

Global organization of terrestrial plant–nutrient interactions

Lars O. Hedin*

Department of Ecology and Evolutionary Biology, 222 Guyot Hall, Princeton University, Princeton, NJ 08544

The global extent of earth system change is challenging plant ecologists and physiologists to understand the organization of plant–nutrient relations across scales of observation, from leaf physiology to biosphere feedbacks. Central to this concern are the roles of nitrogen (N) and phosphorus (P) as the major growth-limiting nutrients for plant communities worldwide (1, 2) and as determinants of key physiological processes such as photosynthetic CO₂ fixation (N-rich enzymes; refs. 3 and 4) and cellular biosynthesis (P-rich RNA and ATP; ref. 5). Thus far, terrestrial ecologists and physiologists have largely focused on local and site-specific insights, with few attempts to understand geographically broad variations in plant–nutrient interactions (however, see refs. 4, 6, and 7), or the factors that may give rise to such trends. On page 11001 of this issue of PNAS, Reich and Oleksyn (8) analyze data from plant species worldwide to document dramatically broad variations in leaf N and P vs. carbon (C) contents as functions of latitude and mean annual temperature (MAT; both factors are highly correlated worldwide). This paper constitutes one of three current and complementary efforts (refs. 8, 9, and A. J. Kerkhoff, B. J. Enquist, J. J. Elser, and W. F. Fagan, unpublished work) to document such global-scale variations in plant nutrient investment, and to search for the factors that govern their origin and maintenance.

Global Trends

Reich and Oleksyn (8) identify two fundamental and geographically broad trends in leaf N and P investment: (i) decreasing leaf P content, and to a lesser degree N content, with decreasing latitude (increasing MAT), and (ii) increasing leaf N:P ratio with decreasing latitude (increasing MAT). The strength of this analysis comes from their use of an extraordinarily rich and diverse data set (cf., ref. 10): 1,280 plant species in 704 genera, across 452 locations worldwide, and covering four angiosperm groups and one conifer group. Across all species and taxonomic groups, the most statistically consistent and striking trend was the shift in leaf N:P ratios which, when expressed on a molar basis, increased from ≈10 at high latitudes to ≈40 in the tropics (Fig. 1). These findings point to the existence of an unexpect-

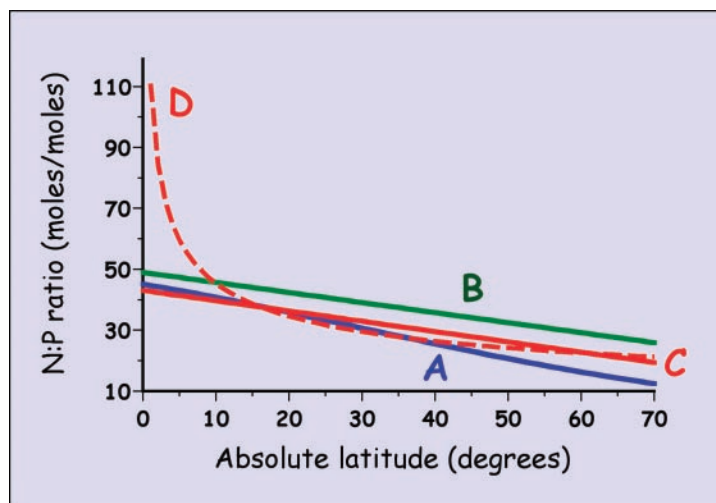


Fig. 1. Regression trends of plant N:P ratios (molar basis) as a function of absolute latitude (degrees): Reich and Oleksyn (ref. 8; blue), Kerkhoff's group (green), and McGroddy *et al.* (ref. 9; red). Line A, Reich and Oleksyn's (8) study of leaf nutrient content in 1,280 plant species from 452 locations worldwide ($\log N:P = 1.30985 - 0.00377 \cdot \text{latitude} - 0.00006 \cdot \text{latitude}^2$; $r^2 = 0.78$; $P < 0.005$). Line B, Kerkhoff's group's study of leaf nutrient content in 1,054 plant species worldwide, binned across 16 latitudes ($N:P = 49 - 0.33 \cdot \text{latitude}$; $r^2 = 0.55$; $P < 0.001$). Line C, McGroddy *et al.*'s (9) study of foliage nutrient content across 59 undisturbed forests worldwide ($N:P = 43.1 - 0.338 \cdot \text{latitude}$; $r^2 = 0.28$; $P < 0.0001$). Line D, McGroddy *et al.*'s (9) study of litterfall nutrient content across 106 undisturbed forests worldwide ($N:P = 111.1 \cdot \text{latitude}^{-0.389}$, $r^2 = 0.43$; $P < 0.0001$).

edly strong, global-scale organization of plant leaf N and P investment across biogeographic and climatic gradients.

What factors cause and maintain these global trends? Reich and Oleksyn (8) develop a series of competing hypotheses that consider either direct effects of temperature on plant N and P physiology, or indirect biogeochemical effects mediated through local soil supplies of N and P. This consideration is where their choice of an extensive data set across diverse species really pays off. They can establish that similar global-scale trends occur within each of five taxonomic groups, and thus find little evidence that taxonomic shifts govern the observed patterns (although they consider that some influence may be caused by shifts in relative abundances of evergreen vs. deciduous plants). They also discount the hypothesis that N and P supply to plants should increase monotonically with MAT worldwide (owing to faster soil recycling in warmer environments), and the idea that higher growth rates in warmer environments should cause lower leaf N:P ratios (owing to high P requirement in RNA and protein synthesis). However, two hypotheses are largely supported: that cold climate may

favor high leaf N and P content relative to C (to offset reduced efficiency of enzymes and metabolites), and that soils may differ in relative N vs. P supply across tropical to temperate regions. In the end, however, Reich and Oleksyn (8) conclude that their data set and analyses do not permit clear separation of these two effects, nor do they discount the possibility of more subtle influences by changes in life forms.

In a second article, McGroddy *et al.* (9) also examine global variations in plant nutrient distributions, but with a focus on entire forested ecosystems rather than individual species. This analysis weights nutrient contents across the biomass and production of all species and individuals within a given forest community; the results therefore are less influenced by rare species, or by averaging across species combinations that do not naturally co-occur. Despite this difference in approach, McGroddy *et al.* (9) document global trends that closely approximate those in Reich and Oleksyn's (8) species-based

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*E-mail: lhedin@princeton.edu.

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analysis, as exemplified by the similar changes in foliar N:P ratios vs. latitude in Fig. 1 (line A vs. C).

These findings (9) shed additional light on factors that may govern these global trends. First, by comparing nutrients in litterfall (i.e., abscised leaves; line D in Fig. 1) against fresh foliage across all forests worldwide, McGroddy *et al.* (9) show that, on average, plants resorb dramatically higher amounts of P (relative to N and C) in tropical forests compared with temperate forests (compare the difference between line D vs. A in Fig. 1). Such resorption is a well known physiological adaptation by which plants conserve nutrients that are in short supply before leaves are abscised and lost as litterfall (11). Second, by using a physiological scaling approach they (9) show that net foliar N and P investment change systematically (relative to C) across forests that differ in aboveground productivity and/or foliar biomass; this finding suggests a dependence of foliar N and P investment on aggregate rates of productivity and nutrient cycling at the ecosystem scale (9).

Interpretation of these two observations suggests strong support for the idea that the global trends in foliar N, P, and C distribution are primarily influenced by economic constraints (i.e., balance of supplies vs. demands at ecosystem scale) on soil P supply in tropical forests, and N supply in temperate forests. The explanation is consistent with ideas (6–7, 12) that lowland tropical soils generally are N-rich but P-poor (owing to prevalence of symbiotic N-fixers and highly weathered soils) whereas temperate forests are N-poor and P-rich (owing to lack of symbiotic N-fixers and less weathered soils).

In a third article (submitted to PNAS), Kerkhoff's group employ a metabolic scaling approach to examine the dependence of plant community productivity on foliar N and P. Based on information from 1,054 plant species distributed worldwide, Kerkhoff's group independently develop a third relationship between leaf N and P content vs. latitude (line B in Fig. 1) and

growing-season temperature. They propose that the apparent lack of temperature dependence in intensity of plant growth (production rate per day of growing season) can be explained by the observed global variations in foliar N and P, with less efficient productivity (expressed per unit foliar N) in tropical than temperate regions.

What impact will these global-scale findings have on the allied fields of ecology, ecological physiology, and biogeochemistry? From a hands-on perspective, they offer well needed guidance for efforts underway to incorporate N and P dynamics within the terrestrial component of coupled earth system models (13). Inclusion of explicit mechanisms of plant-nutrient interactions will better enable these models to simulate long-term biogeochemical controls on plant-atmosphere C exchange worldwide, just as algal C:N:P ratios (so-called Redfield ratios; ref. 14) have been critical for developing models and understanding of global oceanic nutrient cycles (15, 16). The success of this stoichiometric approach in marine ecosystems suggests that these new findings from terrestrial ecosystems may be of considerable importance for developing an integrated understanding of terrestrial ecosystem function. The new terrestrial data also permit stoichiometric comparisons between terrestrial and marine ecosystems. What is perhaps most noteworthy is that terrestrial foliage N:P ratios on average are elevated above the oceanic Redfield ratio of 16 (molar basis), and increasingly diverge from the Redfield ratio with decreasing latitude (Fig. 1). Furthermore, adaptive strategies of nutrient resorption can elevate the N:P consumption ratio even further in land-based plants relative to ocean systems (Fig. 1); this difference needs to be explained.

These new terrestrial findings also raise questions about interactions of nutrients and temperature within physiological processes, and across broad biogeographic, climatic, and taxonomic gradients. For example, whereas Reich and Oleksyn (8)

could not discount the idea of a direct effect of temperature on leaf N and P contents (their prediction: increase in both nutrients relative to C in colder climates), common garden studies of biogeographically and taxonomically distant species across temperature and soil fertility ought to go a long way toward constraining this potential mechanism. In addition, McGroddy *et al.* (9) point to the apparent upper bound to N resorption (relative to P or C) in N-limited high latitude forests (Fig. 1). They speculate that this limit may be caused by universal constraint across species, caused by a significant immobile leaf N pool (17). These questions deserve further attention.

Earth System Evolution

It is perhaps most challenging to understand the role of natural selection and evolutionary adaptation in shaping the observed global patterns in plant nutrient distribution. Ecologists and physiologists have long viewed selection and adaptation as highly localized and individualistic processes, with little evidence of broader spatial feedbacks between ecosystem properties and selective forces on individual plants (18). However, to the degree that forests and aggregate plant communities influence the long-term development of N and P cycles (7), the existence of geographically broad patterns in strategies of plant nutrient investment offers evidence of top-down feedbacks between ecosystem-scale nutrient economies and natural selection of individuals within local environments (e.g., N or P limitation). The emergence of such broad-scale selective pressures on plant nutrient-use strategies does not necessitate a Gaia hypothesis (which is troubled by the potential fallacy of broad-scale group selection) but instead is consistent with the idea of local Darwinian selection within a complex adaptive plant-nutrient system, characterized by top-down as well as bottom-up feedbacks (9, 19). Global management of plants and nutrients within the larger earth-climate system ultimately depends on such understanding.

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