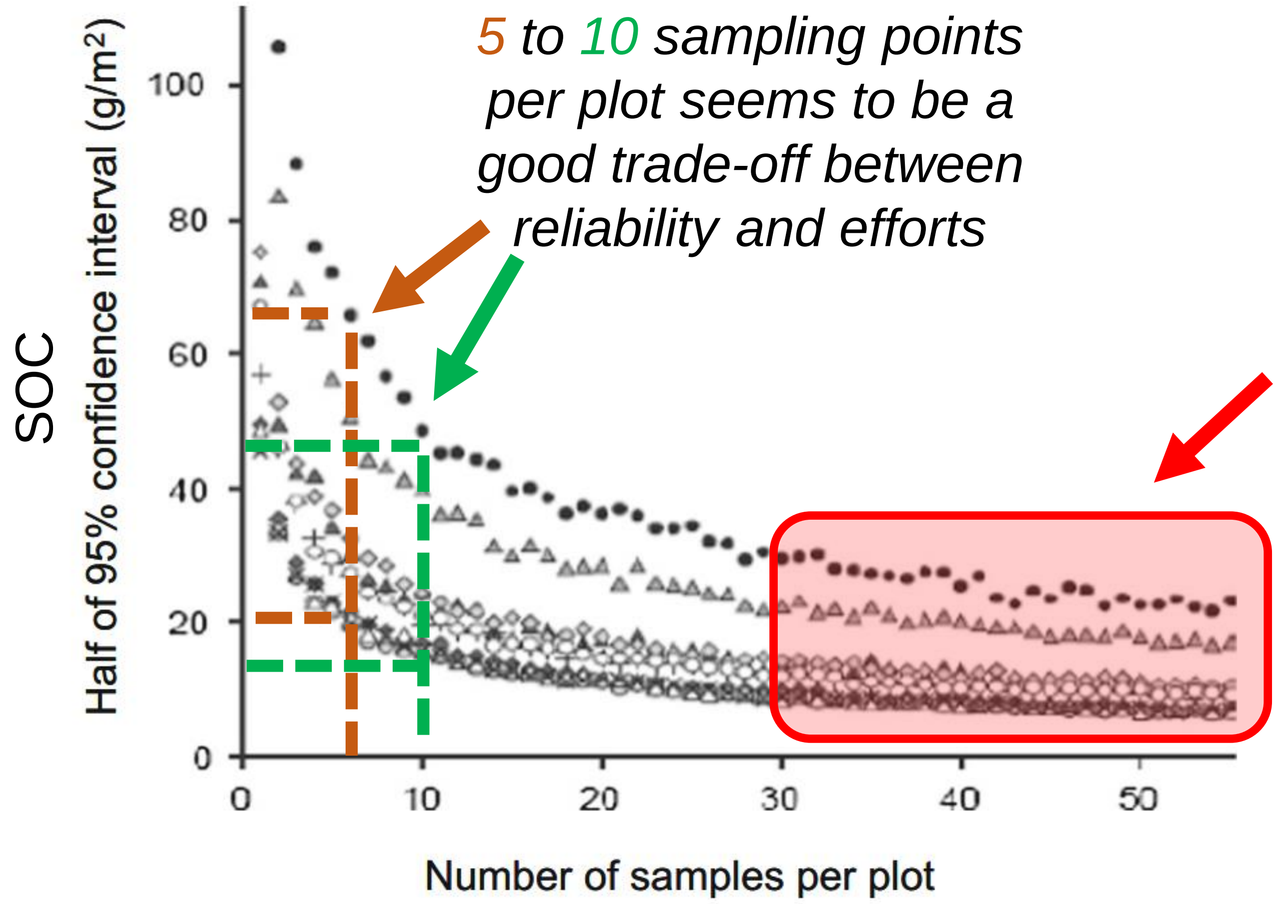
Why “everywhere”?

Soil properties are highly variable in space (horizontal variation)



5 to 10 sampling points per plot seems to be a good trade-off between reliability and efforts

> 30 sampling points per plot should be done only for a very few studied plots

If colleagues require such a sampling design for many plots, require them to come with you to dig.

Vanguelova et al. (2016, Environ Monit Assess, 188:630)

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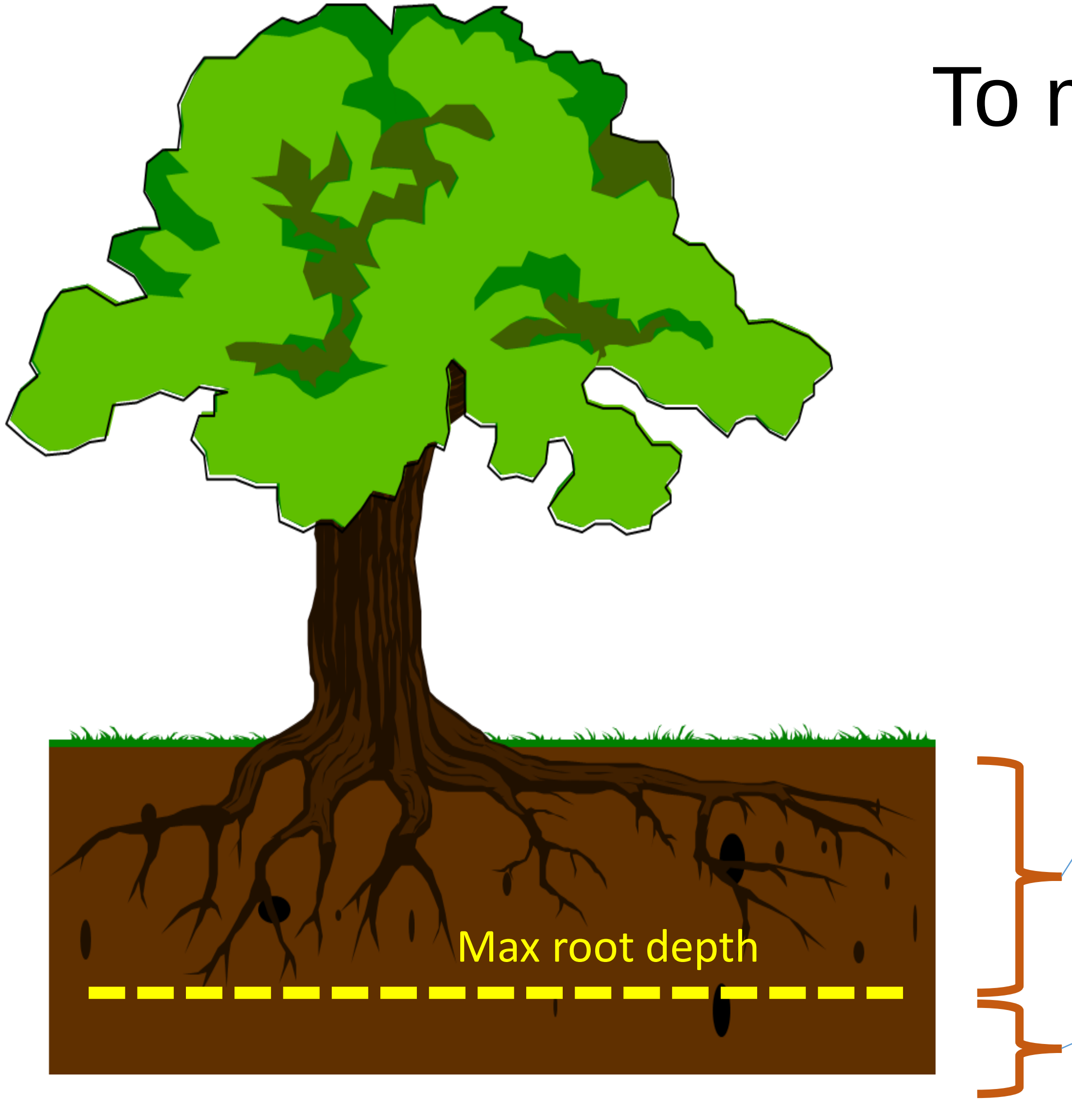
How deep?
To max root depth?



Nutrient chemically available
+ close to tree roots
= bioavailable

Nutrient chemically available
but beyond roots
= unavailable

How deep?
To max root depth?

Cons for digging to max root depth:

- Max root depth can be > 10 meters
- Rocky soils

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How deep?

Table 4 R^2 of logarithmic regressions between phosphorus content in aboveground biomass and stock of citric acid extractable phosphorus in the soil

Foliage P content = *f* (soil P content)

Soil depth (cm)	Needle year 1	Needle year 2	Needle year 3	Needle year 4	Needle total	Twig	Branch	Bark	Stem wood
Humus (H)	0.01 n.s.	0.03 n.s.	0.01 n.s.	0.03 n.s.	0.00 n.s.	0.02 n.s.	0.11 n.s.	0.03 n.s.	0.05 n.s.
H+0–5	0.53**	0.32*	0.29*	0.27*	0.02 n.s.	0.15 n.s.	0.03 n.s.	0.14 n.s.	0.02 n.s.
H+0–10	0.65***	0.39*	0.47**	0.39*	0.08 n.s.	0.24*	0.12 n.s.	0.31*	0.03 n.s.
H+0–20	0.65***	0.37*	0.50**	0.46**	0.26*	0.41**	0.21*	0.52**	0.01 n.s.
H+0–30	0.63***	0.36*	0.50**	0.48**	0.27*	0.44**	0.17 n.s.	0.57***	0.01 n.s.
H+0–40	0.64***	0.38*	0.53**	0.52**	0.27*	0.43**	0.14 n.s.	0.60***	0.01 n.s.
H+0–60	0.58**	0.39*	0.52**	0.53**	0.23*	0.38*	0.04 n.s.	0.61***	0.07 n.s.
H+0–80	0.49**	0.39*	0.52**	0.51**	0.15 n.s.	0.25 *	0.00 n.s.	0.52**	0.16 n.s.

The topsoil layer can be a good proxy of the whole soil profile

ORIGINAL PAPER

Importance of soil extractable phosphorus distribution for mature Norway spruce nutrition and productivity

Hadi Manghabati[1] · Wendelin Weis[2] · Axel Göttlein[1]   European Journal of Forest Research (2018) 137:631–642

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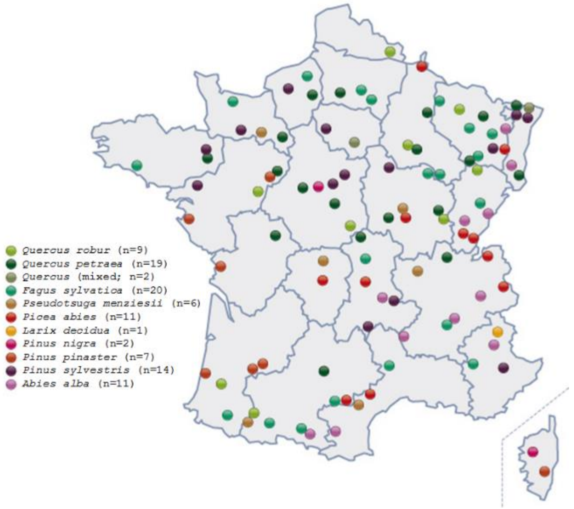

French network of forest long-term monitoring (RENECOFOR)

RENECOFOR

Achat et al. (2018, Ecol. Monog., 88, 408-428)

Table S1: Correlations between nutrient remobilization rates and nutrient stocks at different soil depths# (Spearman's correlation coefficients).

	N remobilization (%) vs. total N stock (Mg ha^{-1})	P remobilization (%) vs. Dyer P stock (kg ha^{-1})	K remobilization (%) vs. echangeable K stock (cmol ha^{-1})	Ca remobilization (%) vs. echangeable Ca stock (cmol ha^{-1})	Mg remobilization (%) vs. echangeable Mg stock (cmol ha^{-1})
All tree species					
0-20 cm	**-0.23**	**-0.36**	**-0.47**	-0.17	**-0.43**
0-40 cm	**-0.26**	**-0.27**	**-0.47**	-0.17	**-0.47**
0-80 cm	**-0.26**	-0.21	**-0.43**	-0.06	**-0.58**
0-100 cm	**-0.25**	**-0.22**	**-0.43**	-0.05	**-0.60**
N_{sites}	*101*††	*85*†	*101*††	*101*††	*101*††

For different nutrients

❌ Discontinuous soil profiles (e.g. planosols)

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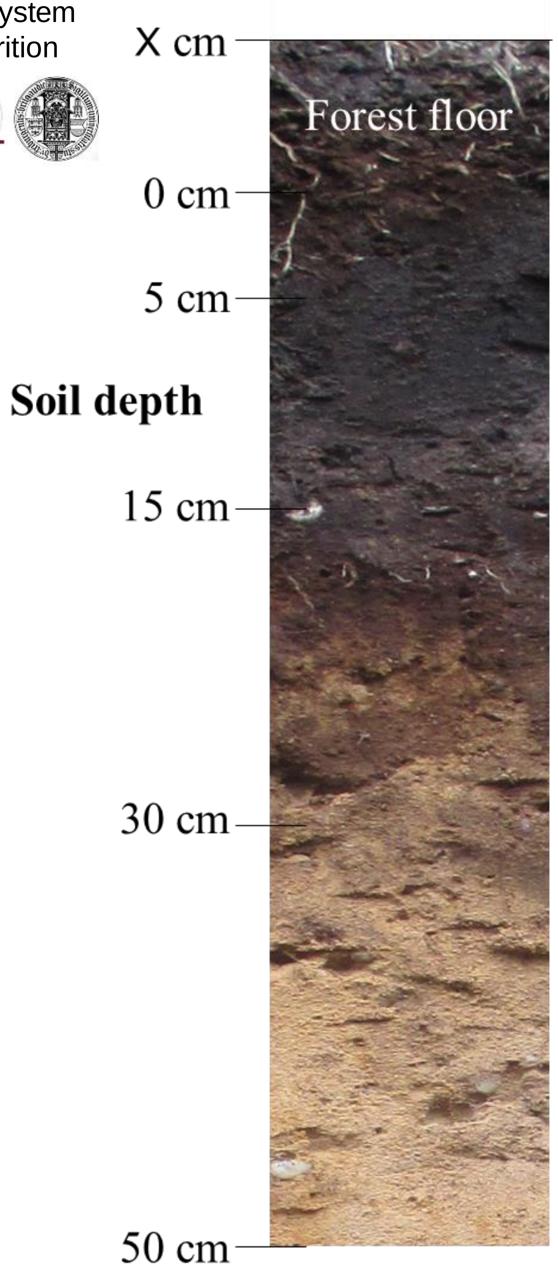
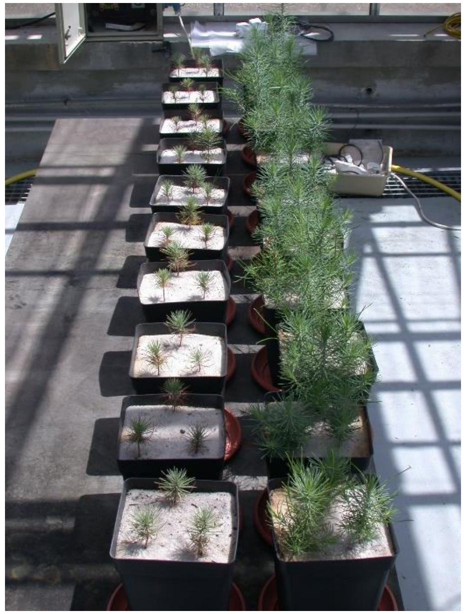
What about the forest floor?



- Preferably take it into account
  - ⇔ nutrient rich
- Above all in case of
  - → seedlings
  - → thick forest floor layer
  - → poor mineral soils
- Maybe not necessary for
  - → adult trees
  - → thin FF layer



Jonard et al. (2009, Ann. For. Res.)

Tree age = 44-187 yrs

Soil depth (cm)	Needle year 1
Humus (H)	0.01 n.s.
H+0–5	<u>0.53</u>**

For measuring what?

- Analysing microbes (C_{mic}, P_{mic}, N_{mic}) or extracellular enzyme activity (EEA) gives generally good information about the nutritional status at the beginning of the web food chain (low homeostasis capacity → more representative of nutrient availability)

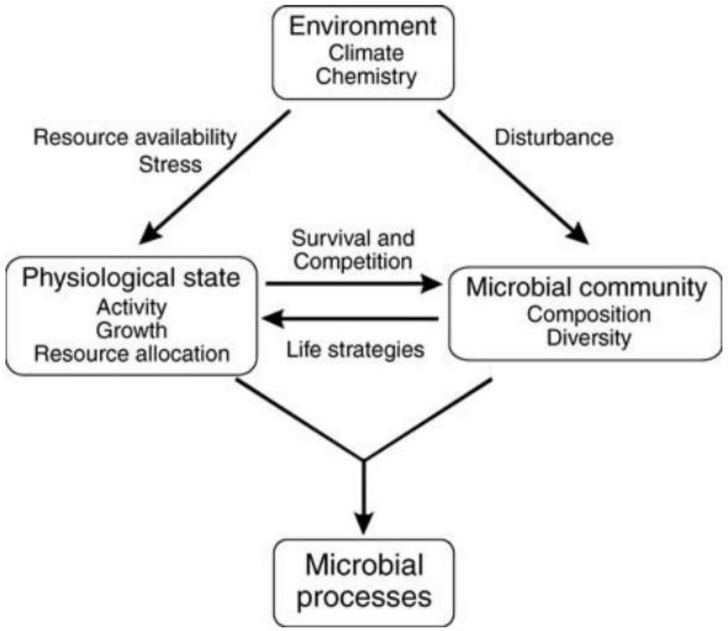


FIG. 1. Links among environmental drivers, microbial physiology, community composition, and ecosystem processes.

Ecology, 88(6), 2007, pp. 1386–1394

MICROBIAL STRESS-RESPONSE PHYSIOLOGY AND ITS IMPLICATIONS FOR ECOSYSTEM FUNCTION

JOSHUA SCHIMEL,[1,4] TERI C. BALSER,[2] AND MATTHEW WALLENSTEIN[3]

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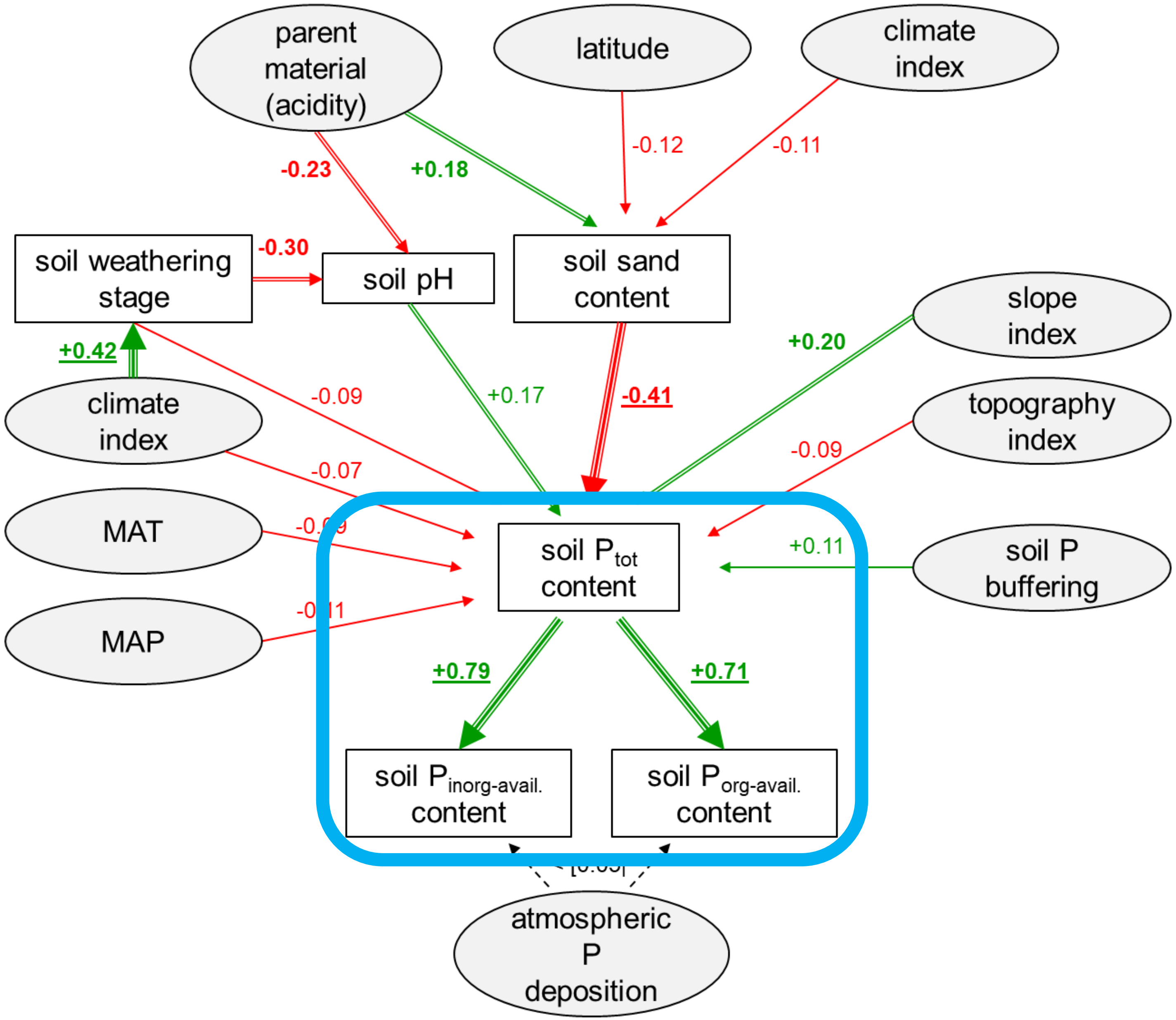
Soil nutrient content?

- There are usually good correlation values among different fractions of the same nutrient

- Total content could be a good proxy



Third set of conclusions in a nutshell:

Cons for digging soils in nutrition studies:

- Could be a tough task
- May need experience to define the best sampling design

Pros for digging:

- Clay is good for skin & fieldwork reinforces the team spirit
- Soil is crucial for understanding ecosystem nutrition

Final thoughts:

"*Ecosystem Nutrition*" (such as "*Soil Health*") seems easy to understand, but is in practice poorly defined

➔ Make clear what aspect of the ecosystem nutrition is to be studied (nutrient reservoir, plant growth…)

"*Ecosystem nutrition*" may be ≠ "Tree nutrition" ≠ "Microbe nutrition" ≠ "Soil nutrient content"

➔ Define the ecosystem compartment, or process, to be assessed

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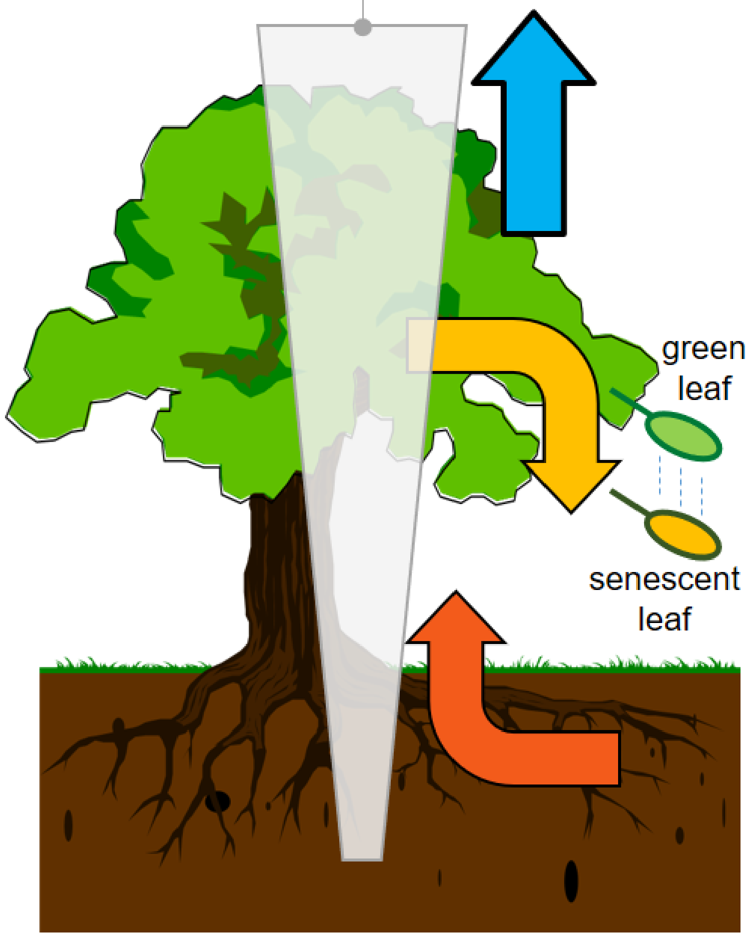
Final thoughts:

Integration level of the nutritive status of ecosystem & importance of homeostatic processes of regulation

If possible, assess all



Plant growth — *Actual nutrient limitation*

Leaf nutritive status — *Actual nutrient stress*

Soil supply — *Potential nutrient limitation*

Let's start discuss!

Looking for forest nutrition

More slides…

Forewords: sharing the same concepts

Nutrition:

“*Metabolism of nutrients in order to assimilate them for the growth, maintenance and functioning of the body*”

⬄ not only related to growth

⬄ nutrient-deficient plants may maintain high growth rate

Fertility:

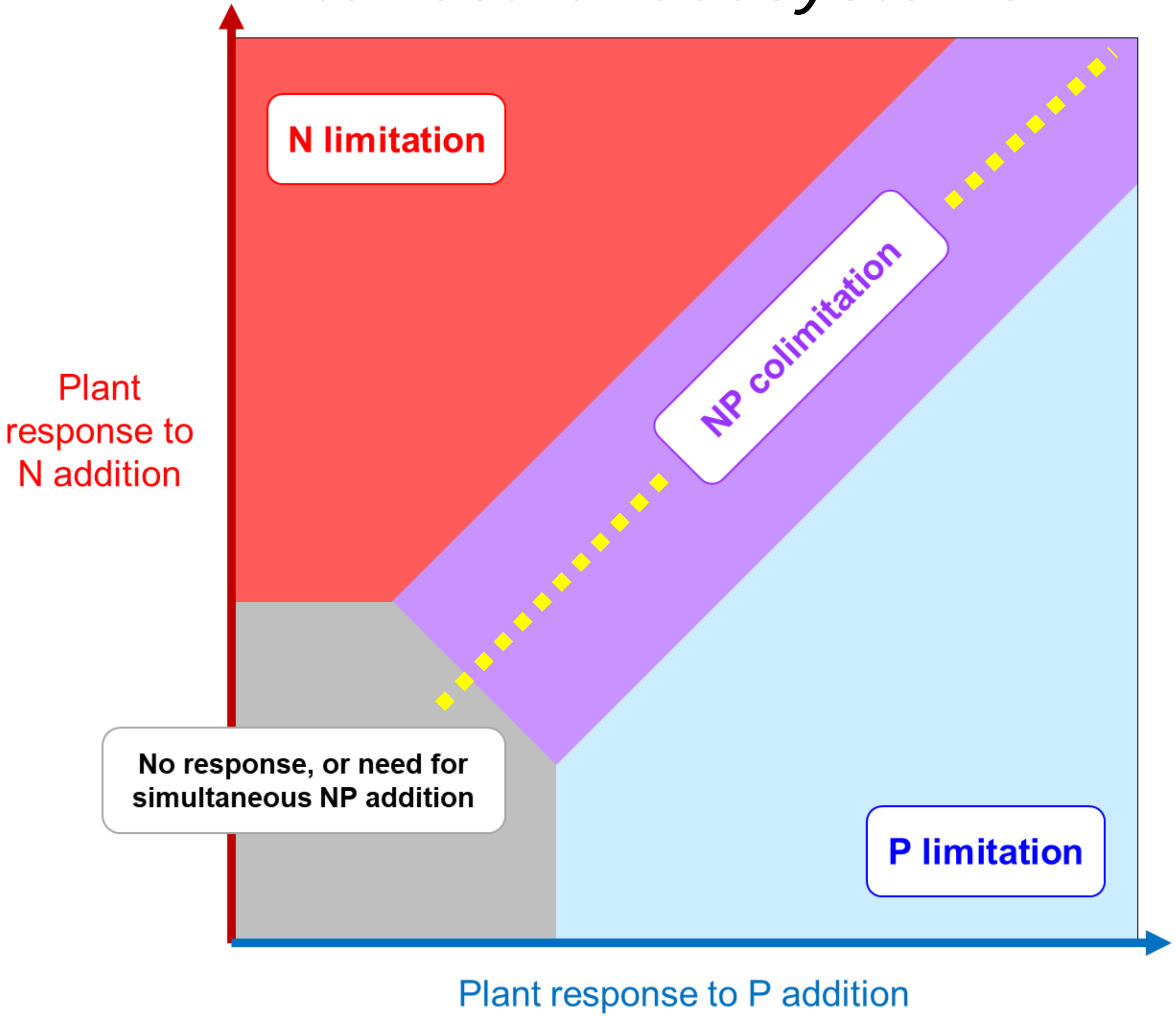
“*Related to the ability to produce in large quantities*”

⬄ fertile soils are not necessarily rich in nutrients

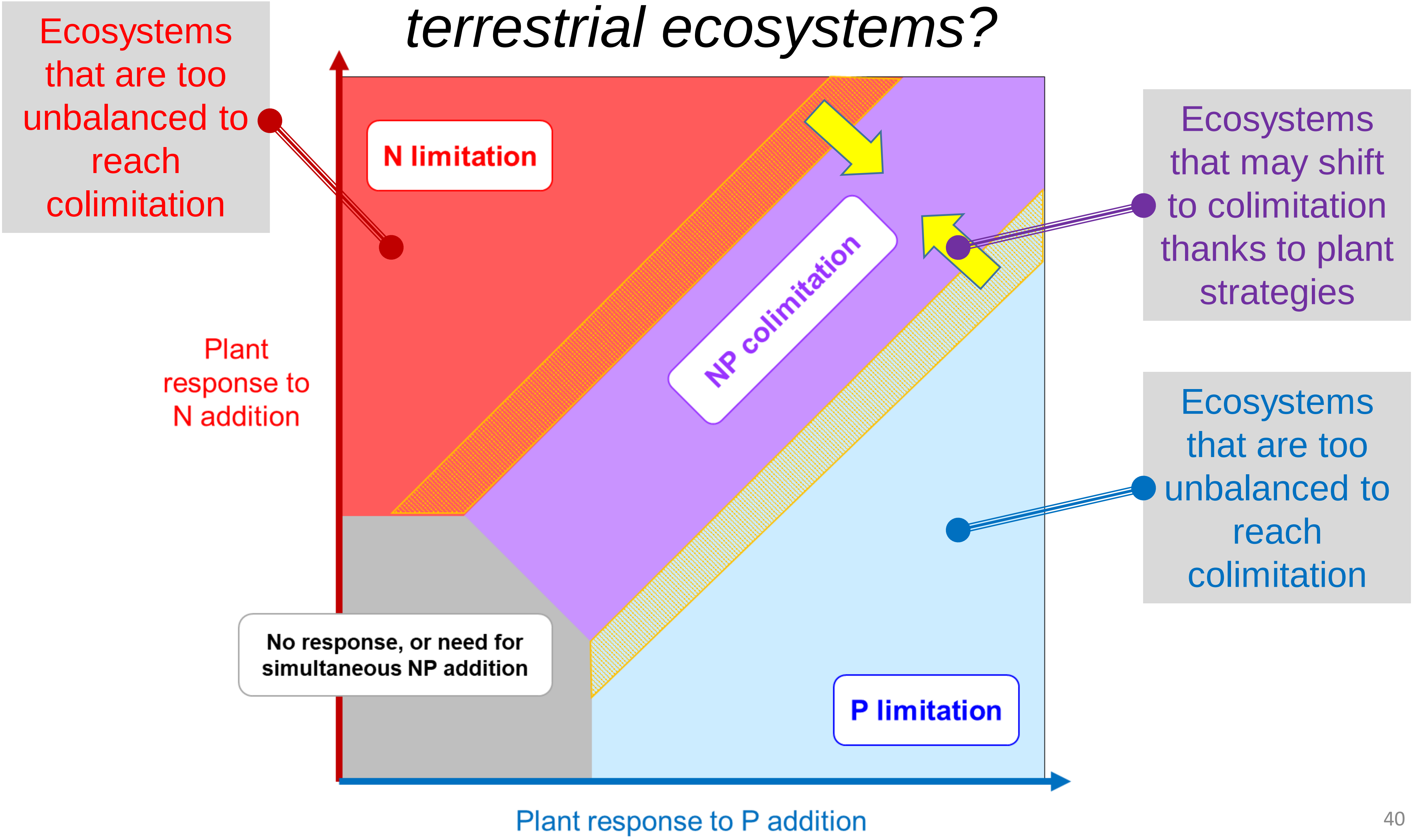
⬄ nutrient-poor soils can be relatively fertile

provided that plants are adapted to local conditions

Why NP colimitation does not dominate terrestrial ecosystems?



Why NP colimitation does not dominate terrestrial ecosystems?



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CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Ecology, 95(3), 2014, pp. 668–681

Assessing nutrient limitation in complex forested ecosystems: alternatives to large-scale fertilization experiments

Benjamin W. Sullivan,[1,4] Silvia Alvarez-Clare,[1] Sarah C. Castle,[1] Stephen Porder,[2] Sasha C. Reed,[3,5] Laura Schreeg,[2] Alan R. Townsend,[3] and Cory C. Cleveland[1]

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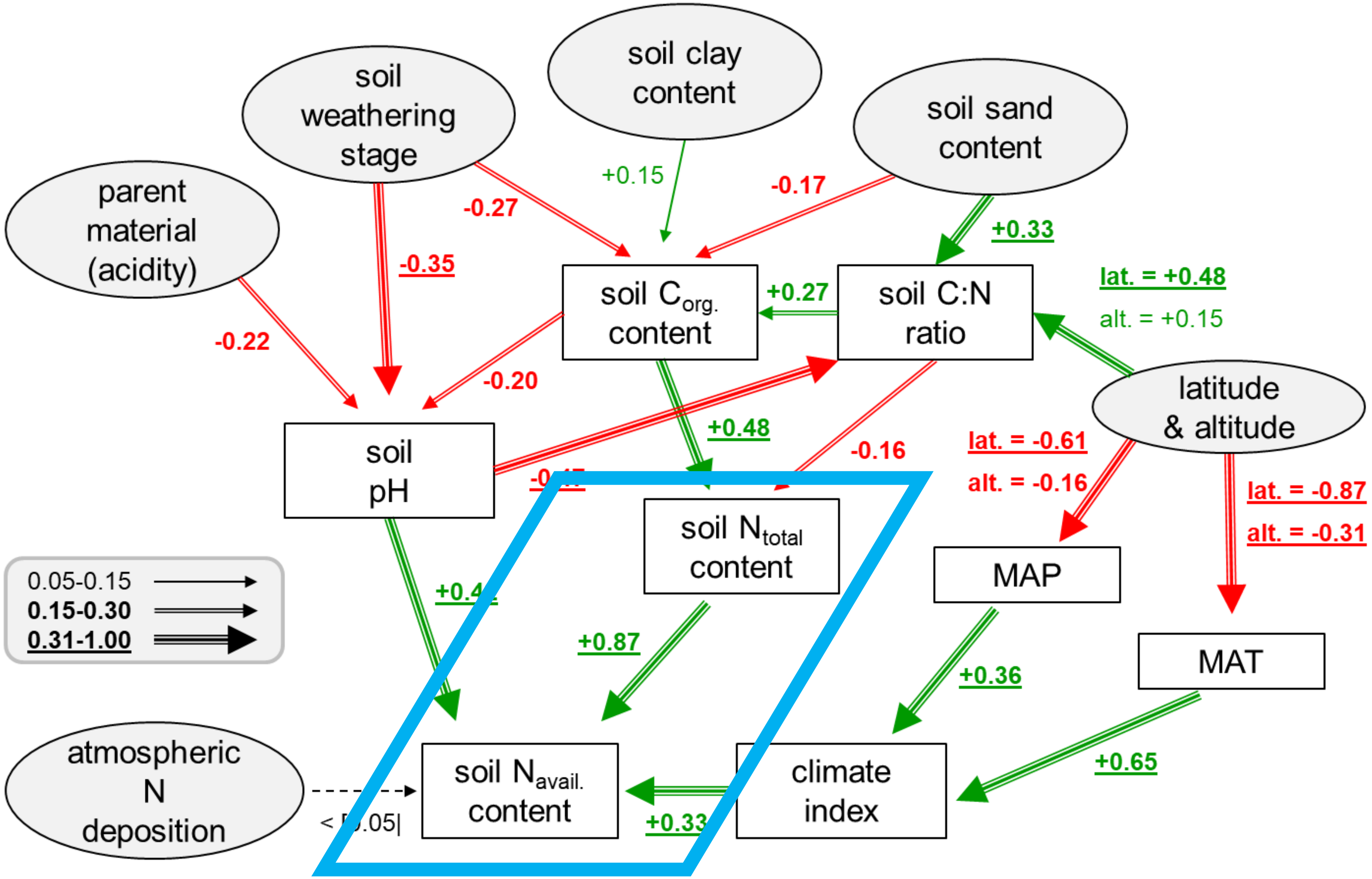
Soil nutrient content?

- There are hundreds of different methods to quantify nutrient pools in soils !!
- But, there are usually good correlation values among different fractions of the same nutrient



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RESEARCH ARTICLE

Functional Ecology
BRITISH ECOLOGICAL SOCIETY

Decoupling between growth rate and storage remobilization in broadleaf temperate tree species

Frida I. Piper

3. Radial growth was not related to seasonal minimum NSC or nutrient concentrations and pools in either the evergreens or deciduous angiosperms; thus, faster growth was not associated with greater remobilization of C or nutrient stores. Furthermore, larger trees grew faster than smaller ones, but did not have higher remobilization. Deciduous species had higher year-round whole-tree NSC and nutrient concentrations than evergreens; however, both groups had similar BRI and seasonal minimum concentrations and pools of NSCs and nutrients.

DFG

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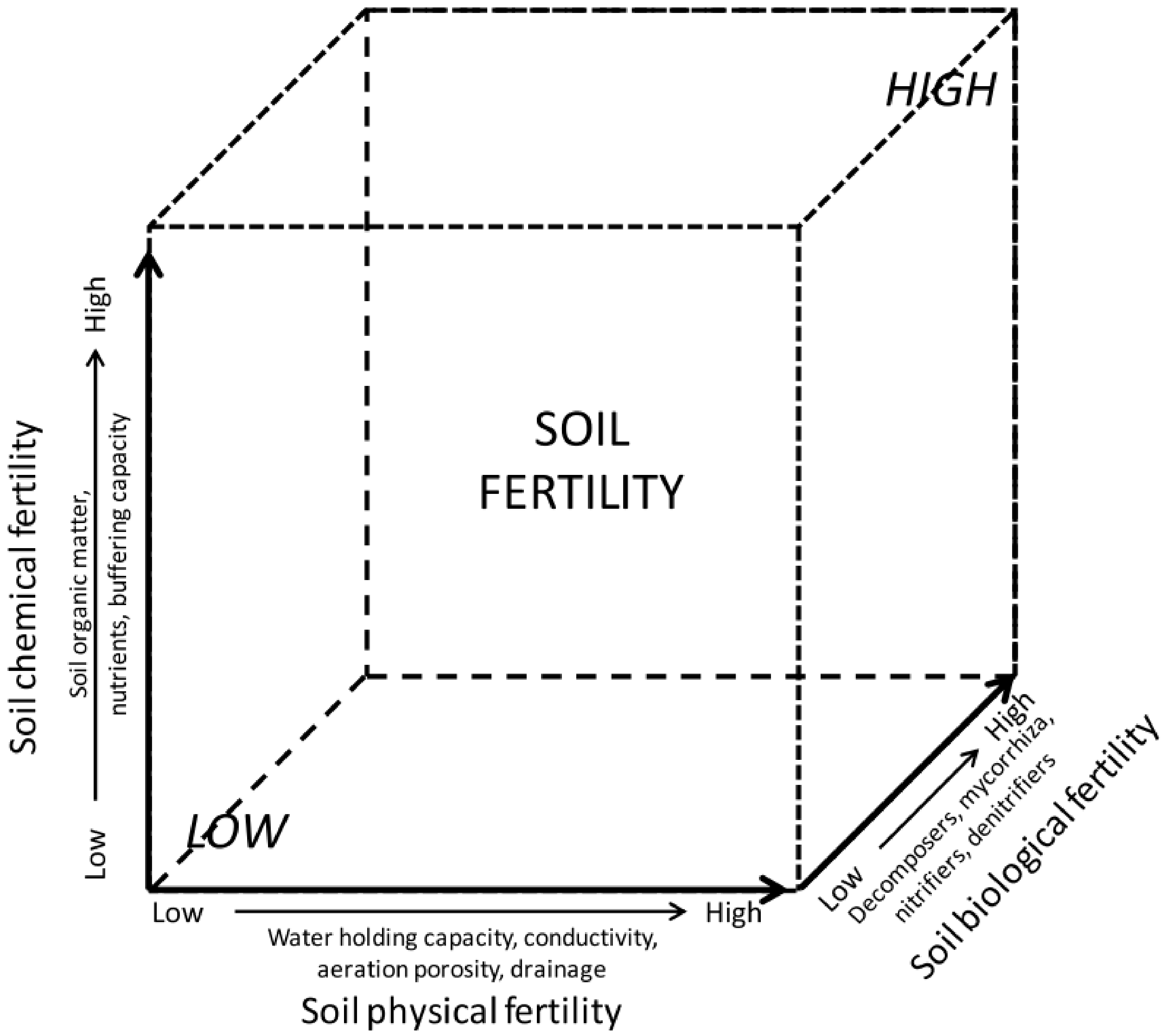

Fig. 1. Schematic overview of soil fertility, defined by biological, chemical and physical properties.

Hansson et al. (2020, For. Ecol. Manage., 461, 117843)

SPP 1685:
Ecosystem
Nutrition

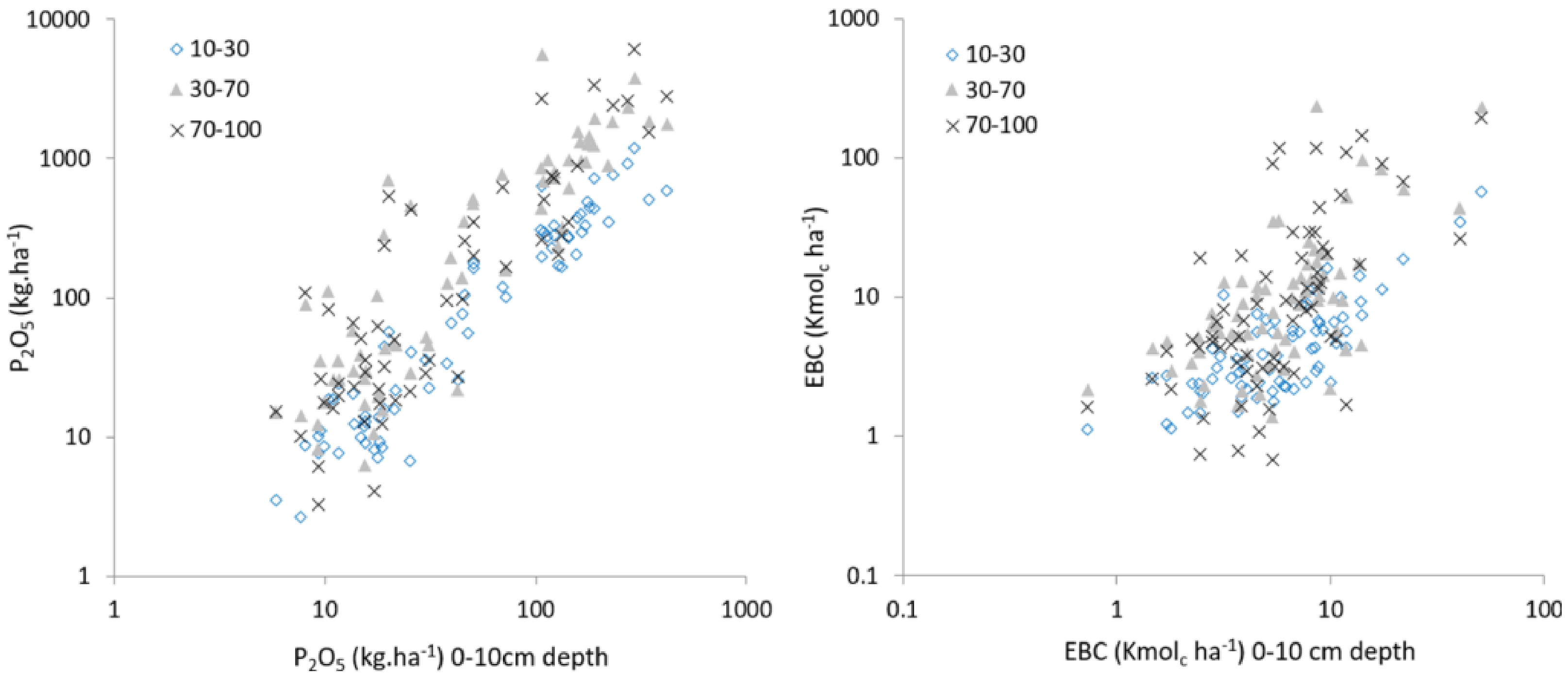

Fig. 4. Relationship between available P_2O_5 pools (kg ha^{-1}) at 0–10 cm depth and in soil layers 10–30 cm, 30–70 cm and 70–100 cm (a) and EBC stocks (kmol$_c$ ha^{-1}) at 0–10 cm depth and in soil layers 10–30 cm, 30–70 cm and 70–100 cm (b) across 49 forest sites.

Hansson et al. (2020, For. Ecol. Manage., 461, 117843)

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At all scales, nutrient limitation depends on:

- Climate (control of organic matter [N,P] recycling)
- Soil age (↗ N, ↘ P)
- Biological activity (e.g. N fixation, P-enzymes)
- Human activity (e.g. N deposition)
- Geology (P content of the soil parent material)

By the way, the 5 key-drivers of soil formation and soil functioning (Dokuchaev, 1883; Jenny, 1941)

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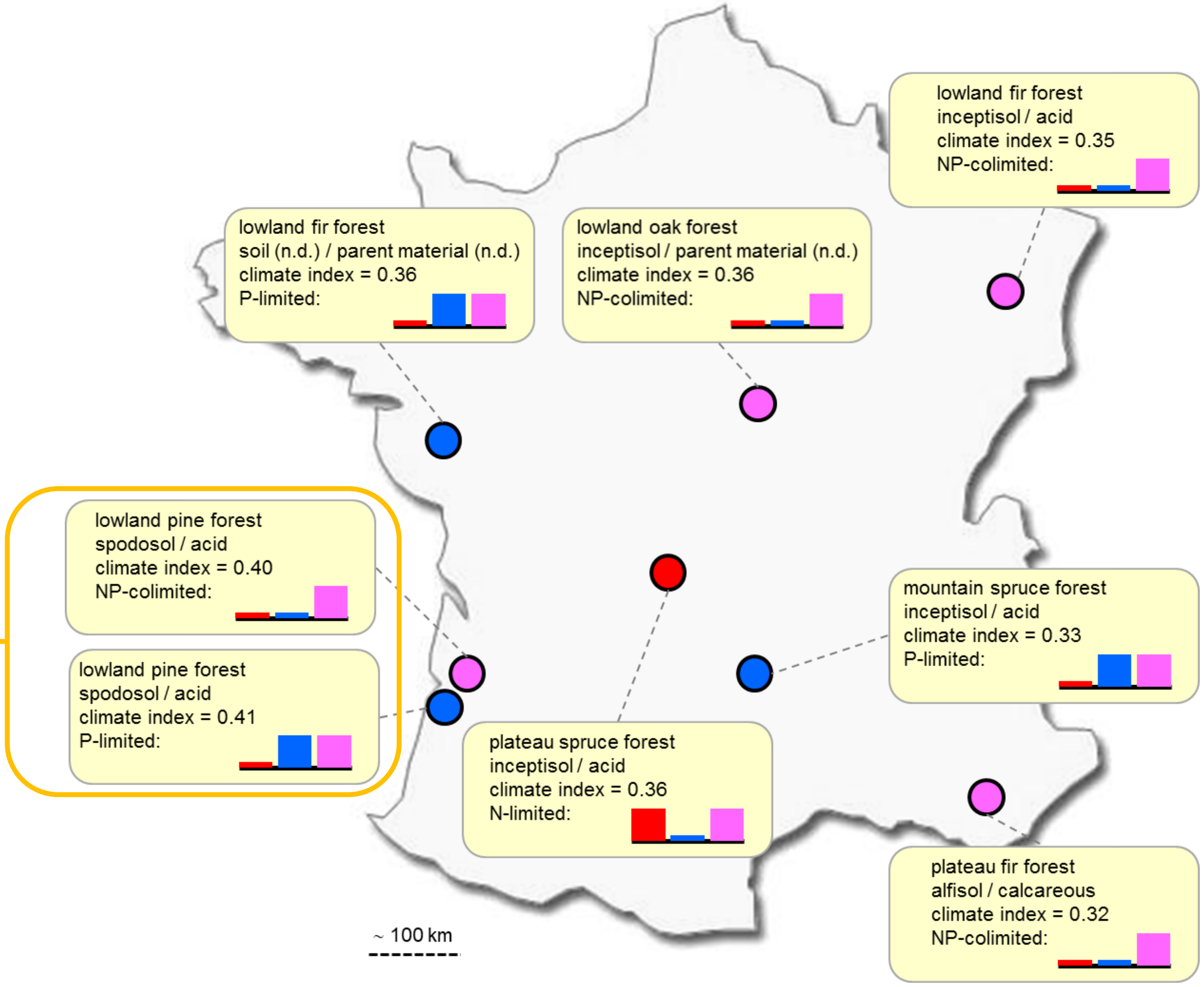
Nutrient limitations vary also at the regional scale, and at the local scale:

Local scale



N limitation: n =1

NP colimitation: n = 4

P limitation: n = 3