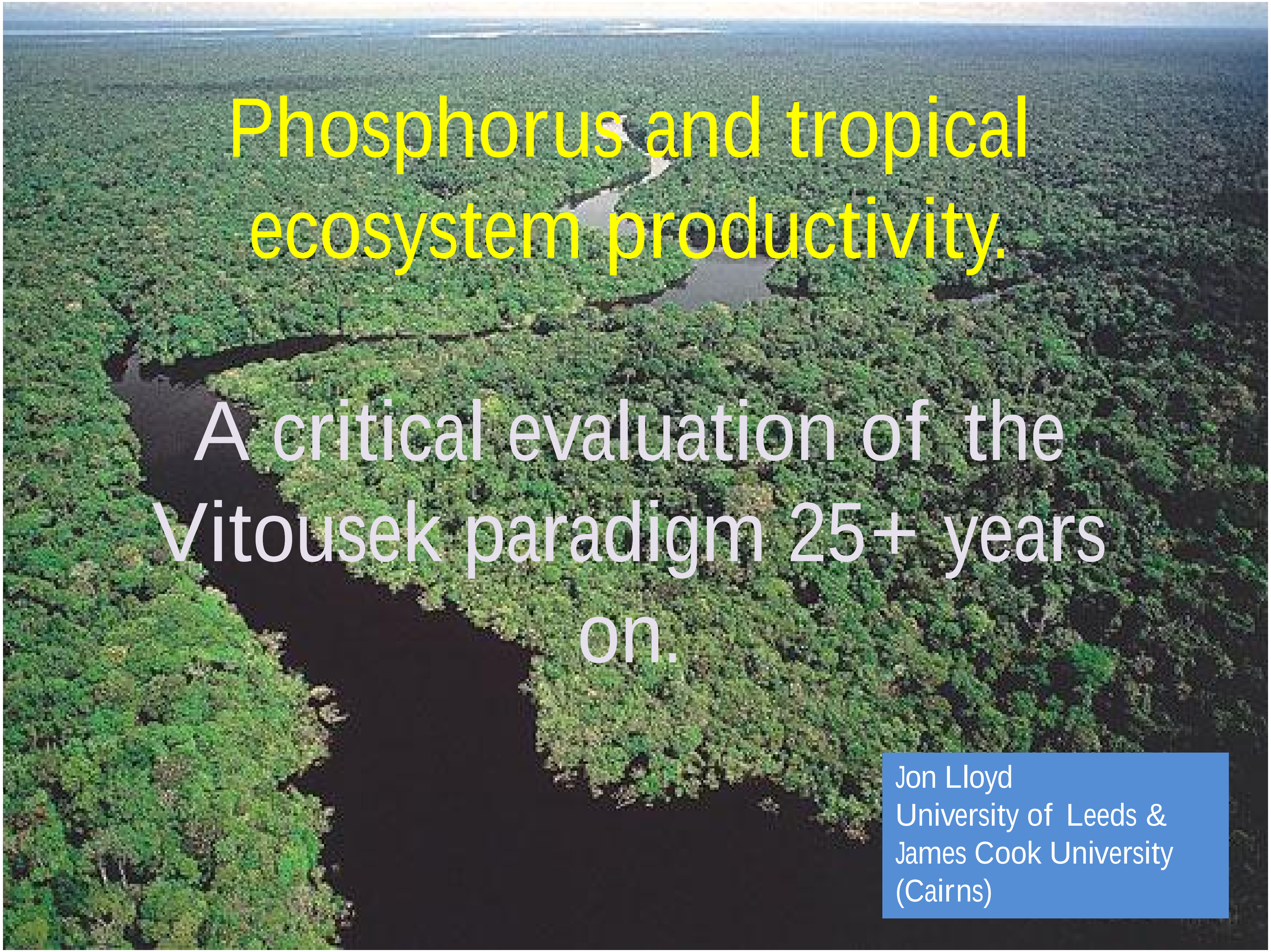


Phosphorus and tropical ecosystem productivity.

A critical evaluation of the Vitousek paradigm 25+ years on.

Jon Lloyd
University of Leeds &
James Cook University
(Cairns)

Phosphorus

- After nitrogen , phosphorus is the next most important “macronutrinet”

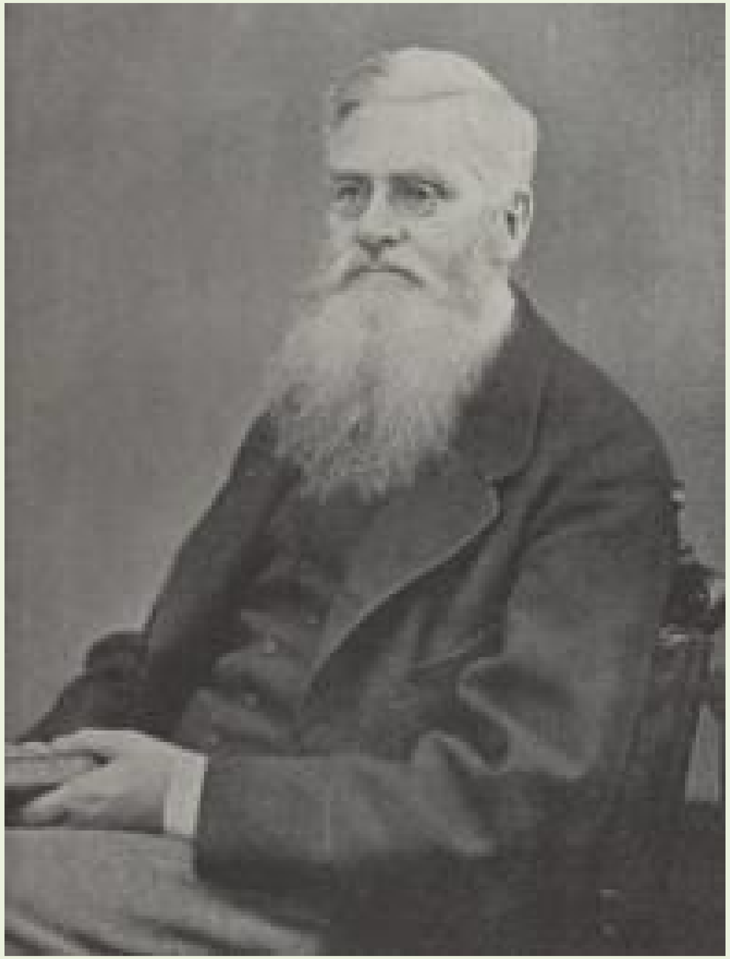
- Required for
  - ADP/ATP production
  - in membranes
  - in nucleic acids
  - can also be found in appreciable amounts (as phosphate) is the vacuole

Phosphorus cycling

- Unlike nitrogen, phosphorus cycling includes significant inorganic (mineral) reactions that make it much more difficult to study.
  - These reactions also tend to interfere with the availability of phosphorus in organic cycles.
  - They also complicate the measurement of various forms of P.
- A second major difference isthat gaseous P (phosphine PH_3) is negligible in biogeochemical cycles and can be ignored.
- Nitrogen and phosphorus have very different ultimate origins.

Early notions were that tropical forests were lush..

so they must have a high soil fertility!



Western Amazonia

Central and Eastern Amazonia

This view of tropical soil fertility gradually changed

Indeed, by the 1970s, it was more or less accepted that virtually all tropical soils were old, infertile and unsuitable for agriculture (!)

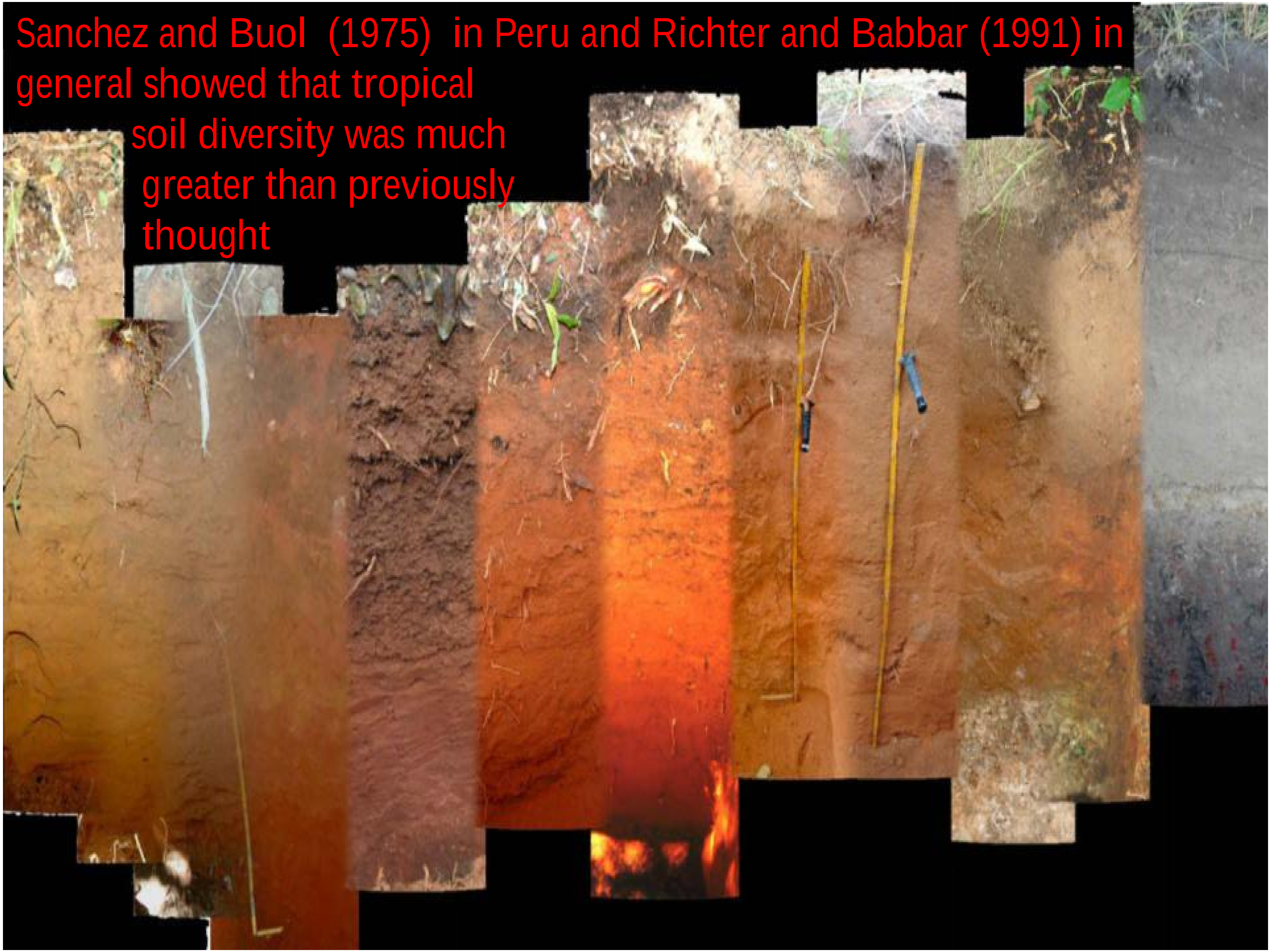
Reviewed in:

Biogeosciences, 8, 1415–1440, 2011
www.biogeosciences.net/8/1415/2011/
doi:10.5194/bg-8-1415-2011

Biogeosciences

Soils of Amazonia with particular reference to the RAINFOR sites

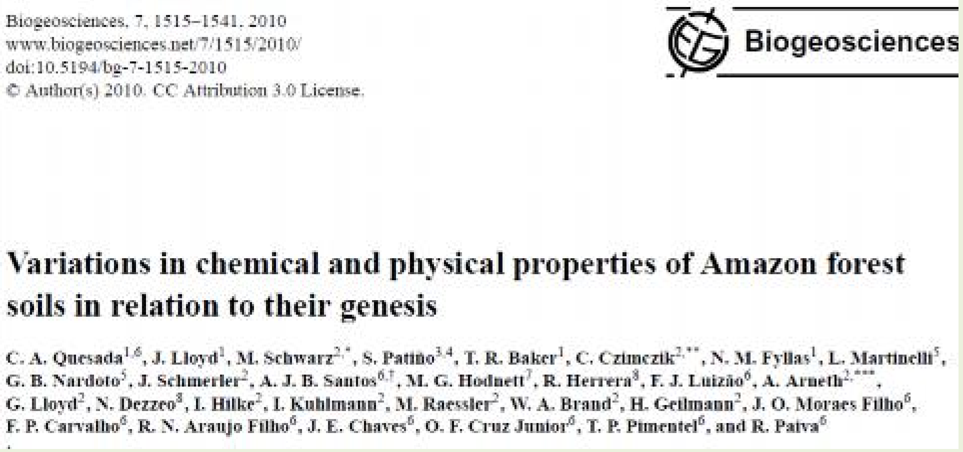
C. A. Quesada[1,2], J. Lloyd[1,3], L. O. Anderson[4], N. M. Fyllas[1], M. Schwarz[5,*], and C. I. Czimczik[5,**]



Sanchez and Buol (1975) in Peru and Richter and Babbar (1991) in general showed that tropical soil diversity was much greater than previously thought

Diversity in tropical soil fertility is massive

So we must be careful in making generalisations!



Biogeosciences, 7, 1515–1541, 2010
www.biogeosciences.net/7/1515/2010/
doi:10.5194/bg-7-1515-2010

Biogeosciences

Variations in chemical and physical properties of Amazon forest soils in relation to their genesis

C. A. Quesada[1,6], J. Lloyd[1], M. Schwarz[2,*], S. Patiño[3,4], T. R. Baker[1], C. Czimczik[2,**], N. M. Fyllas[1], L. Martinelli[5], G. B. Nardoto[5], J. Schmerler[2], A. J. B. Santos[6,†], M. G. Hodnett[7], R. Herrera[8], F. J. Luizão[6], A. Arneth[2,***], G. Lloyd[2], N. Dezzeo[8], I. Hilke[2], I. Kuhlmann[2], M. Raessler[2], W. A. Brand[2], H. Geilmann[2], J. O. Moraes Filho[6], F. P. Carvalho[6], R. N. Araujo Filho[6], J. E. Chaves[6], O. F. Cruz Junior[6], T. P. Pimentel[6], and R. Paiva[6]

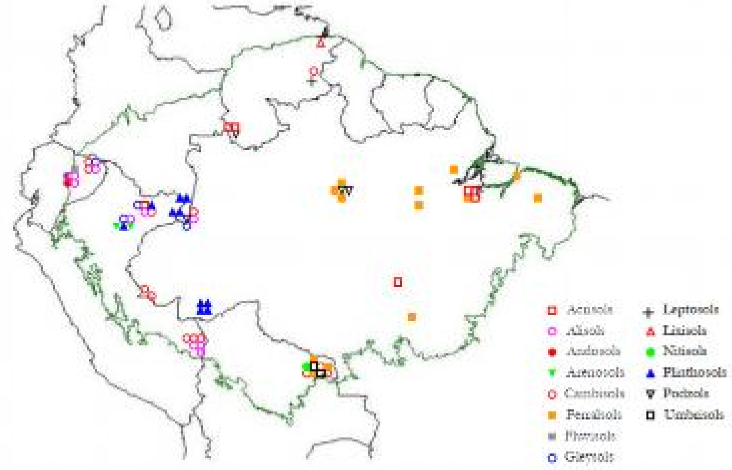
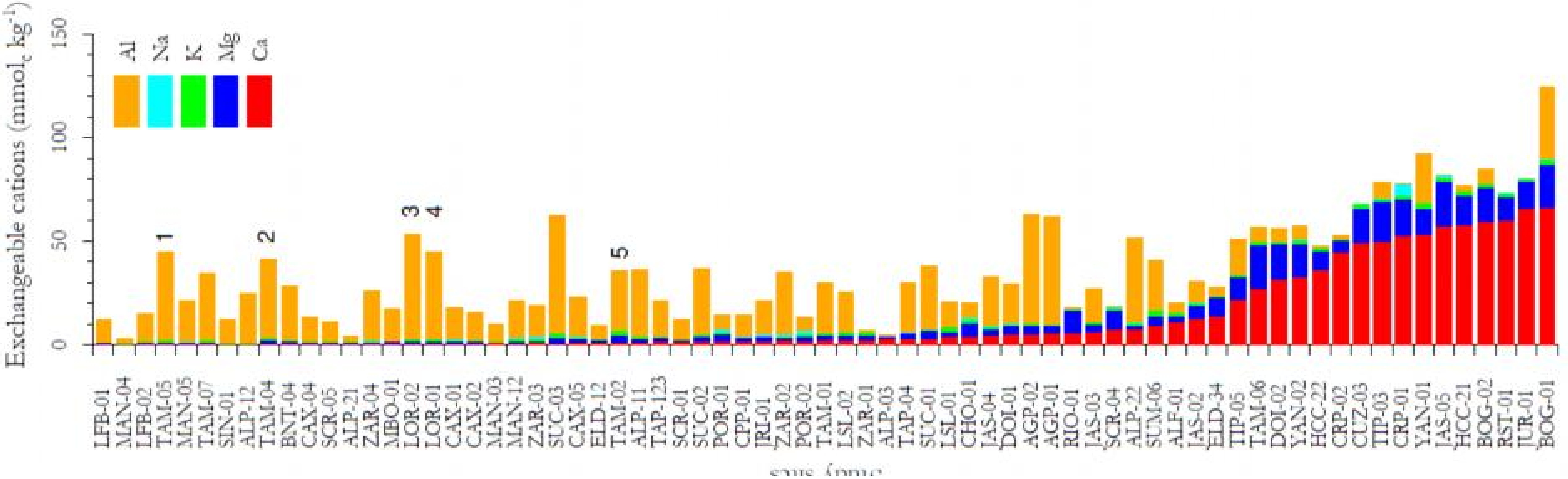
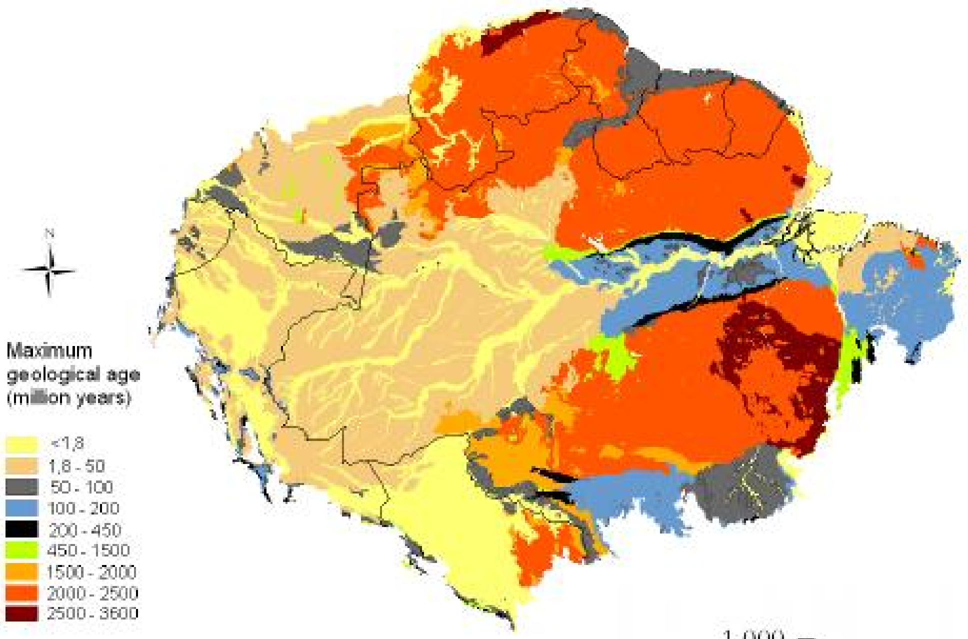


Fig. 1. Distribution of identified soil types across Amazonia.

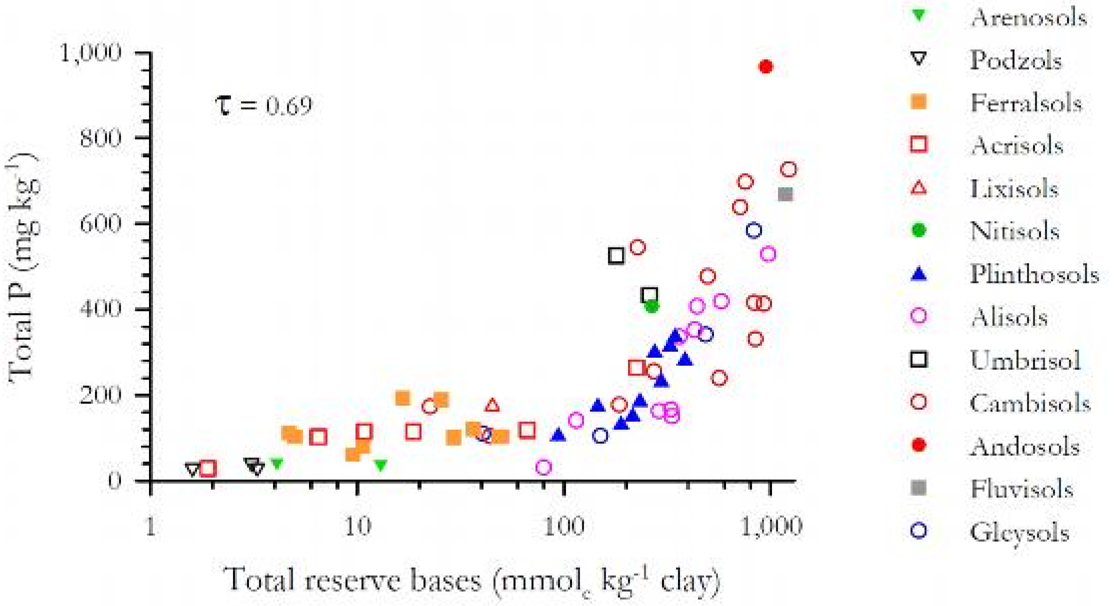


There are good reasons for this

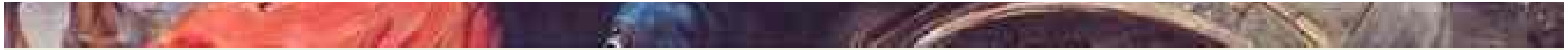


Substrate age

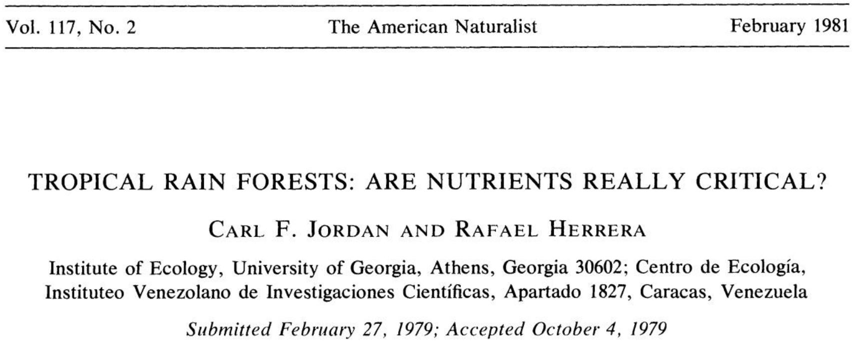
linear-log P / cation relationship



So, all we have to do is relate this variation in soil chemistry to variations in tropical forest productivity ?!



Earliest work focussed on cations, especially calcium



Vol. 117, No. 2 The American Naturalist February 1981

TROPICAL RAIN FORESTS: ARE NUTRIENTS REALLY CRITICAL?

CARL F. JORDAN AND RAFAEL HERRERA

Institute of Ecology, University of Georgia, Athens, Georgia 30602; Centro de Ecología, Instituteo Venezolano de Investigaciones Científicas, Apartado 1827, Caracas, Venezuela

Submitted February 27, 1979; Accepted October 4, 1979

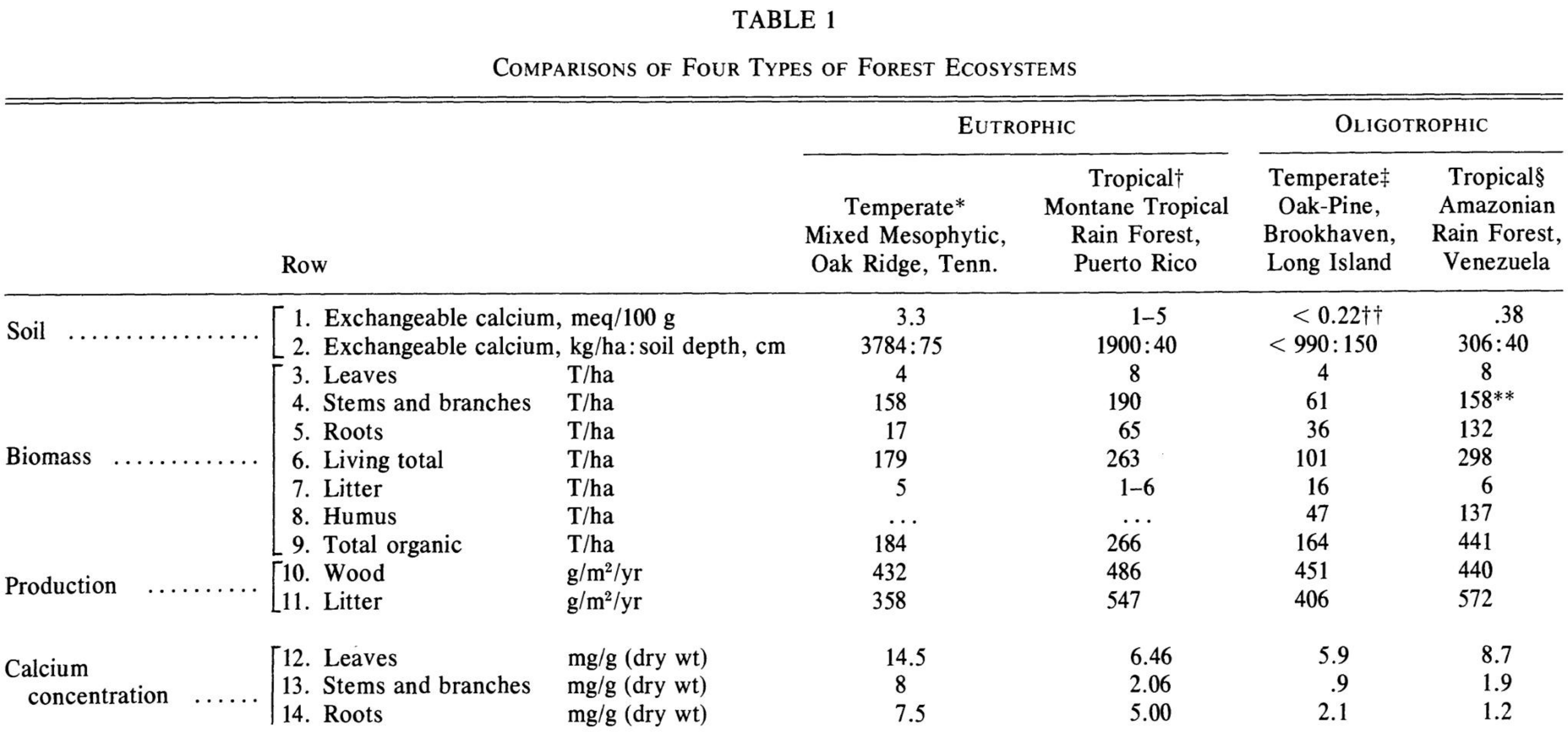
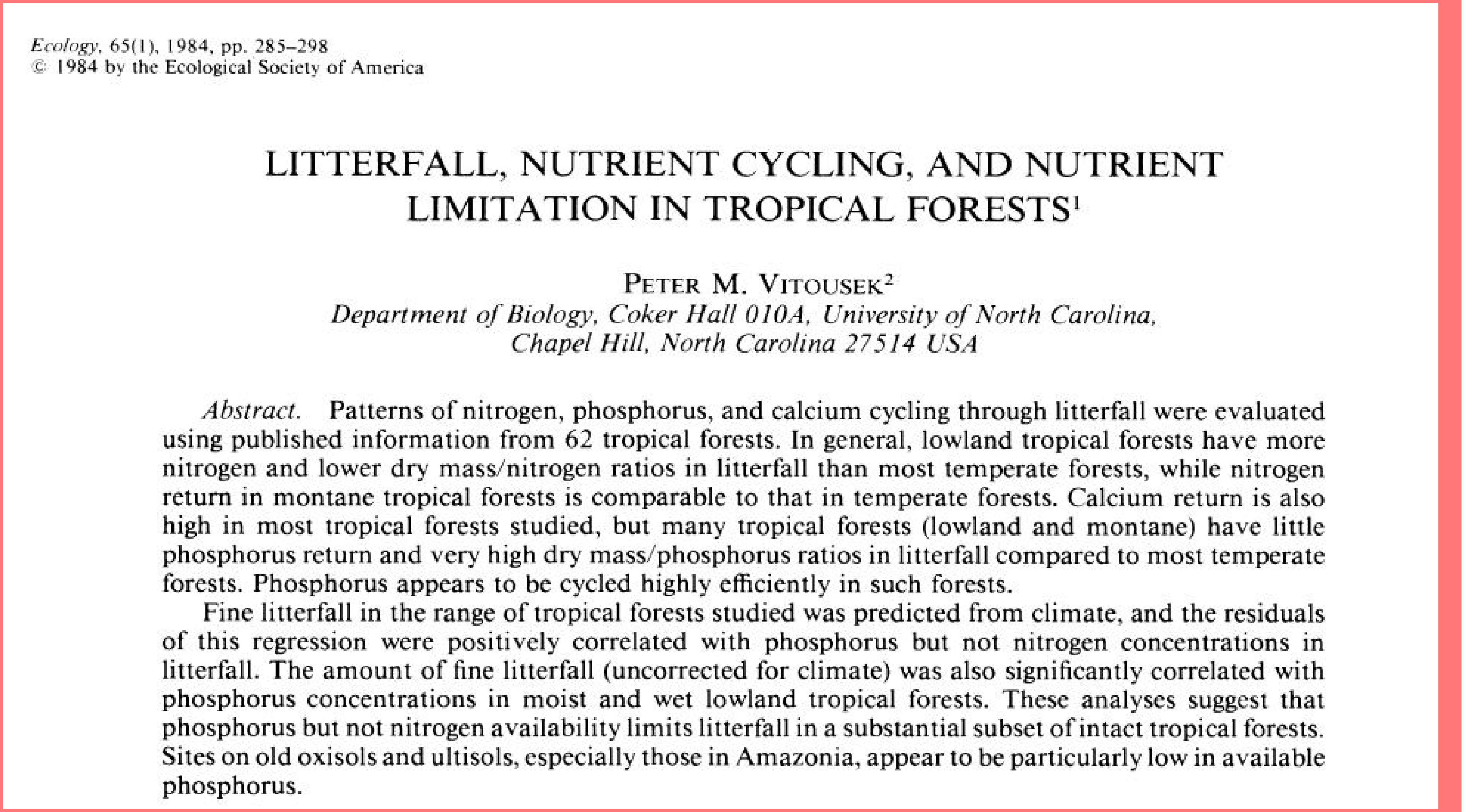


TABLE 1

COMPARISONS OF FOUR TYPES OF FOREST ECOSYSTEMS

	Row		EUTROPHIC		OLIGOTROPHIC	
			Temperate* Mixed Mesophytic, Oak Ridge, Tenn.	Tropical† Montane Tropical Rain Forest, Puerto Rico	Temperate‡ Oak-Pine, Brookhaven, Long Island	Tropical§ Amazonian Rain Forest, Venezuela
Soil	1. Exchangeable calcium, meq/100 g		3.3	1–5	< 0.22††	.38
	2. Exchangeable calcium, kg/ha: soil depth, cm		3784:75	1900:40	< 990:150	306:40
Biomass	3. Leaves	T/ha	4	8	4	8
	4. Stems and branches	T/ha	158	190	61	158**
	5. Roots	T/ha	17	65	36	132
	6. Living total	T/ha	179	263	101	298
	7. Litter	T/ha	5	1–6	16	6
	8. Humus	T/ha	...	...	47	137
	9. Total organic	T/ha	184	266	164	441
Production	10. Wood	g/m²/yr	432	486	451	440
	11. Litter	g/m²/yr	358	547	406	572
Calcium concentration	12. Leaves	mg/g (dry wt)	14.5	6.46	5.9	8.7
	13. Stems and branches	mg/g (dry wt)	8	2.06	.9	1.9
	14. Roots	mg/g (dry wt)	7.5	5.00	2.1	1.2

“but then came the breakout paper”



Ecology, 65(1), 1984, pp. 285–298

LITTERFALL, NUTRIENT CYCLING, AND NUTRIENT LIMITATION IN TROPICAL FORESTS[1]

PETER M. VITOUSEK[2]
Department of Biology, Coker Hall 010A, University of North Carolina,
Chapel Hill, North Carolina 27514 USA

Abstract. Patterns of nitrogen, phosphorus, and calcium cycling through litterfall were evaluated using published information from 62 tropical forests. In general, lowland tropical forests have more nitrogen and lower dry mass/nitrogen ratios in litterfall than most temperate forests, while nitrogen return in montane tropical forests is comparable to that in temperate forests. Calcium return is also high in most tropical forests studied, but many tropical forests (lowland and montane) have little phosphorus return and very high dry mass/phosphorus ratios in litterfall compared to most temperate forests. Phosphorus appears to be cycled highly efficiently in such forests.

Fine litterfall in the range of tropical forests studied was predicted from climate, and the residuals of this regression were positively correlated with phosphorus but not nitrogen concentrations in litterfall. The amount of fine litterfall (uncorrected for climate) was also significantly correlated with phosphorus concentrations in moist and wet lowland tropical forests. These analyses suggest that phosphorus but not nitrogen availability limits litterfall in a substantial subset of intact tropical forests. Sites on old oxisols and ultisols, especially those in Amazonia, appear to be particularly low in available phosphorus.

Primary argument based on the notion of NUTRIENT USE EFFICINCY

- Compared to temperate forests, tropical forests have a low nitrogen use efficiency (and lots of N)
- But especially for P this is the other way around

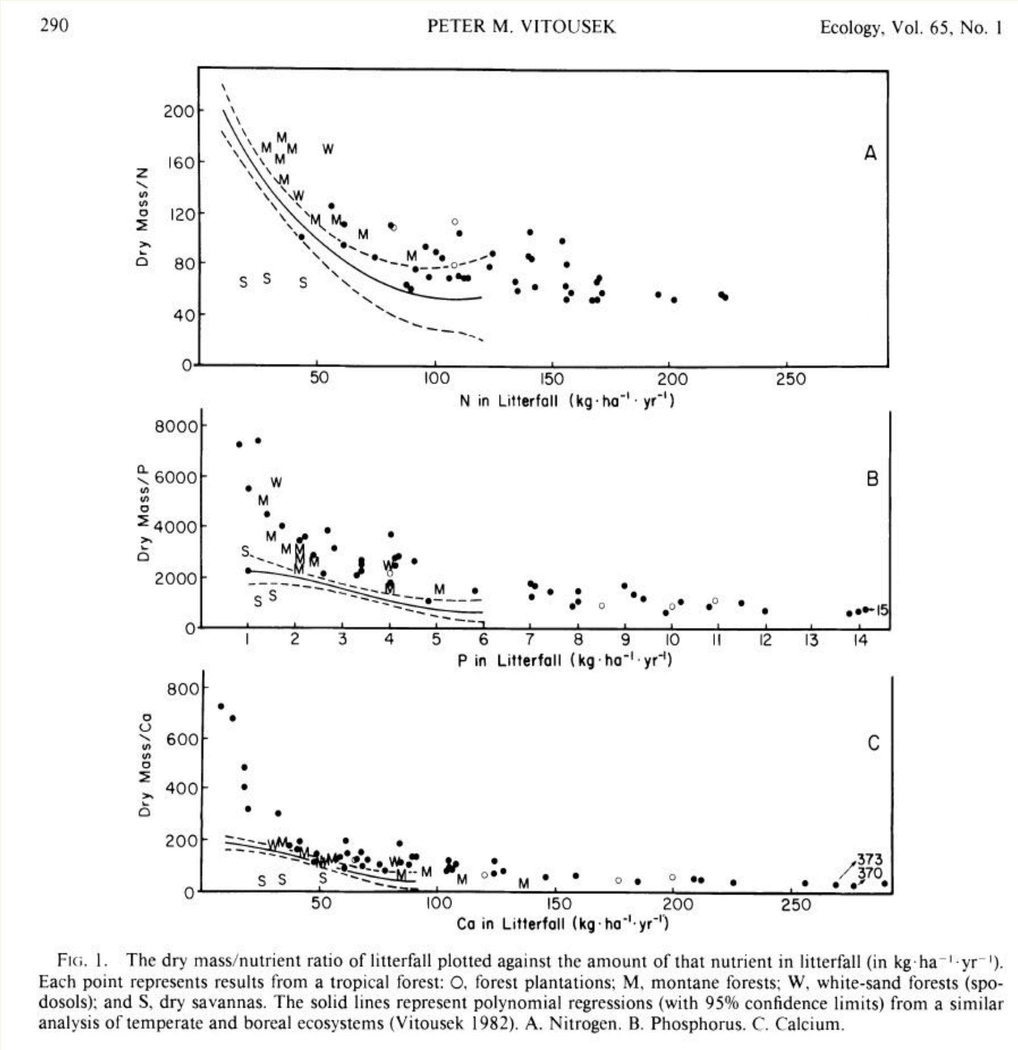
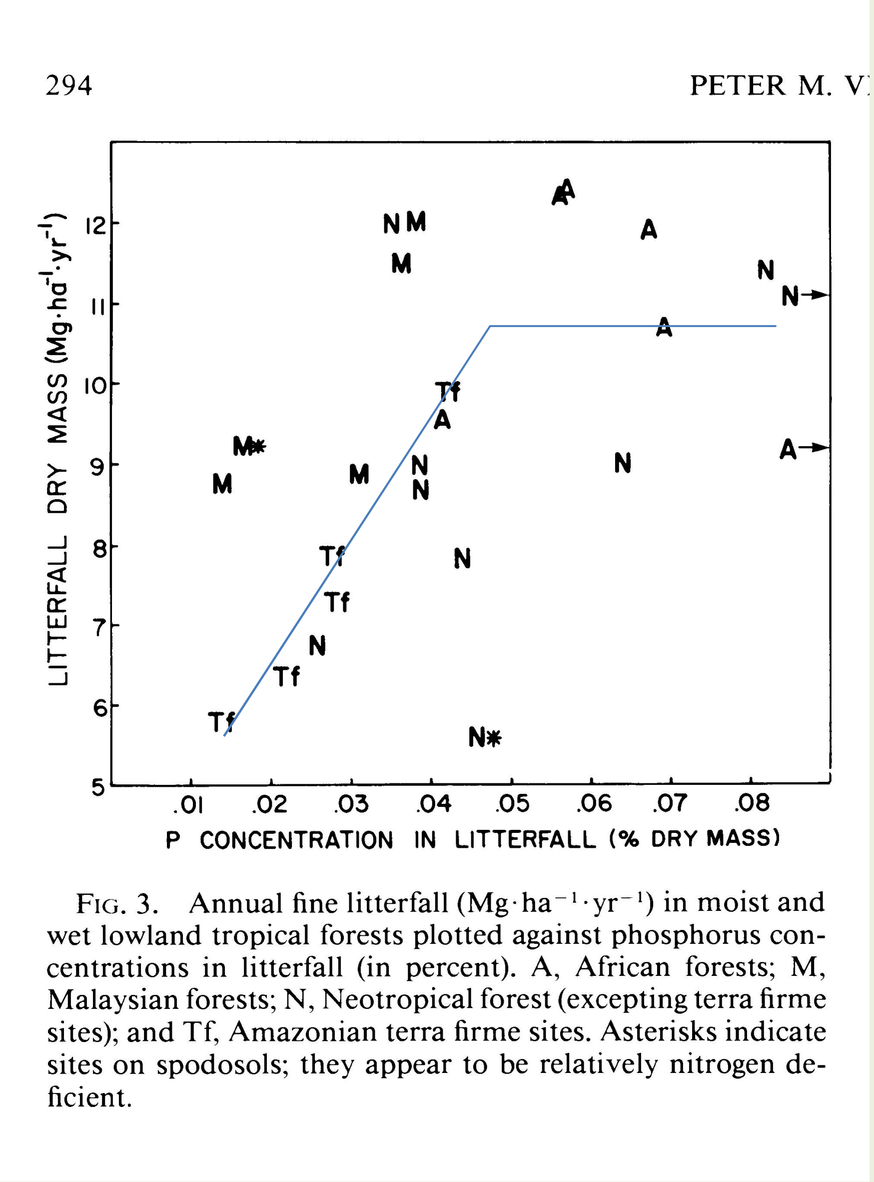

290 PETER M. VITOUSEK Ecology, Vol. 65, No. 1

FIG. 1. The dry mass/nutrient ratio of litterfall plotted against the amount of that nutrient in litterfall (in kg·ha⁻¹·yr⁻¹). Each point represents results from a tropical forest: ○, forest plantations; M, montane forests; W, white-sand forests (spodosols); and S, dry savannas. The solid lines represent polynomial regressions (with 95% confidence limits) from a similar analysis of temperate and boreal ecosystems (Vitousek 1982). A. Nitrogen. B. Phosphorus. C. Calcium.

Based on surrogates of forest P status and productivity

ASSUMPTIONS

- Litterfall ~ new leaf production
- New leaf production ~NPP
- [P] in litterfall reflects that in the canopy itself
- K and Mg (etc) also not important



294 PETER M. V

FIG. 3. Annual fine litterfall (Mg·ha^{-1}·yr^{-1}) in moist and wet lowland tropical forests plotted against phosphorus concentrations in litterfall (in percent). A, African forests; M, Malaysian forests; N, Neotropical forest (excepting terra firme sites); and Tf, Amazonian terra firme sites. Asterisks indicate sites on spodosols; they appear to be relatively nitrogen deficient.

Idea that P should become more limiting founded in pedogenic theory

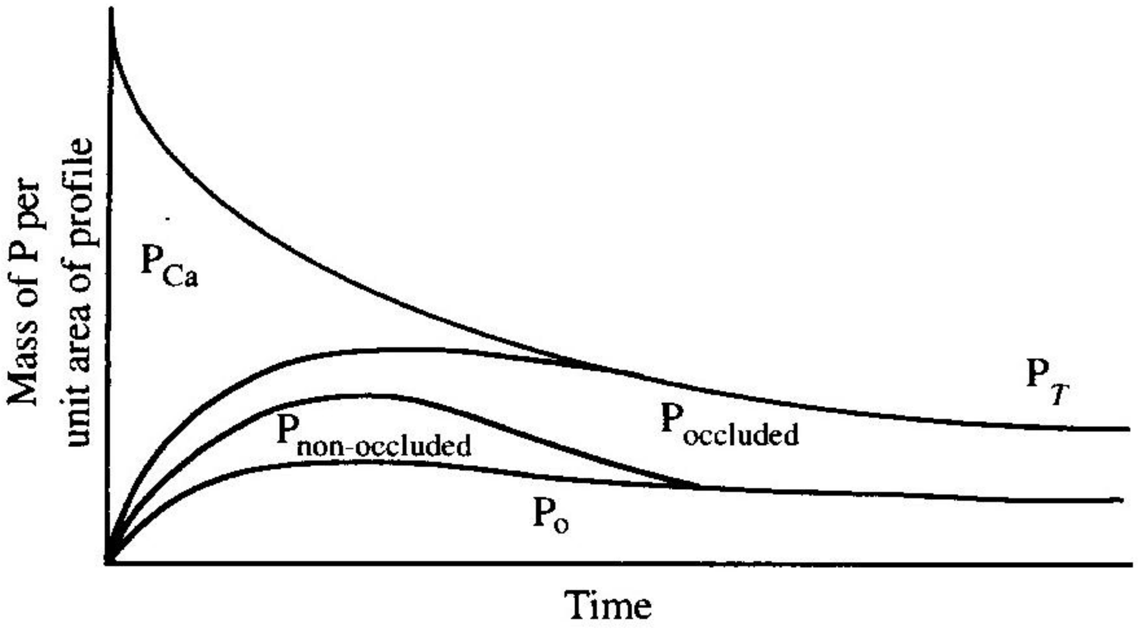


FIG. 1. Walker and Syers' (1976) diagram of P transformations with time. P_{Ca} = calcium phosphates, P_T = total phosphorus, P_o = P bound to organic matter.

Walker T.W. and K. Syers (1976)*Geoderma* 15,1-19

Also evidence that N may be in excess for many tropical forests

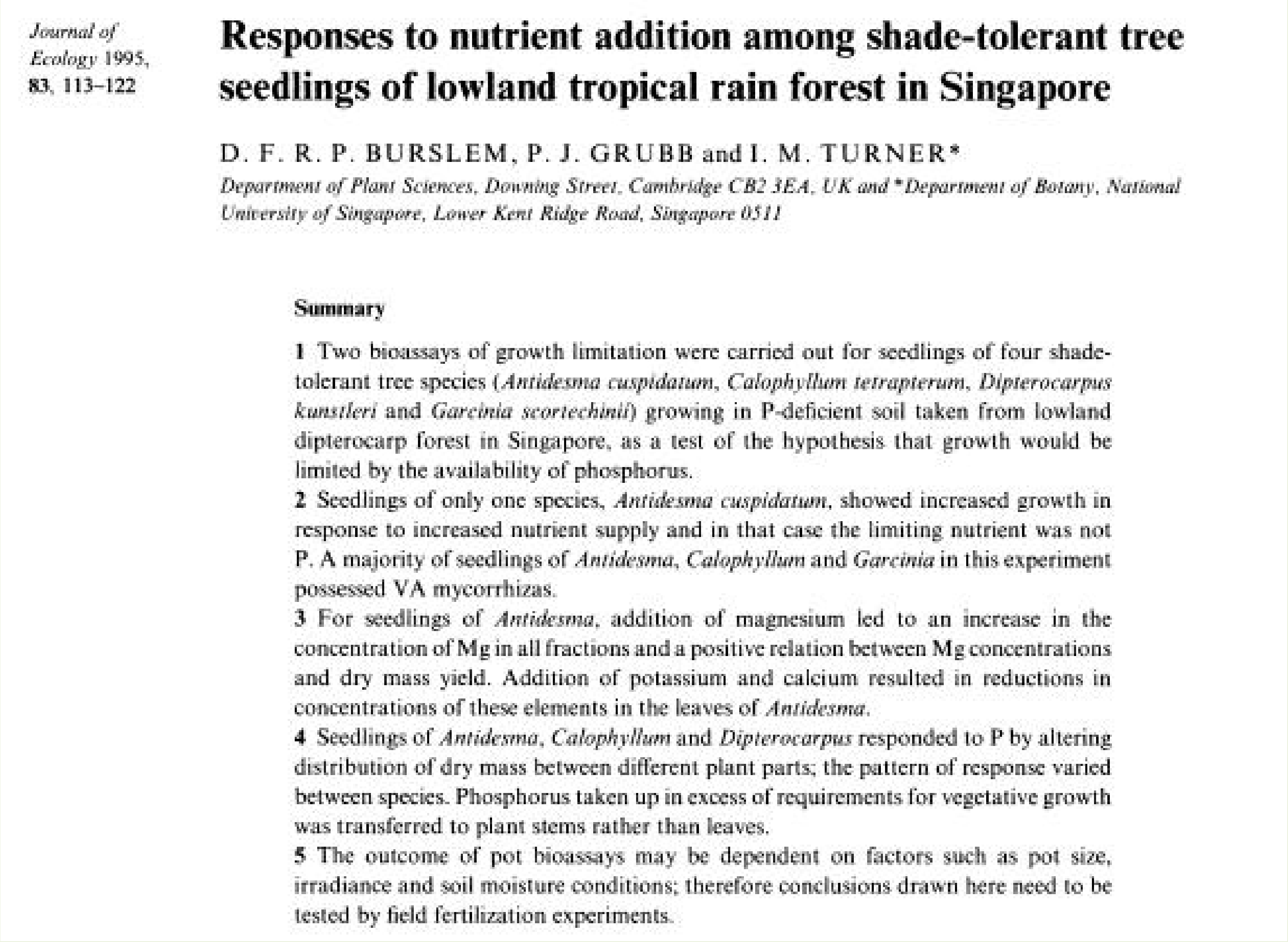
- Relatively high $\delta^{15}N$ for leaves and soil
  - indicates a leaky system
- High rates of N_2O emission
  - indicates a leaky system
- High leaching losses for nitrogen
  - indicates a leaky system
- Most of the species with a N_2-fixing ability don’t bother (most of the time)
  - (most) “mature” tropical forests have nitrogen coming out of their orifices

99.9% of the world has taken one of two approaches to dealing with this theory

- Accepted it uncritically
    - – "(most) tropical forests are phosphorus limited"

- Ignored it completely
    - – "my mental constructs and/or models only deal with temperate zone-like N-limitation concepts"
        - *"so I deal with tropical forests in the same way"*

But not the Poms!



Journal of
Ecology 1995,
83, 113–122

Responses to nutrient addition among shade-tolerant tree seedlings of lowland tropical rain forest in Singapore

D. F. R. P. BURSLEM, P. J. GRUBB and I. M. TURNER*
*Department of Plant Sciences, Downing Street, Cambridge CB2 3EA, UK and *Department of Botany, National University of Singapore, Lower Kent Ridge Road, Singapore 0511*

Summary

1 Two bioassays of growth limitation were carried out for seedlings of four shade-tolerant tree species (*Antidesma cuspidatum*, *Calophyllum tetrapterum*, *Dipterocarpus kunstleri* and *Garcinia scortechinii*) growing in P-deficient soil taken from lowland dipterocarp forest in Singapore, as a test of the hypothesis that growth would be limited by the availability of phosphorus.

2 Seedlings of only one species, *Antidesma cuspidatum*, showed increased growth in response to increased nutrient supply and in that case the limiting nutrient was not P. A majority of seedlings of *Antidesma*, *Calophyllum* and *Garcinia* in this experiment possessed VA mycorrhizas.

3 For seedlings of *Antidesma*, addition of magnesium led to an increase in the concentration of Mg in all fractions and a positive relation between Mg concentrations and dry mass yield. Addition of potassium and calcium resulted in reductions in concentrations of these elements in the leaves of *Antidesma*.

4 Seedlings of *Antidesma*, *Calophyllum* and *Dipterocarpus* responded to P by altering distribution of dry mass between different plant parts; the pattern of response varied between species. Phosphorus taken up in excess of requirements for vegetative growth was transferred to plant stems rather than leaves.

5 The outcome of pot bioassays may be dependent on factors such as pot size, irradiance and soil moisture conditions; therefore conclusions drawn here need to be tested by field fertilization experiments.

Journal of Tropical Ecology (1994) 10:579–599. With 1 figure

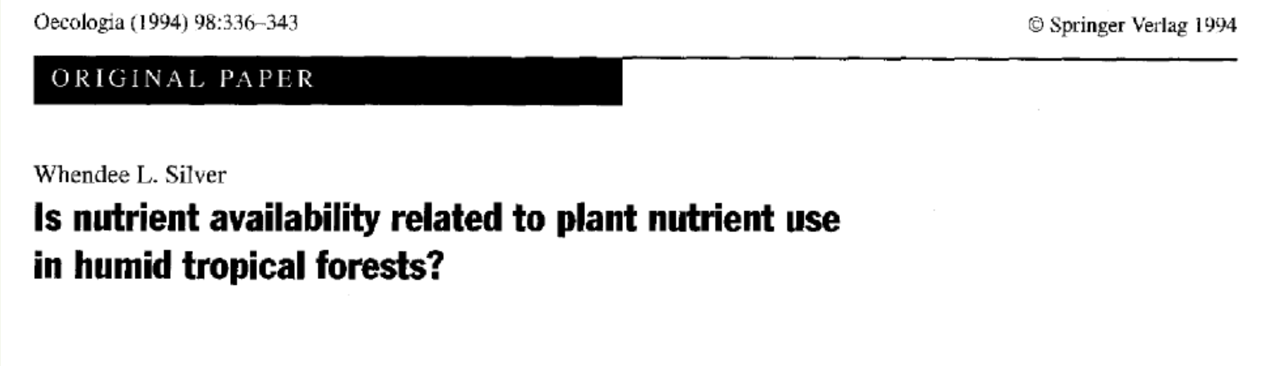
Mineral nutrient status of coastal hill dipterocarp forest and adinandra belukar in Singapore: bioassays of nutrient limitation

D. F. R. P. BURSLEM*, I. M. TURNER† *and* P. J. GRUBB*

**Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EA, UK*
†Department of Botany, National University of Singapore, Lower Kent Ridge Road, Singapore 0511

ABSTRACT. Bioassays of nutrient limitation were carried out for *Melastoma malabathricum* growing on soil from primary lowland dipterocarp rainforest in Singapore, and for *Dillenia suffruticosa* on soil from adinandra belukar, a nutrient-poor secondary forest type dominated by *Adinandra dumosa*. Three questions were addressed. 1. What is the nutrient most limiting to growth in primary forest? 2. What is the nature of nutrient limitation under conditions of adequate P supply? 3. Is there a qualitative difference in the nature of nutrient limitation under primary forest and adinandra belukar? Results showed that there was a strong limitation by P availability in both primary forest and adinandra belukar under the experimental conditions used. Once plants had an adequate P supply, all other nutrients became limiting to growth in primary forest soil. These findings are interpreted as support for the hypothesis that P availability would limit the productivity of moist tropical forests in general in the absence of mycorrhizas; tentative conclusions are drawn on the assumption that most woody tropical plants are mycorrhizal. It is argued that limitation by major cations may be common on old, highly leached tropical rainforest soils.

KEY WORDS: adinandra belukar, *Dillenia suffruticosa*, *Melastoma malabathricum*, nutrients, secondary forest, Singapore, tropical rainforest.

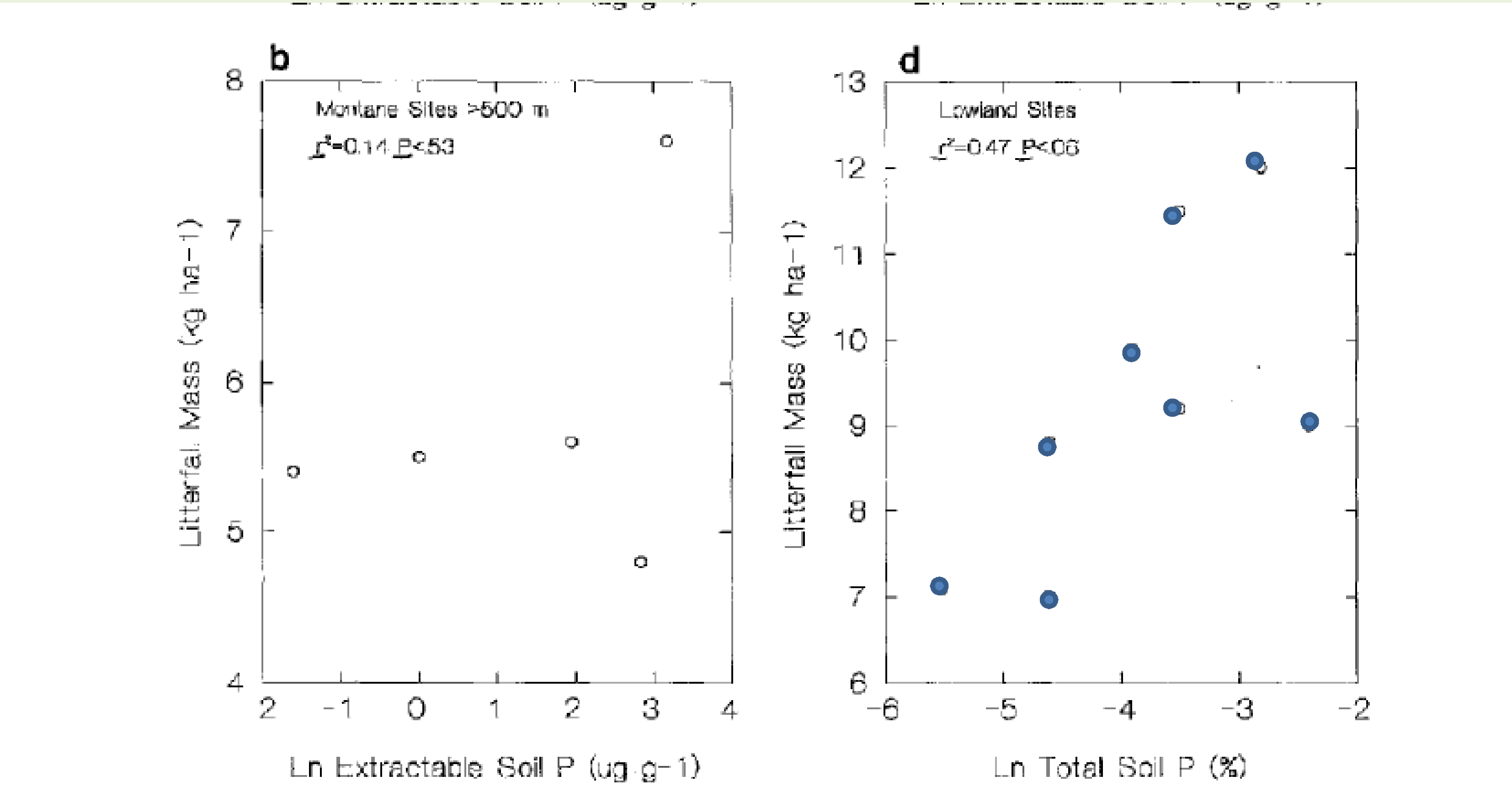


Oecologia (1994) 98:336–343

ORIGINAL PAPER

Whendee L. Silver

Is nutrient availability related to plant nutrient use in humid tropical forests?



Journal of Ecology

Journal of Ecology doi: 10.1111/j.1365-2745.2010.01741.x

Climate is a stronger driver of tree and forest growth rates than soil and disturbance

Marisol Toledo[1,2]*, Lourens Poorter[1,2], Marielos Peña-Claros[1,2], Alfredo Alarcón[2], Julio Balcázar[2], Claudio Leaño[2], Juan Carlos Licona[2], Oscar Llanque[3], Vincent Vroomans[2], Pieter Zuidema[3,4] and Frans Bongers[1]

[1]Forest Ecology and Forest Management Group, Centre for Ecosystem Studies, Wageningen University, PO Box 47, 6700 AA Wageningen, the Netherlands; [2]Instituto Boliviano de Investigación Forestal (IBIF), Casilla 6204, Santa Cruz, Bolivia; [3]Asociación PROMAB, Av. Del Ejército Final, Campus Universitario, Beni, Bolivia; and [4]Ecology and Biodiversity, Institute of Environmental Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, the Netherlands

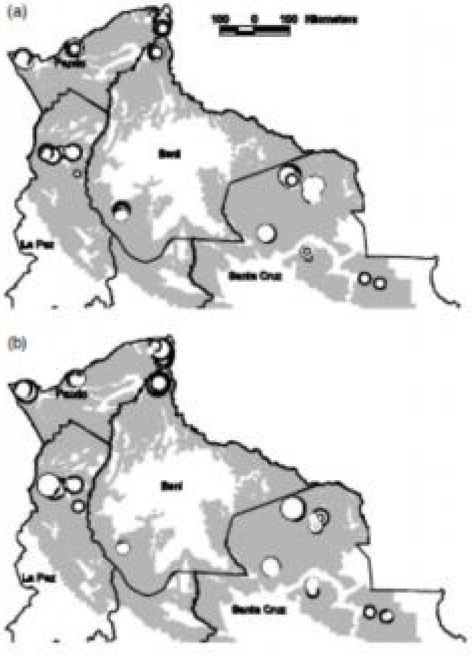
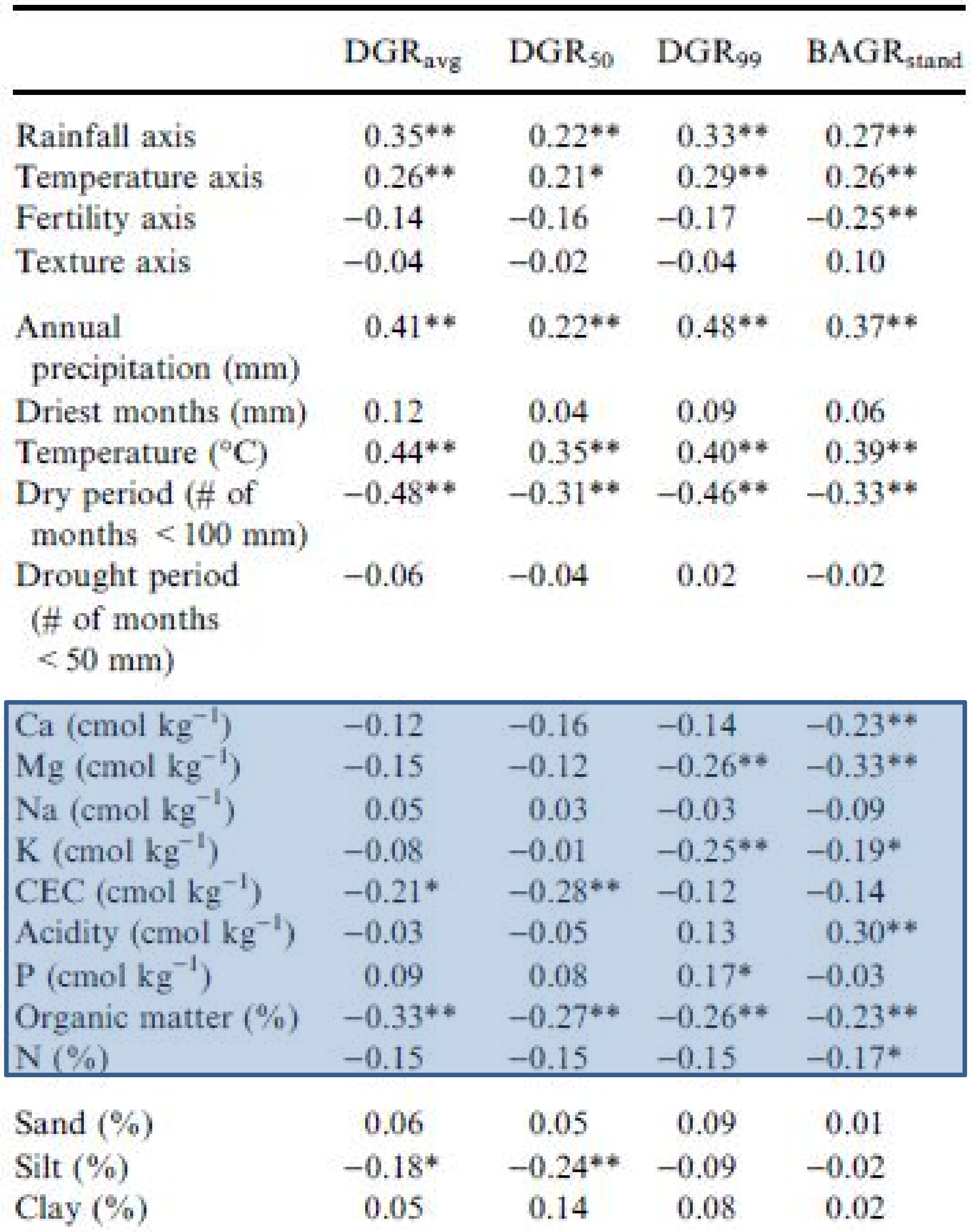


Fig. 1. Variation in (a) average diameter (DGR_{avg}) and (b) stand basal area ($BAGR_{stand}$) growth rates of 165 permanent plots located in four departments (Pando, La Paz, Beni and Santa Cruz) of lowland Bolivia. The size of the symbols scales proportional with the growth rate. Potential forest cover of areas assigned to timber production is indicated in grey. The white areas in Pando pertain to floodplains, in Beni and north of La Paz to savannas, and in Santa Cruz to the Cerrado and Chaco vegetation.



	DGR_{avg}	DGR_{50}	DGR_{99}	$BAGR_{stand}$
Rainfall axis	0.35**	0.22**	0.33**	0.27**
Temperature axis	0.26**	0.21*	0.29**	0.26**
Fertility axis	−0.14	−0.16	−0.17	−0.25**
Texture axis	−0.04	−0.02	−0.04	0.10
Annual precipitation (mm)	0.41**	0.22**	0.48**	0.37**
Driest months (mm)	0.12	0.04	0.09	0.06
Temperature (°C)	0.44**	0.35**	0.40**	0.39**
Dry period (# of months < 100 mm)	−0.48**	−0.31**	−0.46**	−0.33**
Drought period (# of months < 50 mm)	−0.06	−0.04	0.02	−0.02
Ca (cmol kg^{-1})	−0.12	−0.16	−0.14	−0.23**
Mg (cmol kg^{-1})	−0.15	−0.12	−0.26**	−0.33**
Na (cmol kg^{-1})	0.05	0.03	−0.03	−0.09
K (cmol kg^{-1})	−0.08	−0.01	−0.25**	−0.19*
CEC (cmol kg^{-1})	−0.21*	−0.28**	−0.12	−0.14
Acidity (cmol kg^{-1})	−0.03	−0.05	0.13	0.30**
P (cmol kg^{-1})	0.09	0.08	0.17*	−0.03
Organic matter (%)	−0.33**	−0.27**	−0.26**	−0.23**
N (%)	−0.15	−0.15	−0.15	−0.17*
Sand (%)	0.06	0.05	0.09	0.01
Silt (%)	−0.18*	−0.24**	−0.09	−0.02
Clay (%)	0.05	0.14	0.08	0.02

Fair enough: Study was dominated by a rainfall gradient

But (apart from a few other problems)
did they measure the right phosphorus ??!

A five minute course in pedogenesis

1. Older soils are (generally) deeper but less fertile

2. Different elements disappear at different rates

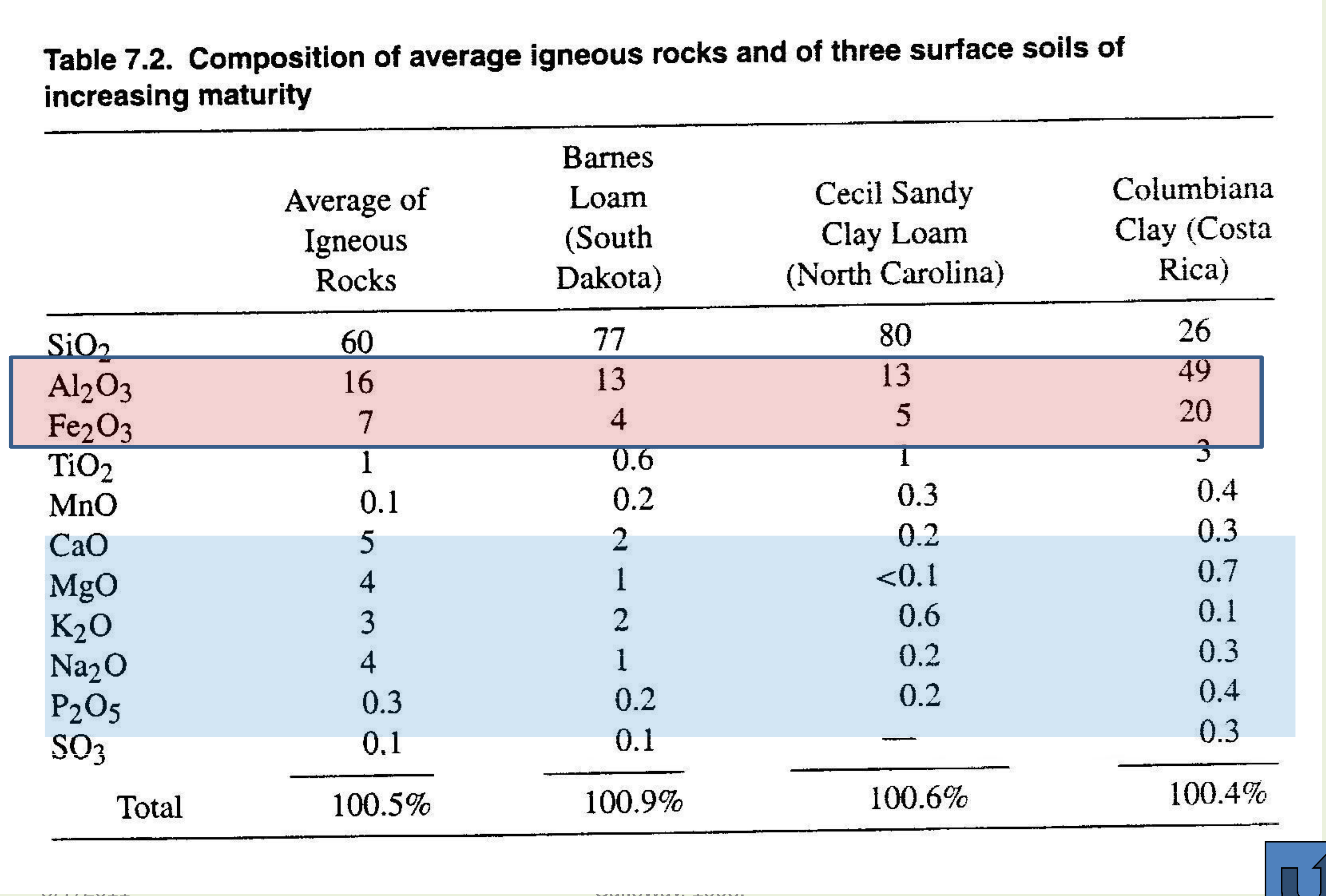


Table 7.2. Composition of average igneous rocks and of three surface soils of increasing maturity

	Average of Igneous Rocks	Barnes Loam (South Dakota)	Cecil Sandy Clay Loam (North Carolina)	Columbiana Clay (Costa Rica)
SiO_2	60	77	80	26
Al_2O_3	16	13	13	49
Fe_2O_3	7	4	5	20
TiO_2	1	0.6	1	3
MnO	0.1	0.2	0.3	0.4
CaO	5	2	0.2	0.3
MgO	4	1	<0.1	0.7
K_2O	3	2	0.6	0.1
Na_2O	4	1	0.2	0.3
P_2O_5	0.3	0.2	0.2	0.4
SO_3	0.1	0.1	—	0.3
Total	100.5%	100.9%	100.6%	100.4%

3. Mineralogy changes as soils develop

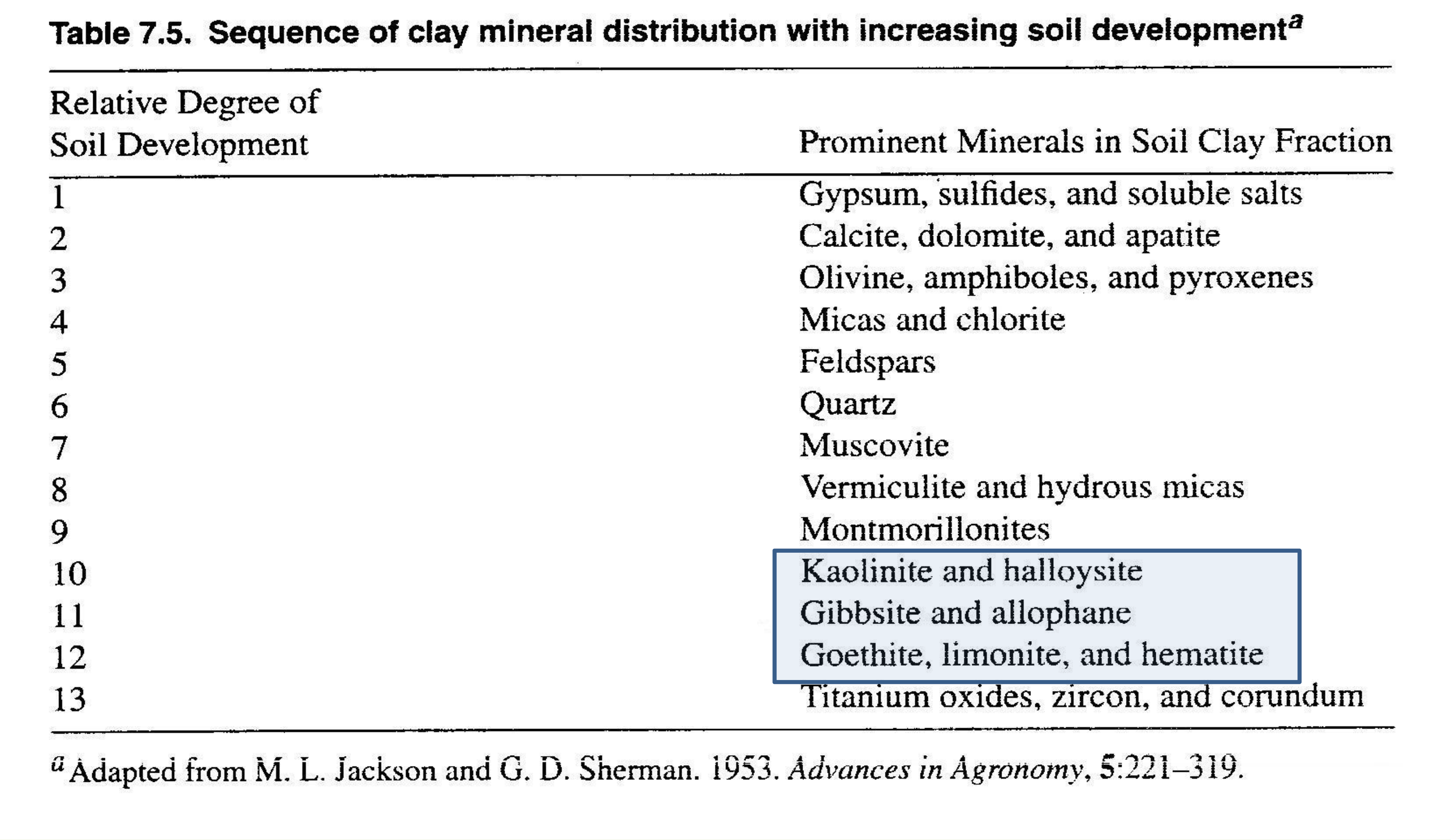


Table 7.5. Sequence of clay mineral distribution with increasing soil development[a]

Relative Degree of Soil Development	Prominent Minerals in Soil Clay Fraction
1	Gypsum, sulfides, and soluble salts
2	Calcite, dolomite, and apatite
3	Olivine, amphiboles, and pyroxenes
4	Micas and chlorite
5	Feldspars
6	Quartz
7	Muscovite
8	Vermiculite and hydrous micas
9	Montmorillonites
10	Kaolinite and halloysite
11	Gibbsite and allophane
12	Goethite, limonite, and hematite
13	Titanium oxides, zircon, and corundum

[a] Adapted from M. L. Jackson and G. D. Sherman. 1953. *Advances in Agronomy*, 5:221–319.

Galloway, 1998.

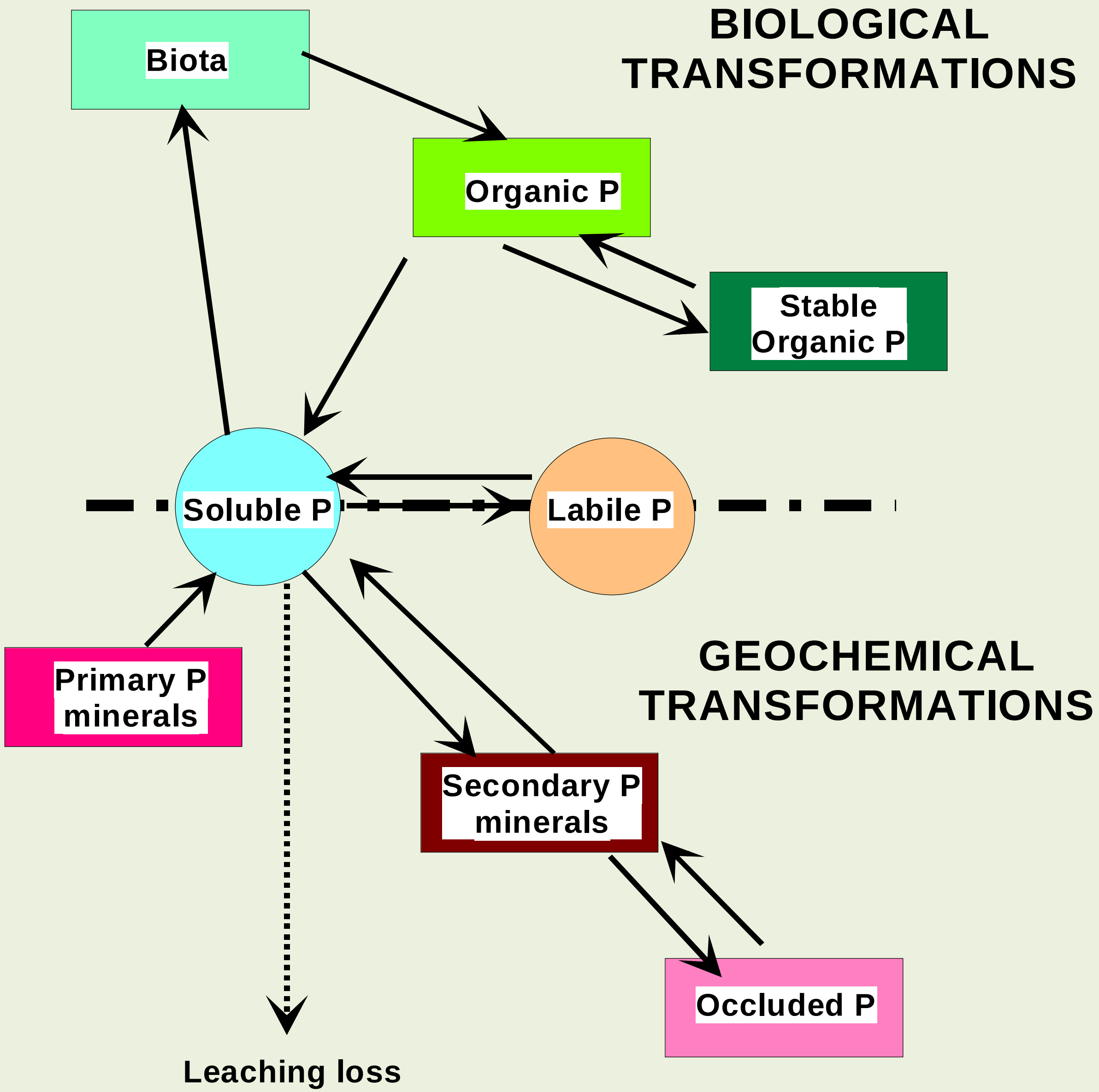
Soil “age effects”

- More highly weathered soils tend to be high in aluminium and iron oxides
- This means phosphorus tends to get “locked up”
- Typically less than 1% of total soil P is available in older soils

Bound forms

- Adsorbed P (attached to Al and Fe irons on the clay surface)
  - Probably to some extent exchangeable
- Occluded P (stuck inside clay particle)
  - Probably “gone for all time” (or at least a very long time)

Soil P transformations



BIOLOGICAL TRANSFORMATIONS

Biota

Organic P

Stable Organic P

Soluble P

Labile P

GEOCHEMICAL TRANSFORMATIONS

Primary P minerals

Secondary P minerals

Occluded P

Leaching loss

RAINFOR CONSORTIUM

- Leeds University (Oliver Phillips, Jon Lloyd)
- Oxford University (Yadvinder Malhi)
- MPI Jena

- Many local collaborators

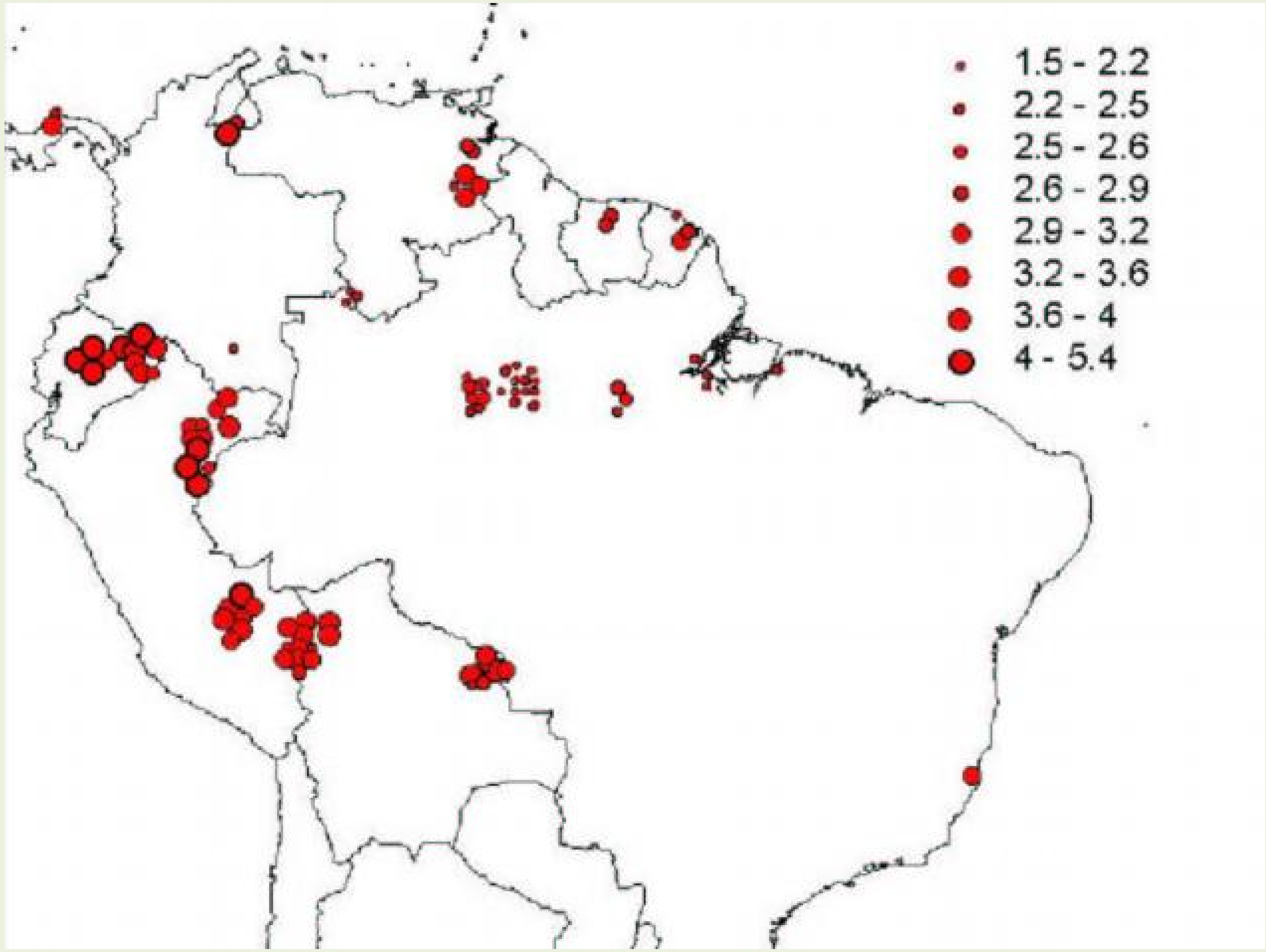
  across Amazonia

  (30 -40)

- Integrated laboratory analyses (Jena, Leeds, Manaus)

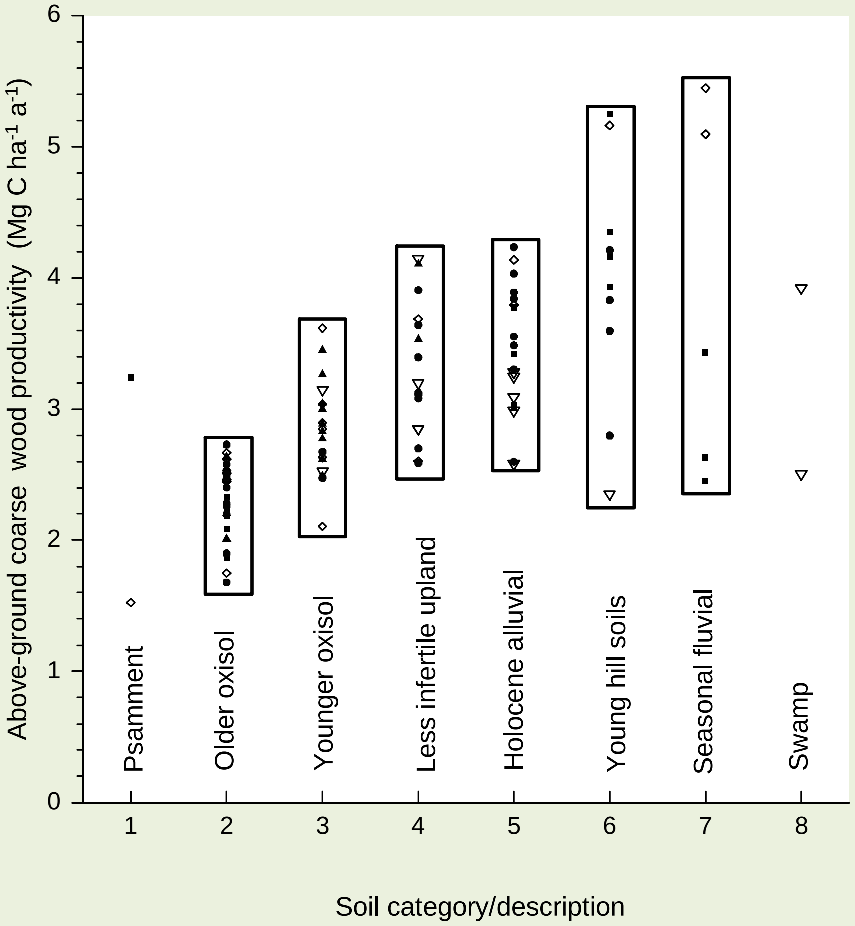
RAINFOR Field Activities 2001-2007

Basin wide variations in stem growth rate



Malhi et al (2004) Global Change Biology

Soil fertility seems to be critical

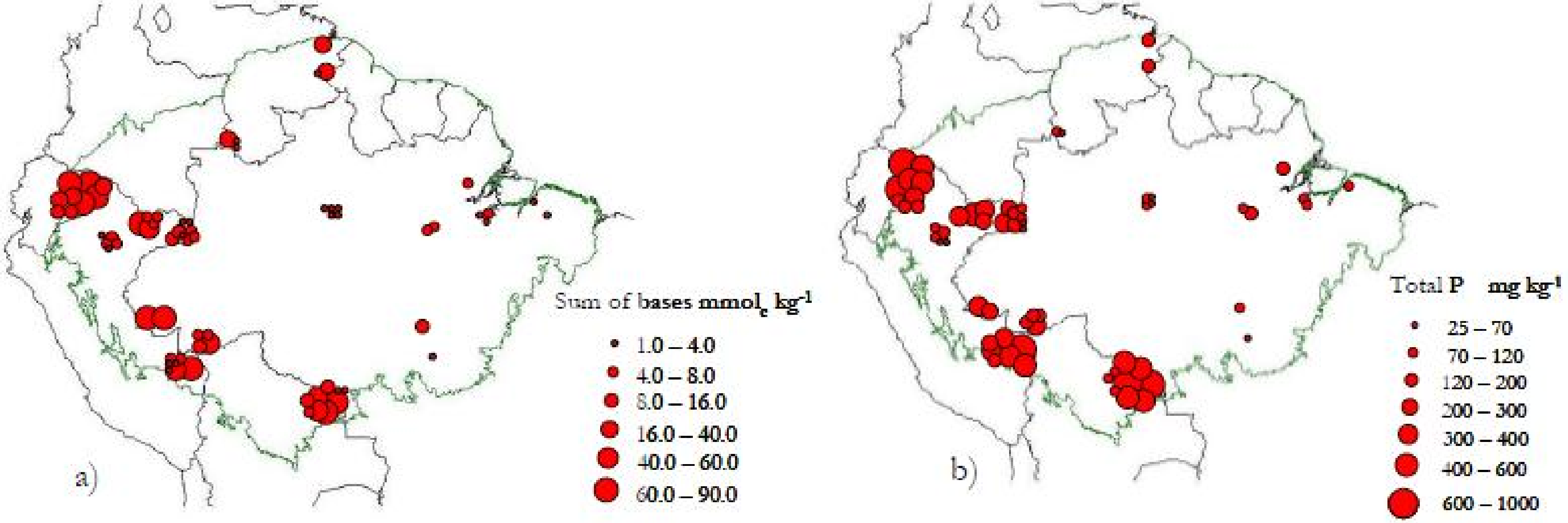


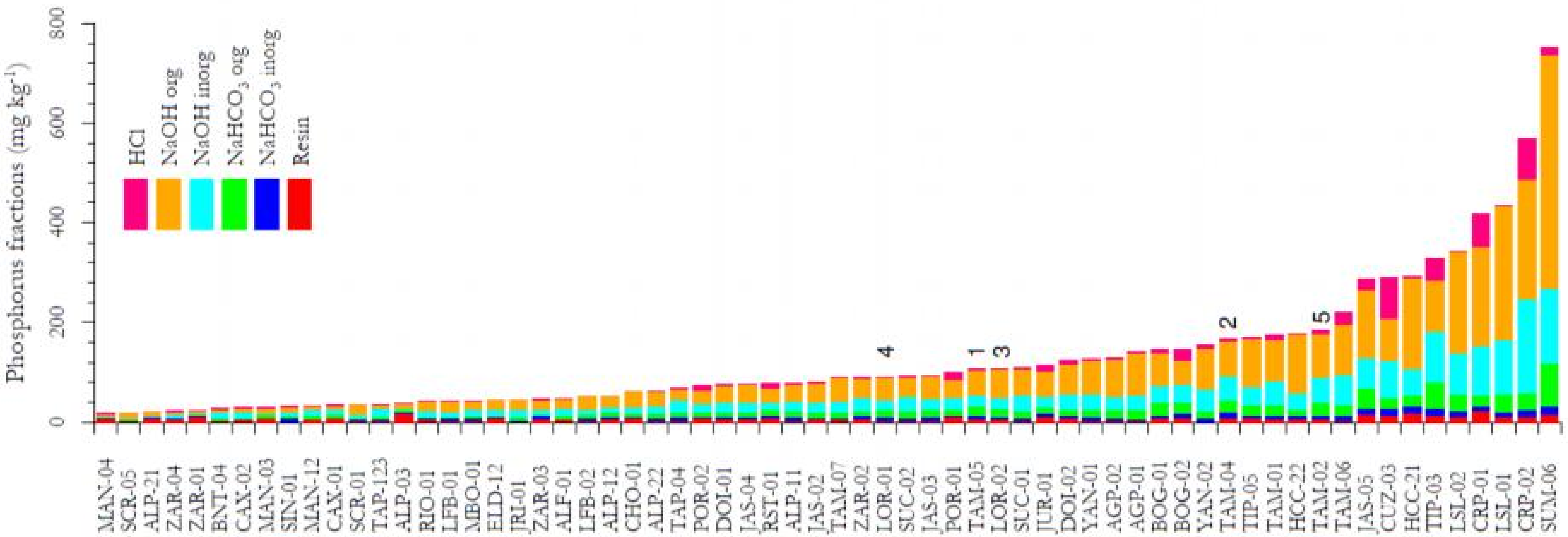
Malhi et al (Global change Biology

But can we pin it down to a specific nutrient ?

- Ph.D thesis work of Carlos (Beto) Quesada at Leeds

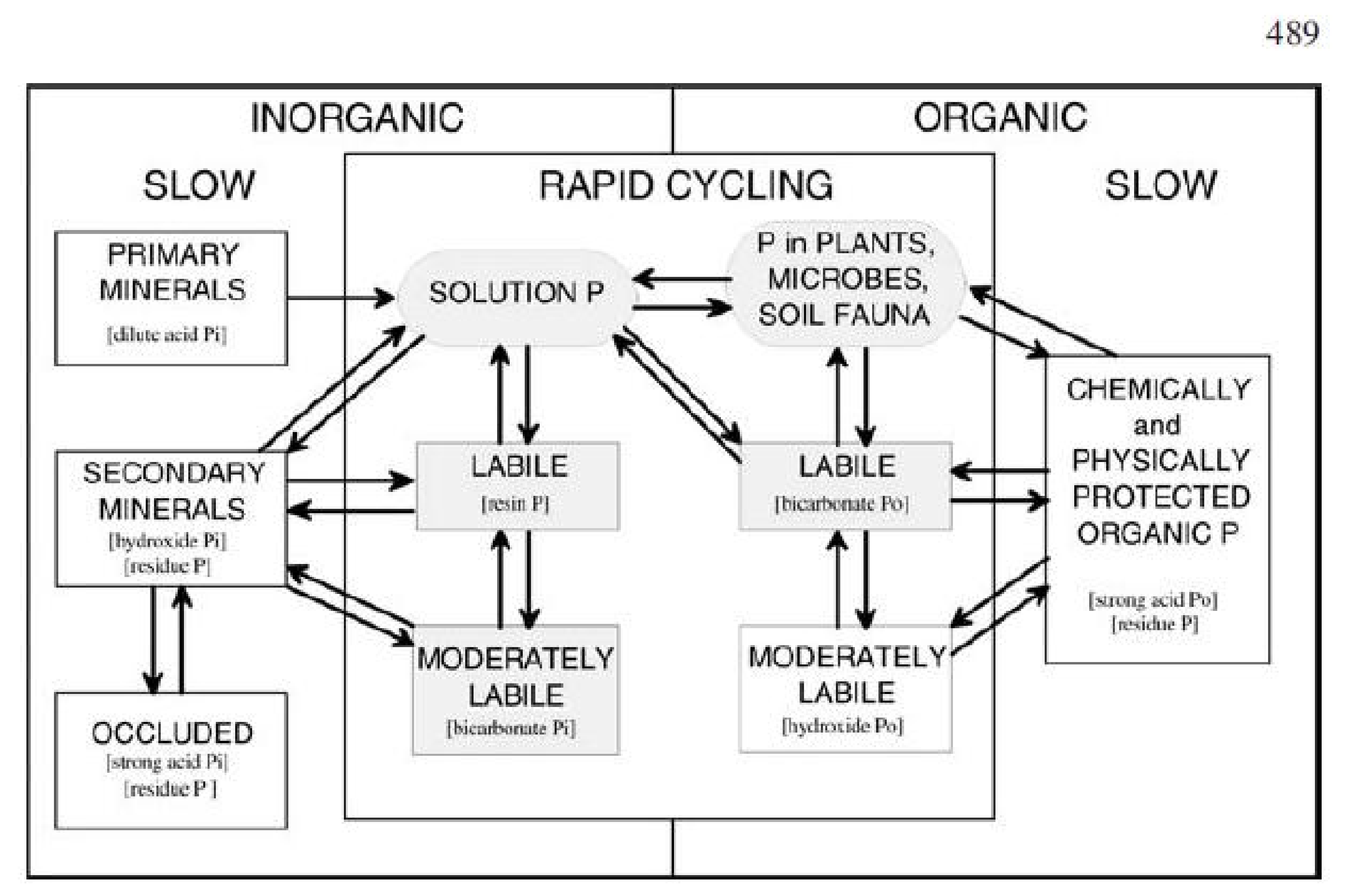
- “Amazon rainforest dynamics in relations to soil chemical and physical conditions”.

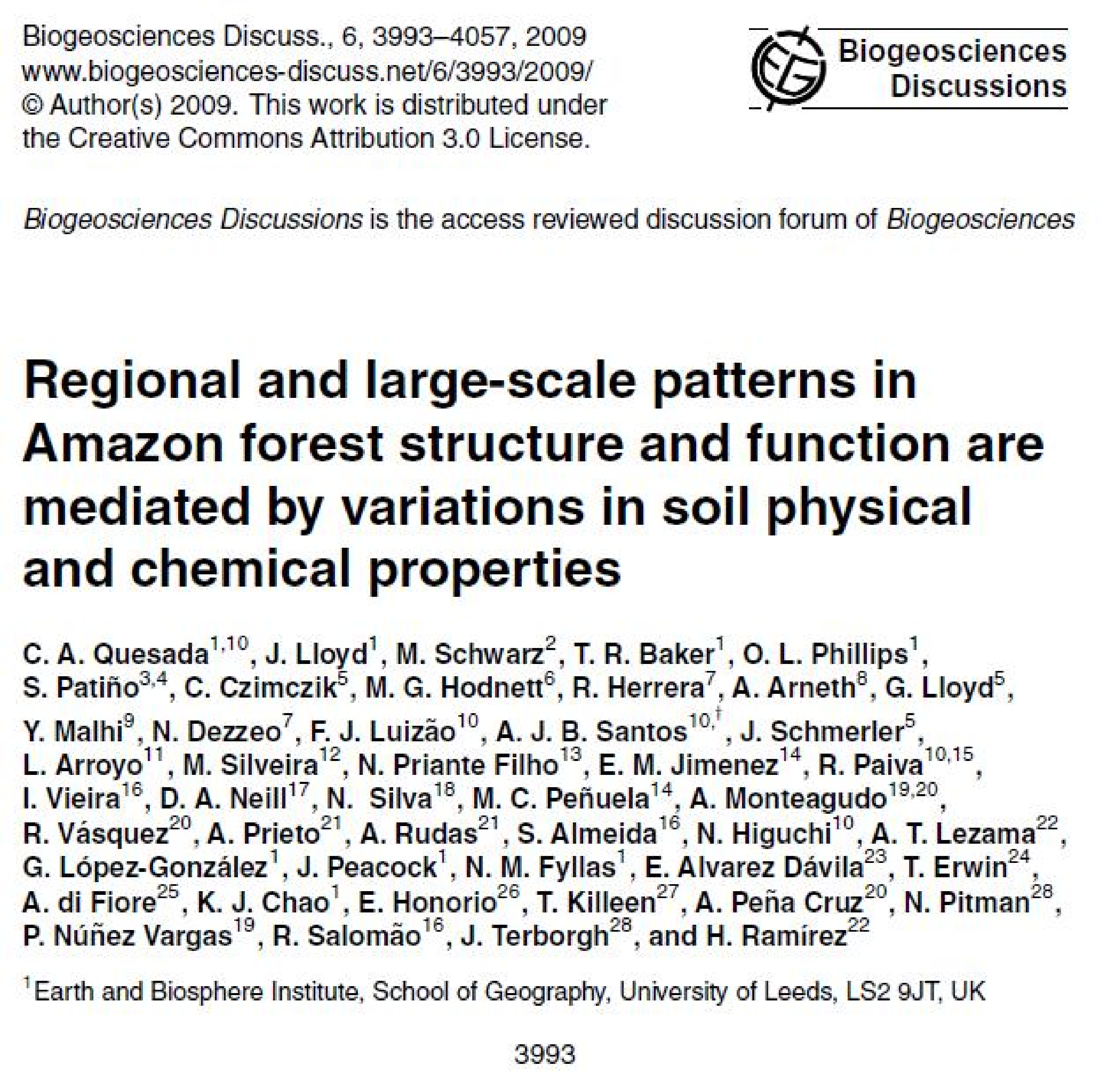




Phosphorus concentrations per extractable fraction for each

Fractionated pools





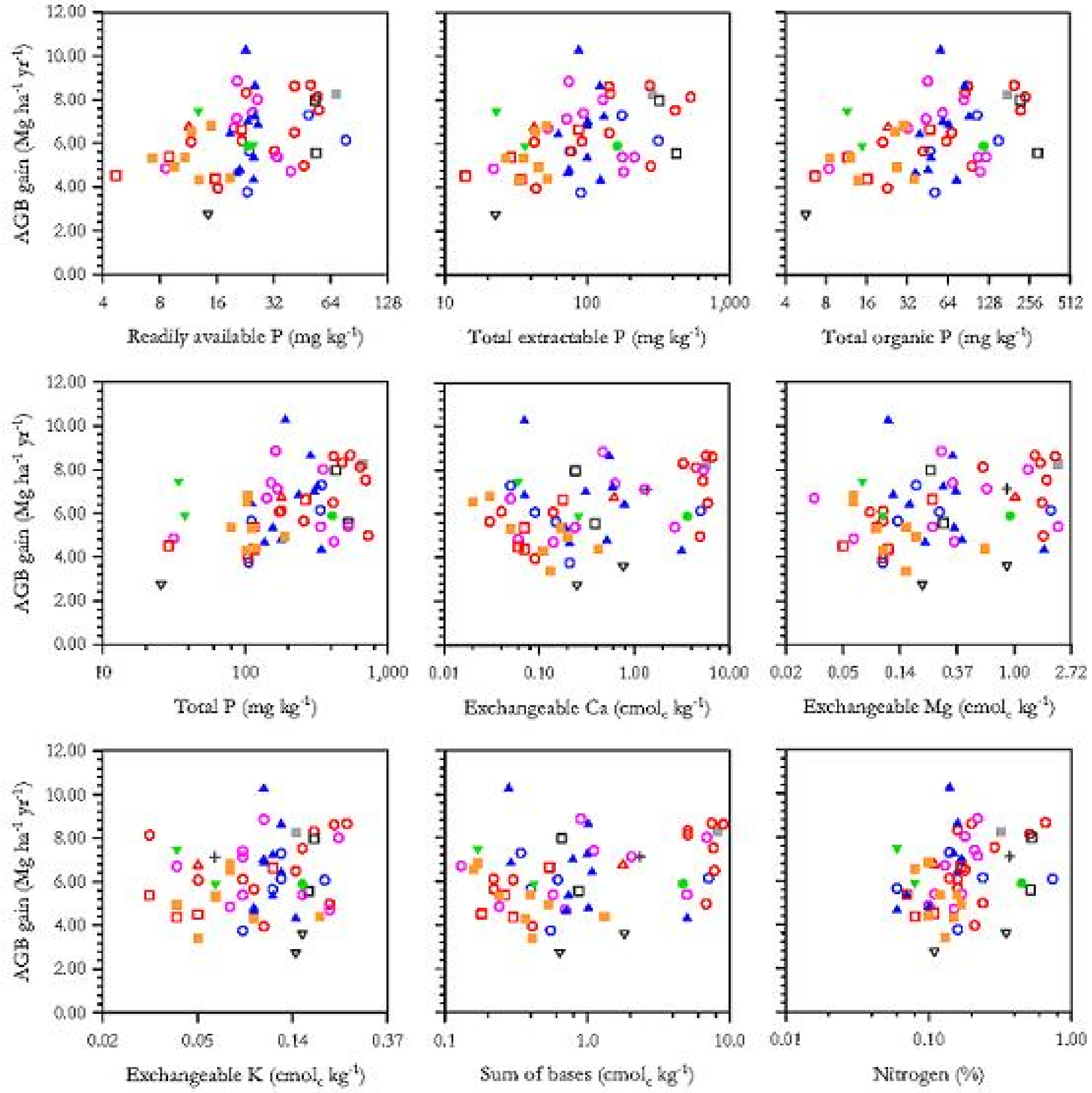
Biogeosciences Discuss., 6, 3993–4057, 2009
www.biogeosciences-discuss.net/6/3993/2009/

Biogeosciences
Discussions

Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties

C. A. Quesada[1,10], J. Lloyd[1], M. Schwarz[2], T. R. Baker[1], O. L. Phillips[1], S. Patiño[3,4], C. Czimczik[5], M. G. Hodnett[6], R. Herrera[7], A. Arneth[8], G. Lloyd[5], Y. Malhi[9], N. Dezzeo[7], F. J. Luizão[10], A. J. B. Santos[10,†], J. Schmerler[5], L. Arroyo[11], M. Silveira[12], N. Priante Filho[13], E. M. Jimenez[14], R. Paiva[10,15], I. Vieira[16], D. A. Neill[17], N. Silva[18], M. C. Peñuela[14], A. Monteagudo[19,20], R. Vásquez[20], A. Prieto[21], A. Rudas[21], S. Almeida[16], N. Higuchi[10], A. T. Lezama[22], G. López-González[1], J. Peacock[1], N. M. Fyllas[1], E. Alvarez Dávila[23], T. Erwin[24], A. di Fiore[25], K. J. Chao[1], E. Honorio[26], T. Killeen[27], A. Peña Cruz[20], N. Pitman[28], P. Núñez Vargas[19], R. Salomão[16], J. Terborgh[28], and H. Ramírez[22]

[1] Earth and Biosphere Institute, School of Geography, University of Leeds, LS2 9JT, UK


AGB gain (Mg ha^{-1} yr^{-1})
0.00
2.00
4.00
6.00
8.00
10.00
12.00
4
8
16
32
64
128
Readily available P (mg kg^{-1})
10
100
1,000
Total extractable P (mg kg^{-1})
4
8
16
32
64
128
256
512
Total organic P (mg kg^{-1})
10
100
1,000
Total P (mg kg^{-1})
0.01
0.10
1.00
10.00
Exchangeable Ca (cmol$_c$ kg^{-1})
0.02
0.05
0.14
0.37
1.00
2.72
Exchangeable Mg (cmol$_c$ kg^{-1})
0.02
0.05
0.14
0.37
Exchangeable K (cmol$_c$ kg^{-1})
0.1
1.0
10.0
Sum of bases (cmol$_c$ kg^{-1})
0.01
0.10
1.00
Nitrogen (%)

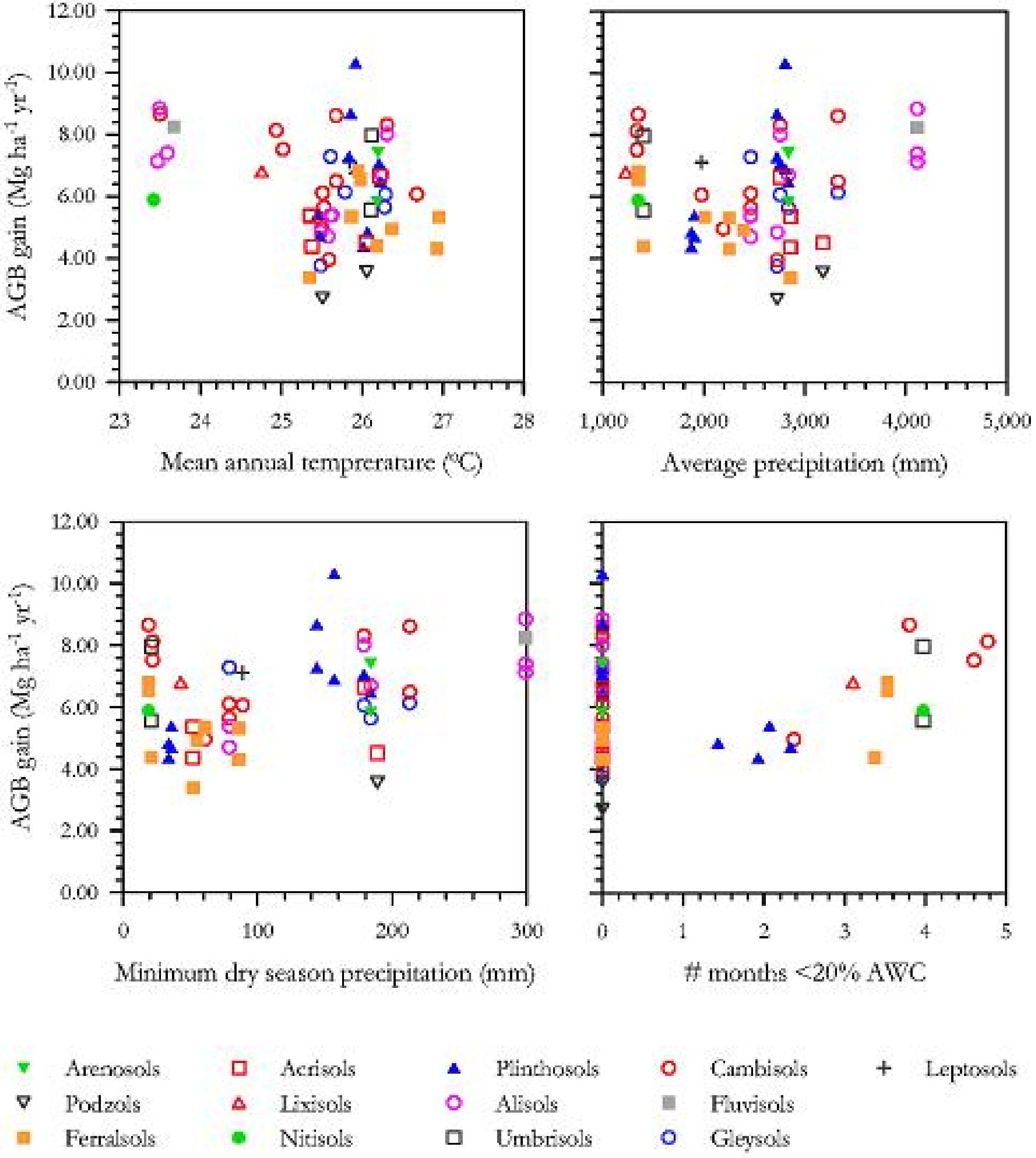


Fig. 9. Relationships between above ground biomass gain and climatic factors.

Observations are not independent (spatially autocorrelated)

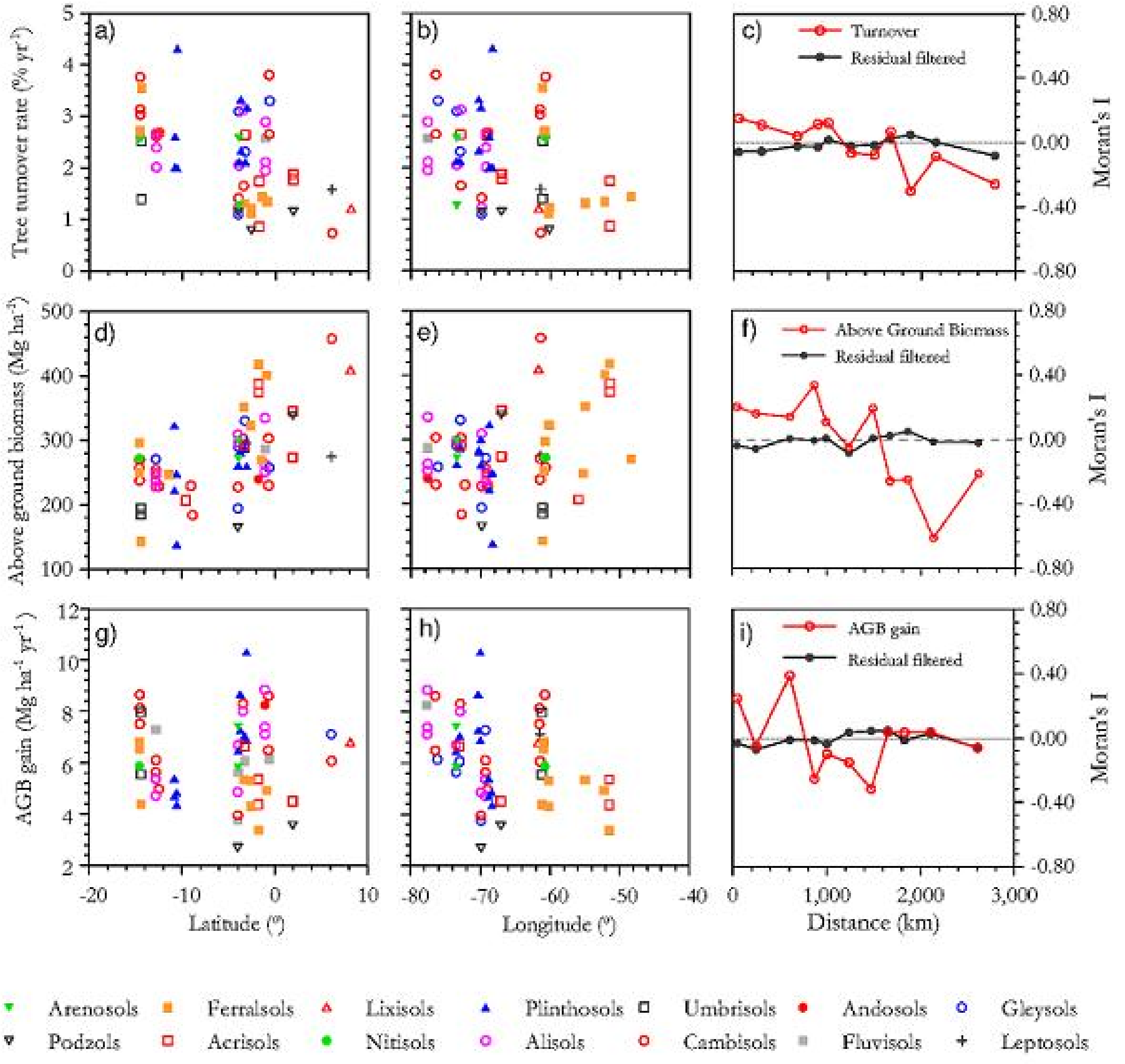
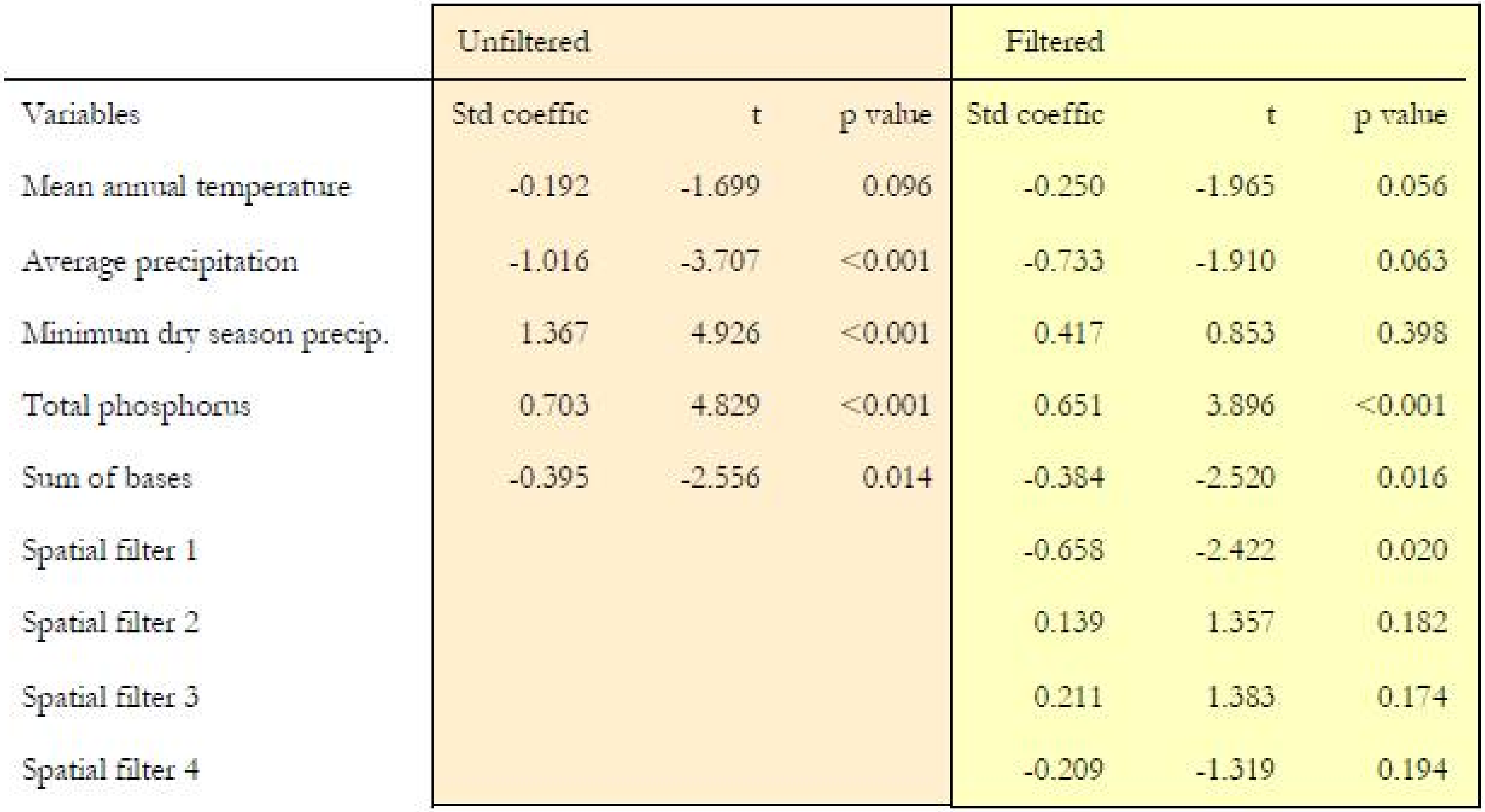


Fig. 2. Correlations of tree turnover, above ground biomass gain and above ground biomass with the geographic space. Moran's *I* correlograms are also given showing spatial autocorrelation but with spatial filters being able to effectively remove its effect from regression residuals.

TOTAL soil phosphorus is the most important predictor

-BUT also climate and perhaps cations



	Unfiltered			Filtered		
Variables	Std coeffic	t	p value	Std coeffic	t	p value
Mean annual temperature	-0.192	-1.699	0.096	-0.250	-1.965	0.056
Average precipitation	-1.016	-3.707	<0.001	-0.733	-1.910	0.063
Minimum dry season precip.	1.367	4.926	<0.001	0.417	0.853	0.398
Total phosphorus	0.703	4.829	<0.001	0.651	3.896	<0.001
Sum of bases	-0.395	-2.556	0.014	-0.384	-2.520	0.016
Spatial filter 1				-0.658	-2.422	0.020
Spatial filter 2				0.139	1.357	0.182
Spatial filter 3				0.211	1.383	0.174
Spatial filter 4				-0.209	-1.319	0.194

Conclusion

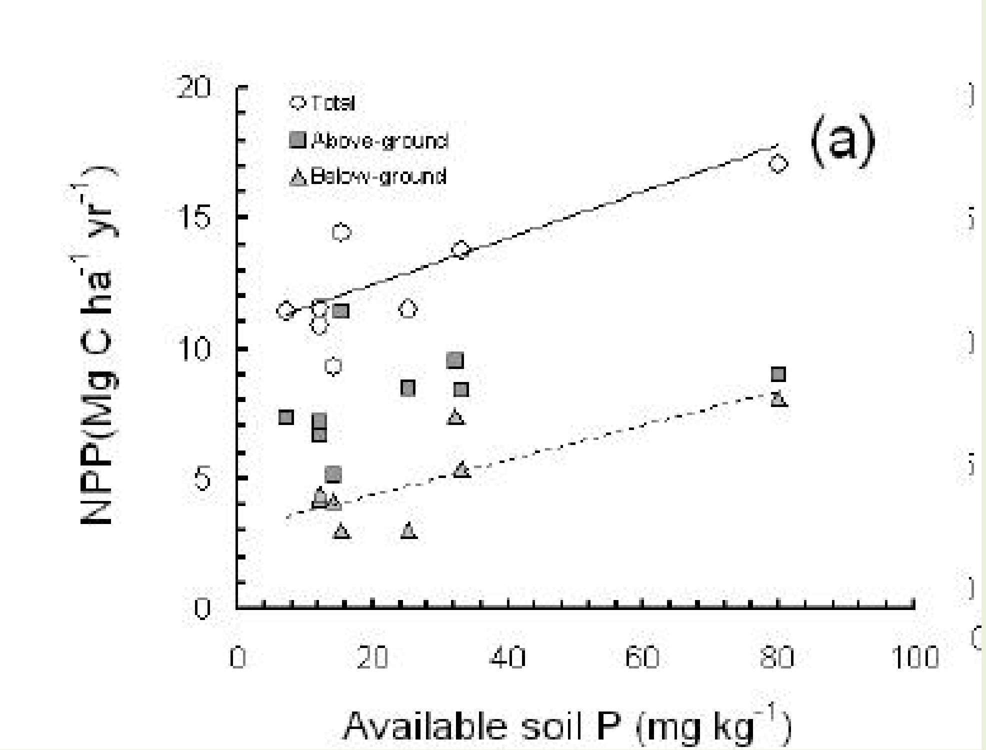
- Vitousek probably right
  - Although exchangeable cations and soil [P] correlate, it is total soil phosphorus that is the best predictor of above ground NPP.
- Probably this translates to total NPP

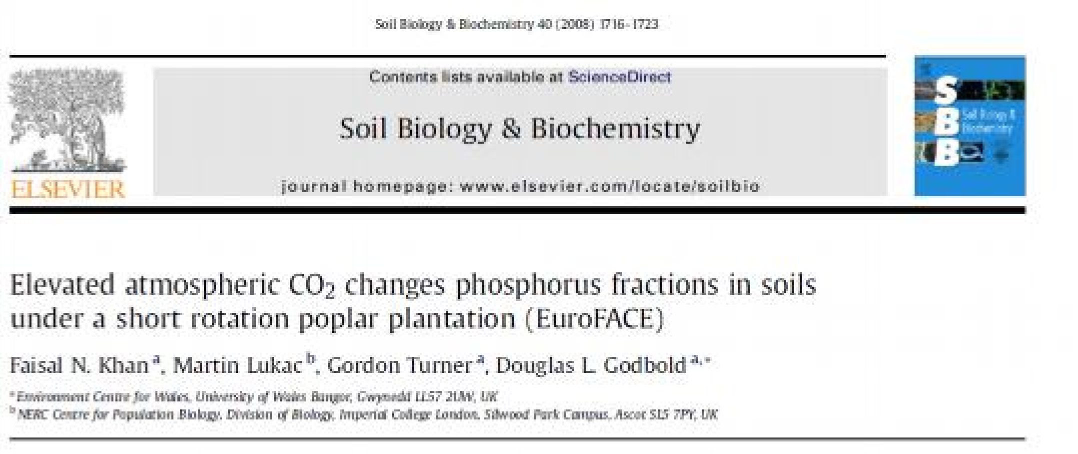
Biogeosciences, 6, 2759–2778, 2009
www.biogeosciences.net/6/2759/2009/

Biogeosciences

Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils

L. E. O. C. Aragão[1,2], Y. Malhi[1], D. B. Metcalfe[1,2], J. E. Silva-Espejo[3], E. Jiménez[4], D. Navarrete[4,5], S. Almeida[6], A. C. L. Costa[7], N. Salinas[1,3], O. L. Phillips[9], L. O. Anderson[1], E. Alvarez[4], T. R. Baker[9], P. H. Goncalvez[7,8], J. Huamán-Ovalle[3], M. Mamani-Solórzano[3], P. Meir[12], A. Monteagudo[13], S. Patiño[4], M. C. Peñuela[4], A. Prieto[14], C. A. Quesada[9,10,11], A. Rozas-Dávila[3], A. Rudas[15], J. A. Silva Jr.[7], and R. Vásquez[13]





Soil Biology & Biochemistry 40 (2008) 1716–1723

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journal homepage: www.elsevier.com/locate/soilbio

Elevated atmospheric CO_2 changes phosphorus fractions in soils under a short rotation poplar plantation (EuroFACE)

Faisal N. Khan[a], Martin Lukac[b], Gordon Turner[a], Douglas L. Godbold[a,*]

[a] Environment Centre for Wales, University of Wales Bangor, Gwynedd LL57 2UW, UK
[b] NERC Centre for Population Biology, Division of Biology, Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK

This may have important implications for tropical forest [CO_2] responses!

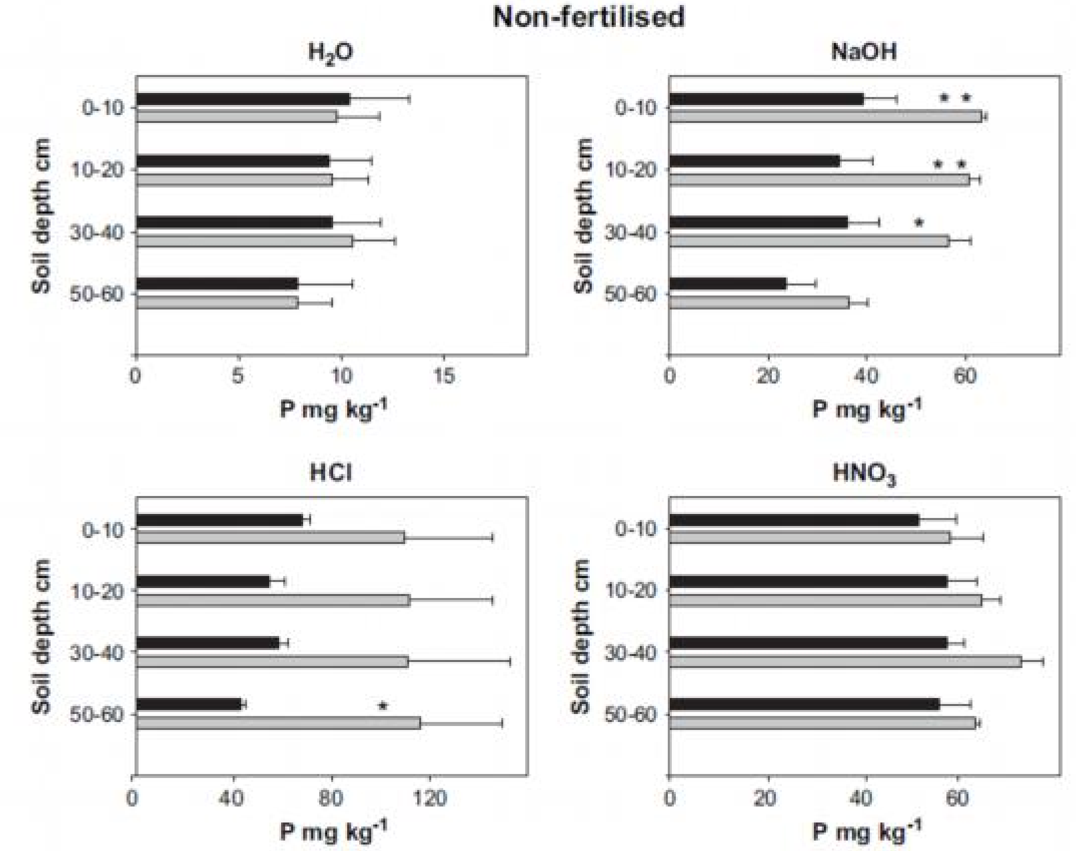


Fig. 2. The concentration of Mo-reactive P in water, NaOH, HCl and HNO_3 extracts of soils from different soil depths in 3 genotypes of *Populus* grown for 5 years under ambient (■) and elevated atmospheric CO_2 (▒). Data shown are means of pooled values for the genotypes (±S.E.). Asterisks show a significant difference between the ambient and FACE treatment at each depth (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

But life is never so simple

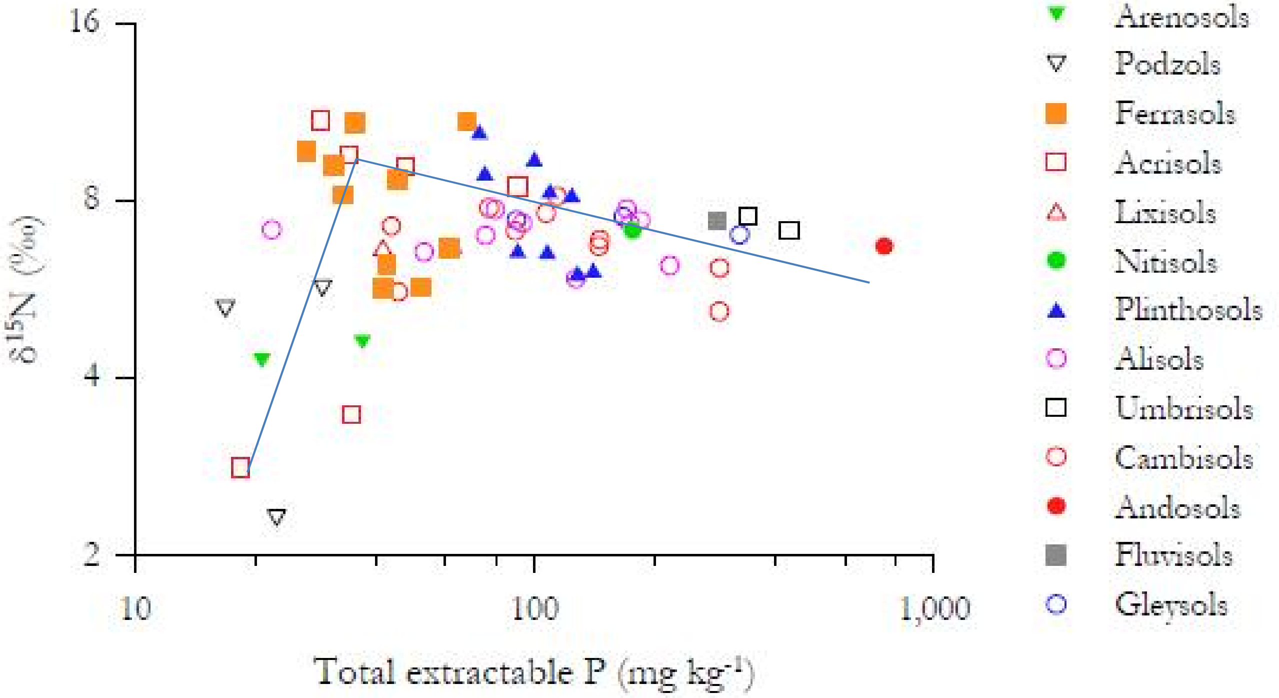
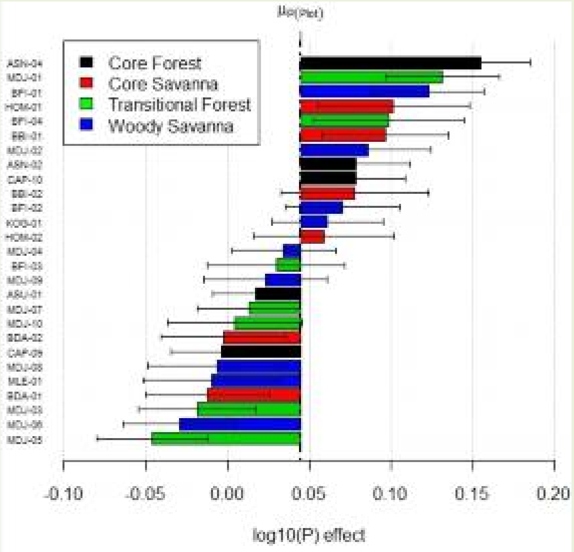


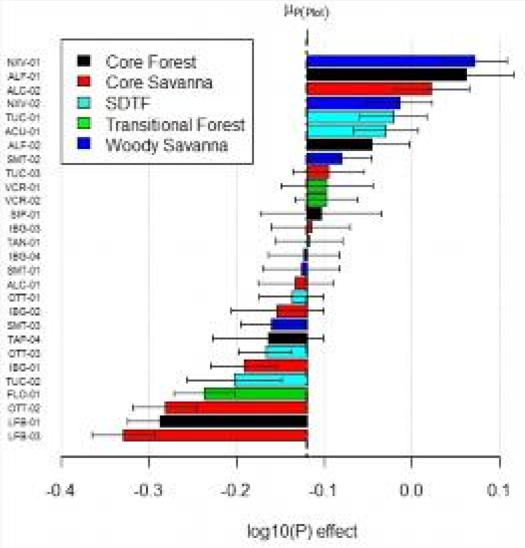
Fig. 11. Relationship between soil $\delta^{15}N$ and the total extractable P pool.

And savannas seem to be much more N-limited at first sight

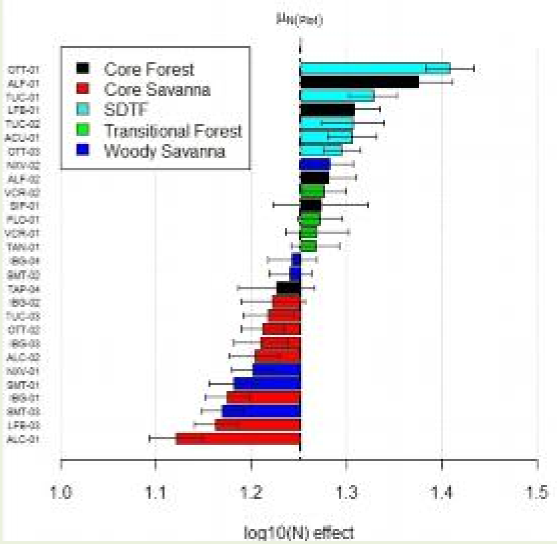
South America

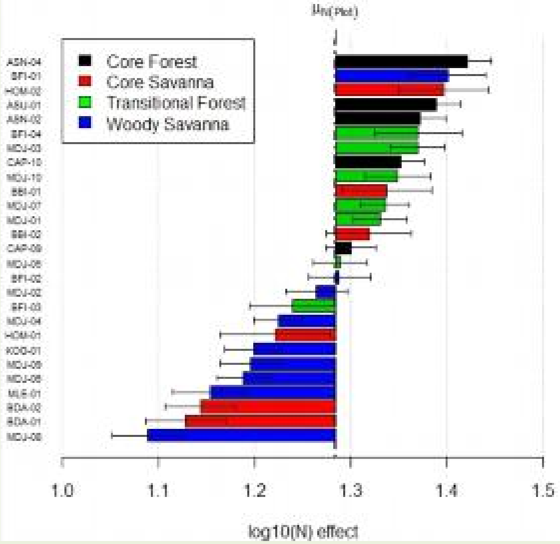
Africa





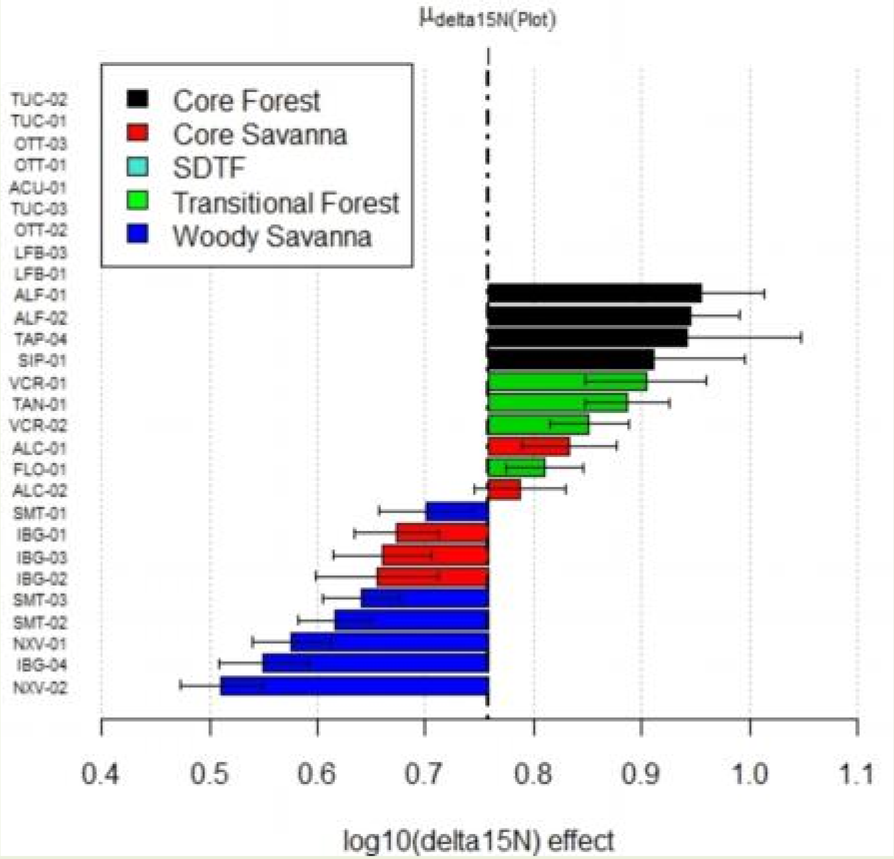
Phosphorus

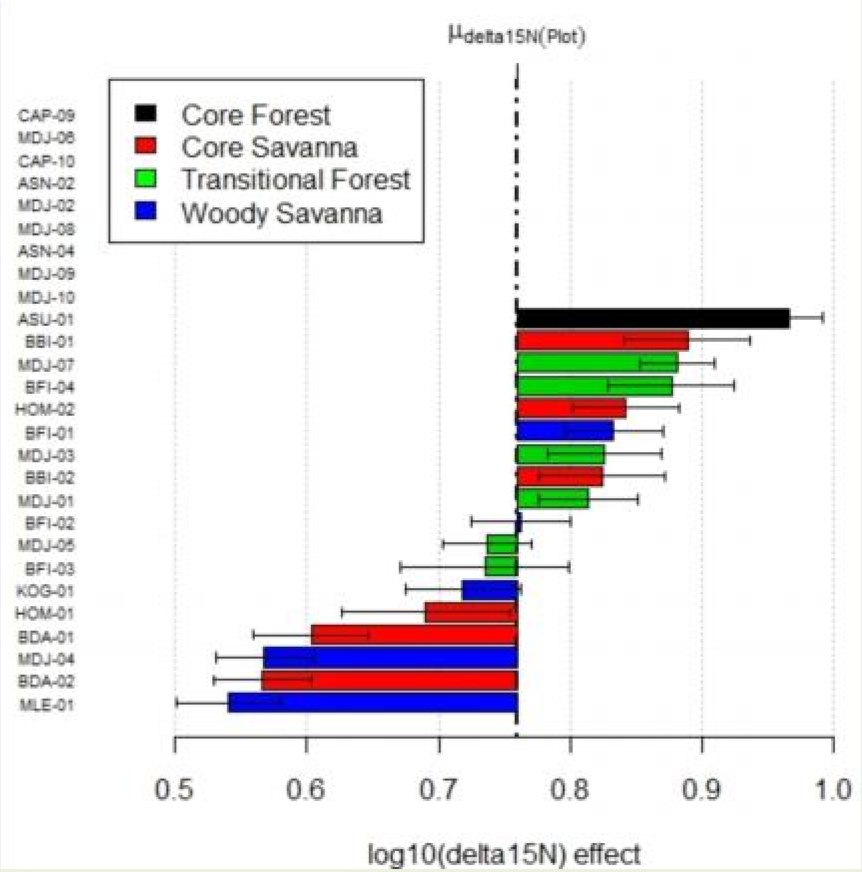




Nitrogen

Also reflected in a very different $\delta^{15}N$





Very different (self-perpetuating ?) biogeochemical cycles probably operate in closely located ecosystems