

LETTER

Testing the Growth Rate vs. Geochemical Hypothesis for latitudinal variation in plant nutrients

C. E. Lovelock,^{1*} I. C. Feller,²
M. C. Ball,³ J. Ellis⁴ and B. Sorrell⁴

¹Centre for Marine Studies and
School of Integrative Biology,
University of Queensland,
St Lucia, Queensland 4072,
Australia

²Smithsonian Environmental
Research Center, Edgewater,
MD 20132, USA

³Ecosystem Dynamics Group,
Research School of Biological
Sciences, Australian National
University, Canberra, ACT 2601,
Australia

⁴National Institute of Water and
Atmospheric Science, PO Box
11-115, Hamilton, New Zealand

*Correspondence: E-mail:
c.lovelock@uq.edu.au

Abstract

Two hypotheses have been proposed to explain increases in plant nitrogen (N) and phosphorus (P) concentrations with latitude: (i) geochemical limitation to P availability in the tropics and (ii) temperature driven variation in growth rate, where greater growth rates (requiring greater nutrient levels) are needed to complete growth and reproduction within shorter growing seasons in temperate than tropical climates. These two hypotheses were assessed in one forest type, intertidal mangroves, using fertilized plots at sites between latitudes 36° S and 27° N. The N and P concentrations in mangrove leaf tissue increased with latitude, but there were no trends in N : P ratios. Growth rates of trees, adjusted for average minimum temperature showed a significant increase with latitude supporting the Growth Rate Hypothesis. However, support for the Geochemical Hypothesis was also strong; both photosynthetic P use efficiency and nutrient resorption efficiency decreased with increasing latitude, indicating that P was less limiting to metabolism at the higher latitudes. Our study supports the hypothesis that historically low P availability in the tropics has been an important selective pressure shaping the evolution of plant traits.

Keywords

Ecological stoichiometry, N : P ratio, nitrogen, nutrient resorption, phosphorus.

Ecology Letters (2007) 10: 1154–1163

INTRODUCTION

The availability of nitrogen (N) and phosphorus (P) is important in determining primary production in both marine and terrestrial ecosystems. Nitrogen is an essential component of all enzymes and phosphorus is vital for protein synthesis forming an essential component of RNA (Elser *et al.* 2003). The concentration of N and P in tissues also influences the rates of ecological processes, for example, grazing, parasitism and decomposition have been observed to be influenced by the stoichiometry of N and P within tissues (Sturner & Elser 2002; Güsewell 2004).

In the marine environment the ratio of N : P and deviation from the Redfield ratio of 16 : 1 has been used as a tool to understand biological processes in the oceans, including interactions between the ocean, the atmosphere and the terrestrial environment and how these processes have changed through time (Redfield 1958; Lenton & Watson 2000). Recently, biologists have begun to probe terrestrial ecosystems for evidence of a terrestrial 'Redfield ratio', seeking to use biological stoichiometry to understand the evolution and ecology of organisms (e.g. Woods *et al.*

2003; Elser 2006) and ecosystems (McGroddy *et al.* 2004; Schade *et al.* 2005).

A number of recent broad-scale surveys of leaf nutrient concentrations from the terrestrial literature suggest a general pattern, where N : P is high at tropical latitudes and decreases as latitude increases and temperatures decline (Güsewell 2004; McGroddy *et al.* 2004; Reich & Oleksyn 2004; Kerkhoff *et al.* 2005). Reich & Oleksyn (2004) advanced two hypotheses to explain this pattern. First, they advanced the Geochemical Hypothesis, where tropical soils are geologically older and more weathered resulting in higher N : P ratios in tropical latitudes, i.e. supply of P is low relative to N (Vitousek 1984; Vitousek & Sanford 1986; Crews *et al.* 1995). Second, they suggested that temperature-related physiological processes result in higher rates of C gain relative to P availability at low latitudes, i.e. P is diluted in tissues in tropical compared to temperate latitudes. Kerkhoff *et al.* (2005) presented similar trends in N : P over latitude, but modified the second hypothesis in line with the Growth Rate Hypothesis (Elser *et al.* 2000). The Growth Rate Hypothesis is based on observations that rapid growth results in a high demand for P used in the ribosomes for

synthesis of mRNA relative to demand for N, leading to low N : P ratio in rapidly growing organisms (Elser *et al.* 2000). Kerkhoff *et al.* (2005), following Woods *et al.* (2003) suggested that because growth rates are accelerated in cooler climates as a response to compressed growing seasons, P demanding biosynthetic components (e.g. ribosomes) are more abundant in tissues of temperate than tropical species. Moreover, it follows from the Growth Rate Hypothesis and earlier theoretical work of Odum & Pinkerton (1955) that nutrient use efficiency for metabolic processes, for example, photosynthetic nutrient use efficiency, would also increase with growth rate (Sternner & Elser 2002), at least for a range of growth rates (Odum & Pinkerton 1955), leading to the expectation that nutrient use efficiency of metabolic processes should increase with decreasing temperature and increasing latitude. Indeed, photosynthetic nutrient use efficiency and nitrogen use efficiency of production have been observed to increase with altitude and decreasing temperature (e.g. Körner & Diemer 1987; Kerkhoff *et al.* 2005).

In addition to N : P ratios being sensitive to nutrient availability (Güsewell *et al.* 2003; Güsewell 2004) and growth rates (Elser *et al.* 2003; Ågren 2004), N : P ratios are strongly influenced by vegetation or forest type (Güsewell 2004; McGroddy *et al.* 2004; Reich & Oleksyn 2004; Rejmankova 2005). McGroddy *et al.* (2004) suggested, in contrast to Aerts (1996), that (i) the biome (i.e. forest type), or the biogeochemistry of differing biomes may exert a strong selection pressure on N : P ratio and (ii) the nutrient resorption efficiency, or the efficiency with which plants resorb nutrients prior to leaf abscission is an important process that varies among biomes and is a trait that has evolved in response to limited soil nutrient availability.

Trees have perennial tissues and can store and translocate nutrients between organs. Resorption of nutrients during tissue senescence often contributes as much to the nutrient content of growing leaves as direct nutrient uptake from soils (Chapin & Kedrowski 1983; Feller 1995; Aerts 1996; Killingbeck 1996; Wright & Westoby 2003). Nutrient resorption is strongly influenced by nutrient availability (Pugnaire & Chapin 1993; Feller 1995; Aerts 1996; Güsewell 2004; Rejmankova 2005). A simple model has been proposed by Wright & Westoby (2003) where high nutrient resorption efficiency reflects the high cost of nutrient acquisition from the soil (i.e. low nutrient availability) compared to the costs of remobilization of nutrients from senescing leaves. Support for the Geochemical Hypothesis should arise if nutrient resorption efficiency, particularly for phosphorus, is higher at low latitudes and declines with increasing latitude (Oleksyn *et al.* 2003; Wright & Westoby 2003; Güsewell 2004, 2005; McGroddy *et al.* 2004; Rejmankova 2005).

Although Sternner & Elser (2002) did not directly consider nutrient resorption efficiency of higher plants in their models, we might expect that high growth rates because of compressed growing seasons (Kerkhoff *et al.* 2005) would result in high demand for nutrients, and thus resorption efficiency should increase with decreasing temperature and at higher latitudes, similar to the pattern expected with nutrient use efficiency. In mountain birch, nitrogen resorption efficiency increased with declining temperature (Nordell & Karlsson 1995) providing some support for the sensitivity of nitrogen resorption efficiency to temperature and thus possibly to variation in growth rate. Additionally, Oleksyn *et al.* (2003) found that pines from higher latitudes had higher nutrient resorption efficiency than genotypes from lower latitudes (Oleksyn *et al.* 2003). However Oleksyn *et al.* (2003) interpreted the gradient in nutrient resorption efficiency from pines of different latitude as reflecting nutrient availability of the area of origin rather than variation in growth rate with latitude. The Growth Rate Hypothesis and Geochemical Hypothesis offer a range of predictions for the variation of nutrient resorption efficiency over latitude and thus provide a means of exploring the applicability of these hypotheses over large geographic scales.

Here, we present results of a series of experimental fertilization studies between latitude 36° S and 27° N in one forest type, mangroves. Mangrove forests occur in the intertidal zone on protected coasts in both tropical and subtropical latitudes closely following the distribution of seagrass and coral reefs (from 35° S to 27° N, Duke *et al.* 1998). They have very low species diversity compared to other tropical forests, with high levels of vicariance (Duke *et al.* 1998). Over the Indo-West Pacific and Atlantic East Pacific biogeographic provinces the dominant species belong to the same genera: *Avicennia* and *Rhizophora*. Mangrove forests with their low species diversity and common species with wide geographic distributions provide an excellent system in which to test hypotheses of how and why nutrient concentrations in plant tissues vary over latitude.

Within the context of our fertilization experiments, where wide ranges in growth rates are observed, we investigate how nutrient use efficiency varies with growth rate and over latitude. We test whether growth rates, adjusted for temperature, increase with increasing latitude as suggested by Kerkhoff *et al.* (2005). Furthermore, we assess whether photosynthetic nutrient use efficiency increases with growth rates as predicted by the Growth Rate Hypothesis or whether they are negatively correlated with latitude, as predicted by the Geochemical Hypothesis.

Finally, we assess how nutrient resorption efficiency varies with growth rates and over latitude. While the Growth Rate Hypothesis suggests there should be higher

resorption efficiency where growth rates are accelerated, i.e. at higher latitudes to compensate for short growing seasons and enhanced nutrient demand, the Geochemical Hypothesis predicts the opposite trend, of high nutrient resorption efficiency in low P tropical environments.

METHODS

Site descriptions

This study was conducted using 10 mangrove forest sites (see Table S1, which is published as supporting information on the Ecology Letters website), three sites are from the Caribbean, and five sites from Australia and two sites from New Zealand. Sites vary from latitude 36° S to 27° N, ranging in average minimum temperatures from 11 to 27 °C, and average maximum temperatures from 19 to 32 °C. Sites also span a large variation in average annual rainfall from 0.3 m in Exmouth to over 3.5 m in Bocas del Toro, Panama. Many of the sites have forests of variable height within the site. Most of the sites were dominated by species within the genus *Rhizophora* L. or *Avicennia* L., with the exception of the Hinchinbrook Channel in Queensland where *Ceriops tagal* (Perr.) C.B. Rob. (Rhizophoraceae) dominates the dwarf forests. Tidal range was microtidal in the Caribbean sites (*c.* 0.5–1 m) and macrotidal in the Australian and New Zealand sites (up to 3.5 m). Sediments also varied, from sand in dwarf forest in Florida and the Hinchinbrook Channel to highly organic sediments (mangrove peat) that is > 80% carbon in Twin Cays, Belize and Bocas del Toro, Panama.

Complete sites descriptions, including description of fertilization plots have been previously published for Belize (Feller *et al.* 2002), Florida (Feller *et al.* 2003) and Bocas del Toro (Lovelock *et al.* 2004). In North Queensland, the mangroves at Cape Cleveland in Chunda Bay have previously been described by Clarke (2004). Our site was situated on the landward edge of the Bay in a stand of dwarf *C. tagal* and *Avicennia marina* (Forsk.) Vierh. on the edge of the saltflats. Our site at Port Douglas was in dwarf *A. marina* forest high in the intertidal at the southern end of Sandfly Creek which has previously been described by Trott *et al.* (2004). In the Hinchinbrook Channel the site is on the landward edge of the Channel at a site 25 km south of the town of Cardwell. There is a narrow fringing forest of *Rhizophora lamarckii* Montr. growing on highly organic sediments, which gives way to an extensive stand of dwarf (< 1.5 m) *C. tagal* that is growing on coarse sand. A description of the mangroves of the Hinchinbrook Channel can be found in Clough (1998). In Exmouth the sites were situated in Mangrove Bay on the western side of the North West Cape and in Giralia Bay in the Exmouth Gulf. A general site description is available in Alongi *et al.* (2003).

The region is extremely arid (< 30 cm rainfall per year). The mangroves in the Exmouth region are dominated by *A. marina*. The site was situated on the Southern side of the Bay in a stand of dwarf (< 1.5 m) trees. Two sites from New Zealand are used in this study, both having monospecific stands of *A. marina*. Waikopua is close to the city of Auckland. The site is muddy due to high rates of sediment deposition due to clearing and agricultural land use in the adjacent terrestrial ecosystem. A full site description of Waikopua can be found in Ellis *et al.* (2004). The second site in New Zealand was situated in the Whangapoua estuary. This site is not heavily impacted by land-use change, and sediments are coarse to fine sands. A general site description can be found in Schwarz (2004).

Experimental design

A total of 18 to 108 trees were randomly selected at each site. Where 81 or more trees were used (i.e. Florida, Belize and Bocas), trees were spread over three random blocks covering 3–4 forest stature categories or zones, dwarf < 1.5 m in height, taller fringing forests > 3 m, and transition forest, 1.5–3 m in height, and in the case of Bocas del Toro a landward transition zone was also included. A similar design was used at Giralia Bay and the Hinchinbrook Channel where 54 trees were used, but where the transition zone was not included. In New Zealand, Giralia Bay, Cape Cleveland and Port Douglas 18–24 trees within a homogenous vegetation type (e.g. dwarf or taller fringing forest) were chosen. In Mangrove Bay, Port Douglas and Cape Cleveland, only dwarf stands were used. Treatments were randomly assigned to trees within sites. Trees were fertilized with nitrogen (N) as urea (45 : 0 : 0) by coring an 8 cm diameter and 30 cm deep hole in the sediment at two locations 50–100 cm at either side of the bole of individual trees and inserting 150 g of urea encased in dialysis tubing into each hole (total dose of 300 g per tree) and resealing it with the soil core, as described in Feller 1995. Trees were fertilized with phosphorus (P) using 300 g triple super-phosphate, P₂O₅ (0 : 45 : 0) in dialysis tubing. Control trees (C) were similarly cored but not fertilized. These treatments were applied twice annually in Belize, Florida, Panama and New Zealand, and annually in all other sites.

Plant growth

As a bioassay of the effects of nutrient treatment on plant growth, we monitored the number of shoots and the length of shoots on five, initially unbranched, shoots (first order) in sunlit positions in the outer part of the canopy of each tree over a 2-year period. To distinguish the growth produced over each interval, we labelled the leaves in the apical

position on each of these shoots at each sampling period (6 months to 1 year). Shoot length and number of new leaves were measured from the previously marked apical position to the base of the current apical bud along the main axis and any lateral shoots as described in Feller (1995). Demographic growth analysis was used to determine the effect of nutrient enrichment on plant growth rates (McGraw & Garbutt 1990; Feller 1995). Demographic absolute growth rates ($\text{DAGR} = [\text{shoot length}_{\text{time}2} - \text{shoot length}_{\text{time}1}] / [\text{time}2 - \text{time}1]$) were calculated for monthly increases in shoot length for the second year after fertilization. To calculate temperature-adjusted growth rates using available climate data sets, DAGR was divided by the mean annual minimum temperature for each site. Although adjustments using degree-days would have been preferable, detailed climate data are only available at a subset of the sites, thus using minimum temperatures facilitated comparison among sites.

Photosynthetic carbon gain

Photosynthetic gas exchange of leaves was measured after the trees had been exposed to the fertilizer treatments for at least 2 years. Measurements were made on a cloudless morning with a portable gas exchange system (LiCor 6400, LiCor Corp., Lincoln, NE, USA), and the leaves were collected afterwards for mineral analysis (see below). Measurements were made on three of the youngest fully developed leaves (usually the penapical leaf pair) per tree using natural light, under ambient temperature, humidity and CO_2 concentrations. After measurements of photosynthesis, leaves were detached; their area was measured (LI 3000A leaf area meter attached to LI 3050 transparent belt conveyer; LiCor Corp.). Leaves were dried to a constant weight at 70 °C and ground to a fine powder. Concentrations of total carbon (C) and N were determined with a CHN Analyzer (Perkin-Elmer 2400, Perkin Elmer, Norwalk, CT, USA) at the Smithsonian Environmental Research Center (Edgewater, MD). Phosphorus concentration was determined using an inductively coupled plasma spectrophotometer (ICP) by Analytical Services (Pennsylvania State University, State College, PA, USA).

Nutrient use efficiency of photosynthetic carbon gain was calculated as photosynthetic C gained per unit N (PNUE) or P (PNUE).

Nutrient concentrations in leaves

Leaves for analyses were harvested in year 2 of the experiment. By that time, all the leaves on the targeted trees had been produced under the influence of the experimental treatment. From a sunlit position in the top of the canopy, we collected fresh, fully mature green leaves

(hereafter referred to as green leaves) from a penapical stem position. We also collected fully senescent (yellow) leaves with a well-developed abscission layer (hereafter referred to as senescent leaves) from a basal position on first-order branches. Senescent leaves were taken directly from the trees to eliminate nutrient loss via leaching and leaf loss by tidal flushing, which happen when litter drops to the forest floor in this mangrove wetland. We assumed that yellow leaves that could be removed from a stem with only slight pressure represented the senescent leaf litter. For each leaf, area was determined. Leaf samples were dried at 70 °C in a convection oven and ground in a Wiley Mill to pass through a 40 (0.38 mm) mesh screen. Concentrations of total carbon (C) and N and mineral nutrients were determined as described above. We also augmented our data set of leaf nutrient concentrations with values obtained from the literature.

Resorption efficiency for either N (NRE%) or P (%PRE) was calculated for each experimental tree as the percentage of N or P recovered from senescing leaves before leaf fall (Chapin and Van Cleve 1989).

Data analysis

Tests of whether %N, %P and the N : P ratio varied over latitude were performed with a data set consisting of 'control' or non-fertilized trees and values from the literature. All other analyses were carried out on a data set that consisted of mean values for site \times zone \times treatment combinations ($N = 3-8$ trees for each mean). Not all parameters are available at all sites. While DAGR, N and P concentrations are available at all sites, photosynthetic nutrient use efficiency and nutrient resorption efficiency was not always available because of inaccessibility of the site, or the availability of senescent leaves during visits to the sites. Data was analysed using the linear models module of the statistical computing package DATA DESK 6.1 (Data Descriptions, Inc. Ithaca, NY, USA). Data were log-transformed prior to analysis. The fixed factors in the models were fertilization treatment or plant family with continuous factors being either latitude or growth rate. Inspecting residual plots assessed the suitability of the models.

RESULTS

Both N and P in mangrove tissues increased significantly with increasing latitude (Fig. 1). Our data were consistent with other published data from mangrove forests. Over all sites, zones and treatments, N : P ratio varied between 16 and 98. The median was 31.98 and the mean ratio of N : P was 36.98 ± 2.20 (Fig. 1). Comparison of trends in mangrove N, P and N : P ratio to those from terrestrial environments show that mangrove N concentrations increase with latitude with a much stronger slope

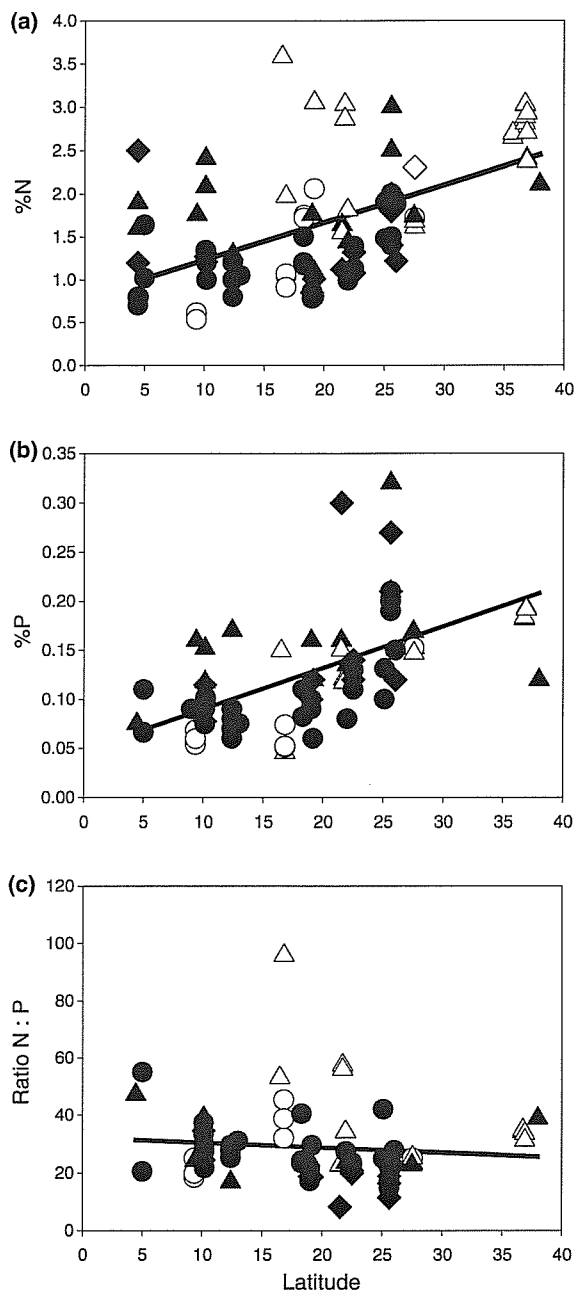


Figure 1 Increase in per cent nitrogen (a), per cent phosphorus (b) and N : P ratio (per cent) (c) in green mangrove leaf tissue over latitude. Closed symbols are values obtained from the literature while open symbols were measured at experimental sites from control trees. Circles are values from the Rhizophoraceae, triangles the Avicenniaceae and diamonds are measurements from other taxa. The lines of best fit are of the form: (a) $\%N = 0.769 + 0.0435 \times \text{Lat.}$, $R^2 = 0.335$, $P < 0.0001$; (b) $\%P = 0.0477 + 4.223 \times \text{Lat.}$, $R^2 = 0.335$, $P < 0.0001$; (c) $N : P = 32.10 - 0.169 \times \text{Lat.}$, $R^2 = 0.01$, $P > 0.05$.

(fivefold greater slope) than in terrestrial plants, but that increases in P with latitude were similar in mangrove and terrestrial vegetation. Variation in N : P over latitude was negative, similar to that in terrestrial plants, but the slope was not significant in the mangrove data (Fig. 1c). The slope of N : P vs. latitude for the mangrove forests was one-third of that observed in terrestrial plants (cf. Reich & Oleksyn 2004).

Over all sites growth rates varied widely (from 0.11 to 5.89 cm months⁻¹). Mean growth rates were 1.82 ± 0.20 cm months⁻¹, and median 1.01 cm months⁻¹. When growth rates were adjusted for minimum temperatures at each site, growth rate significantly increased with increasing latitude (Fig. 2, $R^2 = 0.181$, $P < 0.0001$) although this trend was not evident for unadjusted growth rates. Over all latitudes fertilization treatment did not significantly influence the relationship between temperature-adjusted growth rate and latitude ($F_{2,84} = 1.26$, $P = 0.443$). The relationship between temperature-adjusted growth rate and latitude was also similar for both the Rhizophoraceae and Avicenniaceae (latitude \times family interaction, $P > 0.05$).

Photosynthetic nitrogen and phosphorus use efficiency (PNUE and PPUE) showed significant but weak negative co-variation with temperature-adjusted growth rate (Table 1), but PNUE and PPUE declined significantly and strongly with increasing latitude (Fig. 3). Fertilizer treatments did not significantly affect the relationship between PNUE and PPUE and latitude ($P > 0.05$). Plant families had no significant effect on the patterns in PPUE over latitude. In contrast, significantly different patterns in

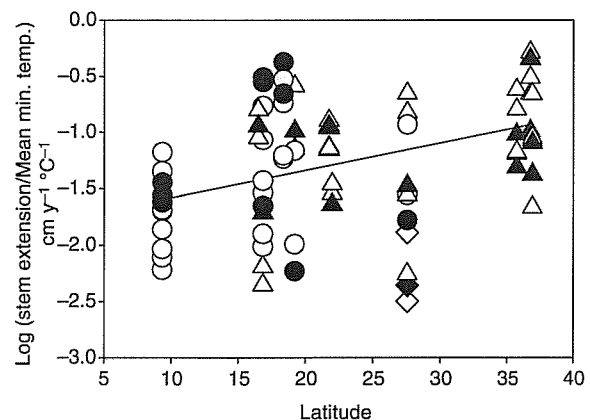


Figure 2 Variation in tree growth rates over latitude. Circles are values from the Rhizophoraceae, triangles the Avicenniaceae and diamonds are measurements from other taxa. Fertilization treatments are: control trees – open, nitrogen fertilized – grey and phosphorus fertilized – black. The line of best fit is of the form $Y = -1.82 + 0.0243 \times \text{Lat.}$, $R^2 = 0.181$, $P < 0.0001$, where Y is the $\log(\text{stem extension}/\text{mean minimum temperature in } ^\circ\text{C})$.

Table 1 Pearson Product Moment correlation (R) between latitude, temperature-adjusted growth rate (DAGR_{TA}), photosynthetic nitrogen and phosphorus use efficiency (PNUE, PPUE, respectively) and nitrogen and phosphorus resorption efficiency (%NRE and %PRE)

	Latitude	Log DAGR_{TA}	%N	%P	N : P	PNUE	PPUE	%NRE	%PRE
Latitude	1								
Log DAGR_{TA}	0.425	1							
%N	0.694	0.495	1						
%P	0.902	0.520	0.750	1					
N : P	-0.063	-0.054	0.428	-0.202	1				
PNUE	-0.408	-0.296	-0.558	-0.369	-0.324	1			
PPUE	-0.783	-0.503	-0.802	-0.891	0.207	0.760	1		
%NRE	-0.061	0.076	-0.478	-0.086	-0.551	0.424	0.351	1	
%PRE	-0.749	-0.234	-0.553	-0.740	0.221	0.400	0.762	0.178	1

Significant correlations ($P < 0.05$) are marked in bold.

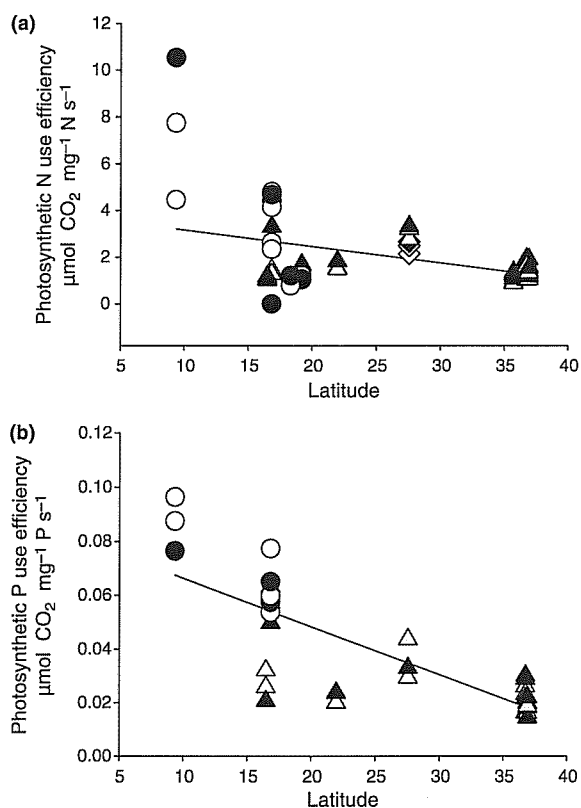


Figure 3 Variation in photosynthetic nitrogen (a) and phosphorus (b) use efficiency over latitude. Circles are values from the Rhizophoraceae, triangles the Avicenniaceae and diamonds are measurements from other taxa. Fertilization treatments are: control trees – open, nitrogen fertilized – grey and phosphorus fertilized – black. The line of best fit is of the form (a) $\text{PNUE} = 3.874 - 0.0708 \times \text{Lat}$, $R^2 = 0.167$, $P < 0.0001$; (b) $\text{PPUE} = 0.0843 - 1.792 \times \text{Lat}$, $R^2 = 0.612$, $P < 0.0001$.

PNUE over latitude were observed (latitude \times family interaction, $F_{1,83} = 38.53$, $P < 0.0001$), with the Rhizophoraceae showing a steeper decline in PNUE with increasing latitude than observed for the Avicenniaceae.

Nutrient resorption efficiency showed no significant correlation with temperature-adjusted growth rate; however, phosphorus resorption efficiency (%PRE), but not nitrogen resorption efficiency (%NRE), showed a strong and significant decline with increasing latitude (Fig. 4,

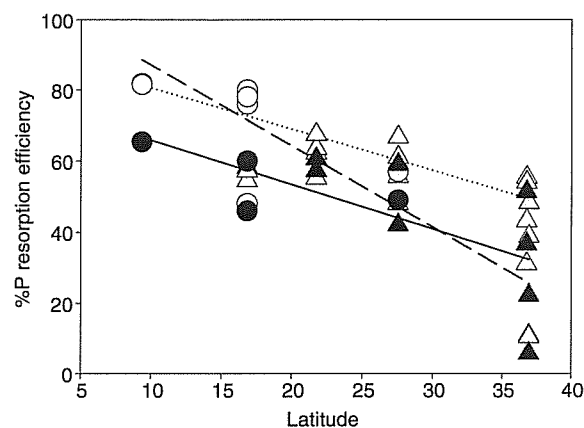


Figure 4 Variation in per cent phosphorus resorption efficiency (%PRE) over latitude. Circles are values from the Rhizophoraceae, triangles the Avicenniaceae and diamonds are measurements from other taxa. Fertilization treatments are: control trees – open, nitrogen fertilized – grey and phosphorus fertilized – black. The lines of best fit are of the form, controls (long dash): $\% \text{PRE} = 109.9 - 2.284 \times \text{Lat}$, $R^2 = 0.825$, $P < 0.0001$; nitrogen (dotted) fertilized: $\% \text{PRE} = 92.19 - 1.162 \times \text{Lat}$, $R^2 = 0.690$, $P < 0.0001$; phosphorus fertilized (solid): $\% \text{PRE} = 78.44 - 1.251 \times \text{Lat}$, $R^2 = 0.495$, $P < 0.0001$.

$R^2 = 0.81$, $P < 0.0001$). Fertilizer treatments showed a significant interaction with latitude ($F_{2,36} = 4.23$, $P = 0.0223$) but plant family did not ($P > 0.05$). %PRE in controls was higher at low latitudes than in fertilized trees and declined much more steeply in controls with latitude than in N- and P-fertilized trees. Additionally, N-fertilized trees had higher %PRE than P-fertilized trees at high latitudes.

DISCUSSION

Our observations that N and P of mangrove leaf tissue increase with latitude (Fig. 1) as did temperature-adjusted growth rates (Fig. 2) support the hypotheses of Sterner & Elser (2002) and Kerkhoff *et al.* (2005) that plants at high latitudes grow faster and contain more nutrients to achieve fast growth, a response that is driven by selection imposed by lower temperatures and compressed growing seasons. Our use of stem extension as a measure of growth rate, without adjustment for differences in wood density and biomass allocation of patterns among different species and over treatments are likely to have contributed to the variation observed in Fig. 2. Growth rate was also significantly correlated with %N and %P of leaf tissue which is also predicted by the Growth Rate Hypothesis (Sterner & Elser 2002; Elser *et al.* 2003). However, there was no trend in decreasing N : P with increasing latitude, contrary to expectations of increasing P demand at cooler more temperate latitudes (Sterner & Elser 2002; Woods *et al.* 2003).

Differences in the strength of the pattern of decline in N : P over latitude in mangroves compared to terrestrial vegetation could be due to a number of processes (Table 2). The near-coastal zone, particularly in estuaries where many mangroves forests occur, are exposed to nutrient pollution by agriculture, urban development and other land-use change, even if the forests themselves are relatively undisturbed (Downing *et al.* 1999; Rivera-Monroy *et al.* 2004). This might explain why foliar N concentrations in mangroves increased with latitude much more strongly than in terrestrial forests (Table 2). An additional cause of greater

increase in N in mangroves with latitude could be the biology of the species from the Avicenniaceae which dominate at high latitudes. Species from the family Avicenniaceae accumulate N-rich glycine betaine as an osmoregulatory compound, although concentrations are low (Popp *et al.* 1985). Although sediment salinities of the temperate sites were not high, enhanced osmotic potential of cells may enhance cold tolerance in *Avicennia* spp. (e.g. Sakamoto & Murata 2000) which could lead to greater than expected increases in leaf N with latitude.

Although there is support for the GRH, our data also support the Geochemical Hypothesis, that low P levels have influenced the evolution of leaf traits, internal plant nutrient cycling and ecosystem processes in tropical vs. temperate latitudes (Vitousek 1984; Vitousek & Sanford 1986; Crews *et al.* 1995; McGroddy *et al.* 2004; Reich & Oleksyn 2004). The Geochemical Hypothesis is supported by our observations that there were strong significant reductions in photosynthetic P use efficiency and in the resorption efficiency of leaf P with increasing latitude. Phosphorus resorption efficiency is a powerful measure of nutrient availability, with plants resorbing a high proportion of P from senescent tissue under P limiting conditions (Pugnaire & Chapin 1993; Feller 1995; Aerts 1996; Reich *et al.* 1997; Güsewell 2004; Rejmankova 2005). Moreover, there was no significant correlation between temperature-adjusted growth rate and %PRE, as predicted by the growth rate hypothesis, suggesting that geochemistry and not the sink strength provided by rapidly growing tissue may have the stronger influence on P resorption efficiency over latitude.

The geochemical signature evident in reductions in PPUE and %PRE with increasing latitude was not greatly influenced by fertilization treatments, despite the large effect of fertilization with limiting nutrients at individual sites (Boto & Wellington 1984; Feller *et al.* 2002, 2003, 2007; Lovelock *et al.* 2004, 2007). This is expected if low P availability was a significant selective pressure over long periods of time, giving rise to populations that are more efficient at resorbing P in the tropics even under ambient conditions of nutrient enrichment (Oleksyn *et al.* 2003). A significant proportion of the variation in %PRE was explained by fertilization treatments, with N and P additions decreasing the slope of the %PRE decline with latitude. Additionally, P fertilization decreased %PRE in the tropics and N fertilization increased %PRE at lower latitudes which is consistent with our knowledge of nutrients that limit growth over latitude (Pugnaire & Chapin 1993; Feller 1995; Aerts 1996; Reich *et al.* 1997; Güsewell 2004, 2005; Rejmankova 2005).

In many studies nutrient resorption efficiency has been found to differ strongly among vegetation types (Güsewell 2004; McGroddy *et al.* 2004; Rejmankova 2005). The current study is the first to show a clear decline in %PRE with

Table 2 Comparison of relationships between linear models best describing the relationships between latitude and leaf nutrient concentrations in a global data set (Reich & Oleksyn 2004) and mangrove leaves

	Data set	Intercept	Slope	R^2	P -value
Log N : P	Mangrove	1.46876	-0.00220	0.01	0.374
	Global	1.37432	-0.00769	0.24	< 0.0001
Log N (mg g ⁻¹)	Mangrove	0.9435	0.0118	0.34	< 0.0001
	Global	1.17942	0.00231	0.04	< 0.0001
Log P (mg g ⁻¹)	Mangrove	-0.2128	0.0146	0.37	< 0.0001
	Global	-0.3246	0.0122	0.34	< 0.0001

latitude within one ecosystem type. Within the mangrove, species from the family Rhizophoraceae dominate in more tropical latitudes and those from the Avicenniaceae become dominant in temperate latitudes (Duke *et al.* 1998), leading to a potential confounding of species and latitude in our data set. However, an analysis including plant family as a fixed effect in the statistical model found no significant family \times latitude interaction suggesting the declining trend of %PRE with latitude is robust and has evolved similarly in two unrelated families of plants.

Direct effects of lower temperature on PNUE and %PRE, leading to reduced PNUE and %PRE cannot be totally dismissed. We might expect in a similar way as proposed for growth (Kerkhoff *et al.* 2005) that photosynthetic carbon gain per degree is higher at low latitudes. If this was the case temperature-adjusted PNUE and PPUE should be enhanced with increasing latitude, but they were not (data not shown). Studies that have directly assessed the effect of temperature on resorption efficiency have found only very small effects (Norby *et al.* 2000; Aerts *et al.* 2005), but there are very few studies. Tateno (2003) investigated the trade-off in deciduous species between extended growth season and low nutrient resorption in one species vs. high resorption efficiency and lower carbon gain associated with earlier senescence in a co-occurring species (Tateno 2003). His models indicated that the species with the extended growing season (at the cost of losing nutrients by not resorbing them) had a significant competitive advantage in the relatively high nutrient environment of the study system. From Tateno (2003) we might expect selection for low resorption in cooler environments if it were advantageous to extend the growing season at the cost of loss of nutrients if nutrient resources were not limiting. Thus, restriction of the growing season in cooler climates could contribute to the steep and strong decline in %PRE with latitude.

Our data, from mangrove forests spanning 30° of latitude, partially support the predictions of the Growth Rate Hypothesis. Specifically, there was an increase in nutrient concentrations in plant tissue with increasing latitude, similar to that observed in other taxa (Reich & Oleksyn 2004) and an increase in temperature-adjusted growth rates, as proposed by Kerkhoff *et al.* (2005). However, declining %PRE and, to a lesser extent, PPUE with increasing latitude, and the strength of these trends even with experimental nutrient enrichment are strong indicators for the presence in the vegetation of a geochemical signature that has evolved in response to historically low P availability in the tropics.

ACKNOWLEDGEMENTS

The research was supported by a WISC award from the American Association for the Advancement of Science and

by awards from the Smithsonian Institution, the New Zealand Foundation for Research, Science and Technology (C01X0024, C01X0215 and C01X0307) and the Australian Research Council (LP0561498 and DP0774491). Thanks to Pip Nichols, Nicole Hancock and many other NIWA staff who assisted with field measurements, and to Rachel Tenni, Anne Chamberlain, Ray Feller and Helen Penrose for field assistance.

REFERENCES

- Aerts, R. (1996). Nutrient resorption from senescing leaves of perennials: are there general patterns? *J. Ecol.*, **84**, 597–608.
- Aerts, R., Cornelissen, J.H.C., van Logtestijn, R.S.P. & Callaghan, T.V. (2005). Climate change has only a minor impact on nutrient resorption parameters in a high-latitude peatland. *Oecologia*, **151**, 132–139.
- Ågren, G.I. (2004). The C:N:P stoichiometry of autotrophs – theory and observations. *Ecol. Lett.*, **7**, 185–191.
- Alongi, D.M., Clough, B.F., Dixon, P. & Tirendi, F. (2003). Nutrient partitioning and storage in arid-zone forests of the mangroves *Rhizophora stylosa* and *Avicennia marina*. *Trees*, **17**, 51–60.
- Boto, K.G. & Wellington, J.T. (1984). Soil characteristics and nutrient status in a northern Australian mangrove forest. *Estuaries*, **71**, 61–69.
- Chapin, F.S. & Kedrowski, R.A. (1983). Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous Taiga trees. *Ecology*, **64**, 376–391.
- Chapin, F.S. III & Van Cleve, K. (1989). Approaches to studying nutrient uptake, use and loss in plants. In: *Plant Physiological Ecology. Field Methods and Instrumentation* (eds Pearcy, R.W., Ehleringer, J.R., Mooney, H.A. & Rundel, P.W.). Chapman and Hall, New York, pp. 55–70.
- Clarke, P.J. (2004). Effects of experimental gaps on mangrove recruitment: lack of habitat partitioning may explain stand dominance. *J. Ecol.*, **92**, 203–213.
- Clough, B.F. (1998). Mangrove forest productivity and biomass accumulation in Hinchinbrook Channel, Australia. *Mangr. Salt. Marsh*, **2**, 191–198.
- Crews, T.E., Kitayama, K., Fownes, J.H., Riley, R.H., Herbert, D.A., Mueller-Dombois, M. *et al.* (1995). Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology*, **76**, 1407–1424.
- Downing, J.A., McClain, M., Twilley, R.R., Melack, J.M., Elser, J., Rabalais, N.N. *et al.* (1999). The impact of accelerating land-use change on the N-cycle of tropical aquatic ecosystems, current conditions and projected changes. *Biogeochemistry*, **46**, 109–148.
- Duke, N.C., Ball, M.C. & Ellison, J.C. (1998). Factors influencing biodiversity and distributional gradients in mangroves. *Glob. Ecol. Biogeogr. Lett.*, **7**, 27–47.
- Ellis, J., Nicholls, P., Craggs, R., Hofstra, D. & Hewitt, J. (2004). Effects of terrigenous sedimentation on mangrove physiology and associated macrobenthic communities. *Mar. Ecol. Prog. Ser.*, **270**, 71–82.
- Elser, J.J. (2006). Biological stoichiometry: a chemical bridge between ecosystem ecology and evolutionary biology. *Am. Nat.*, **168**, S25–S35.

- Elser, J.J., Sterner, R.W., Gorokhova, E., Fagan, W.F., Markow, T.A., Cotner, J.B. *et al.* (2000). Biological stoichiometry from genes to ecosystems. *Ecol. Lett.*, 3, 540–550.
- Elser, J.J., Acharya, K., Kyle, M., Cotner, J., Makino, W., Markow, T. *et al.* (2003). Growth rate-stoichiometry couplings in diverse biota. *Ecol. Lett.*, 6, 936–943.
- Feller, I.C. (1995). Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). *Ecol. Monogr.*, 65, 477–505.
- Feller, I.C., Whigham, D.F., McKee, K.M. & O'Neill, J.P. (2002). Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. *Biogeochemistry*, 62, 145–175.
- Feller, I.C., Whigham, D.F., McKee, K.L. & Lovelock, C.E. (2003). Nitrogen limitation of growth and nutrient dynamics in a mangrove forest, Indian River Lagoon, Florida. *Oecologia*, 134, 405–414.
- Feller, I.C., Lovelock, C.E. & McKee, K.L. (2007). Nutrient addition differentially affects ecological processes of *Avicennia germinans* in nitrogen vs. phosphorus limited mangrove. *Ecosystems*, 10, 347–359.
- Güsewell, S. (2004). N:P ratios in terrestrial plants: variation and functional significance. *New Phytol.*, 164, 243–266.
- Güsewell, S. (2005). Nutrient resorption of wetland graminoids is related to the type of nutrient limitation. *Funct. Ecol.*, 19, 344–354.
- Güsewell, S., Bollens, U., Ryser, P. & Klötzli, F. (2003). Contrasting effects of nitrogen, phosphorus and water regime on first-year and second-year growth of 16 wetland plant species. *Funct. Ecol.*, 11, 754–765.
- Kerkhoff, A.J., Enquist, B.J., Elser, J.J. & Fagan, W.F. (2005). Plant allometry, stoichiometry and the temperature-dependence of terrestrial primary production. *Glob. Ecol. Biogeogr. Lett.*, 14, 585–598.
- Killingbeck, K.T. (1996). Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology*, 77, 1716–1727.
- Körner, C. & Diemer, M. (1987). In situ photosynthetic responses to light, temperature and carbon dioxide in herbaceous plants from low and high altitude. *Funct. Ecol.*, 1, 179–194.
- Lenton, T.M. & Watson, A.J. (2000). Redfield revisited. 2. What regulates the oxygen content of the atmosphere? *Glob. Biogeochem. Cycles*, 14, 249–268.
- Lovelock, C.E., Feller, I.C., McKee, K.L., Engelbrecht, B.M. & Ball, M.C. (2004). The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panama. *Funct. Ecol.*, 18, 25–33.
- Lovelock, C.E., Feller, I.C., Ellis, J., Schwarz, A.M., Hancock, N., Nicholls, P. *et al.* (2007). Mangrove growth in New Zealand estuaries: the role of nutrient enrichment at sites with contrasting rates of sedimentation. *Oecologia*, 153, 633–641.
- McGraw, J.P. & Garbutt, K. (1990). The analysis of plant growth in ecological and evolutionary studies. *Trends Ecol. Evol.*, 5, 251–254.
- McGroddy, M.E., Daufresne, T. & Hedin, L.O. (2004). Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios. *Ecology*, 85, 2390–2401.
- Norby, R.J., Long, T.M., Hartz-Rubin, J.S. & O'Neill, E.G. (2000). Nitrogen resorption in senescing tree leaves in a warmer, CO₂ enriched atmosphere. *Plant Soil*, 224, 15–29.
- Nordell, K.O. & Karlsson, P.S. (1995). Resorption of nitrogen and dry matter prior to leaf abscission: variation among individuals, sites and years in the mountain birch. *Funct. Ecol.*, 9, 326–333.
- Odum, H.T. & Pinkerton, R.C. (1955). Times speed regulator: the optimum efficiency for maximum power output in physical and biological systems. *Am. Nat.*, 43, 331–343.
- Oleksyn, J., Reich, P.B., Zytowski, R., Karolewski, P. & Tjoelker, M.G. (2003). Nutrient conservation increases with latitude of origin in European *Pinus sylvestris*. *Oecologia*, 136, 220–235.
- Popp, M., Larher, F. & Weigel, P. (1985). Osmotic adaption in Australian mangroves. *Vegetatio*, 61, 247–253.
- Pugnaire, F.I. & Chapin, F.S. III (1993). Controls over nutrient resorption from leaves of evergreen Mediterranean species. *Ecology*, 74, 124–129.
- Redfield, A.C. (1958). The biological control of chemical factors in the environment. *Am. Sci.*, 46, 205–221.
- Reich, P.B. & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc. Natl Acad. Sci. U.S.A.*, 101, 11001–11006.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997). From tropics to tundra: global convergence in plant functioning. *Proc. Natl Acad. Sci. U.S.A.*, 94, 13730–13734.
- Rejmankova, E. (2005). Nutrient resorption in wetland macrophytes: comparison across several regions of different nutrient status. *New Phytol.*, 167, 471–482.
- Rivera-Monroy, V.H., Twilley, R.R., Bone, D., Childers, D.L., Coronado Molina, C., Feller, I.C. *et al.* (2004). Conceptual framework to develop long-term ecological research and management objectives in the wider Caribbean region. *BioScience*, 54, 843–856.
- Sakamoto, A. & Murata, N. (2000). Genetic engineering of glycinebetaine synthesis in plants: current status and implications for enhancement of stress tolerance. *J. Exp. Bot.*, 51, 81–88.
- Schade, J.D., Espeleta, J.F., Klausmeier, C.A., McGroddy, M.E., Thomas, S.A. & Zhang, L. (2005). A conceptual framework for ecosystem stoichiometry: balancing resource supply and demand. *Oikos*, 109, 40–51.
- Schwarz, A.M. (2004). Contribution of photosynthetic gains during tidal emersion to production of *Zostera capricorni* in a North Island, New Zealand estuary. *N. Z. J. Mar. Freshw. Res.*, 38, 809–818.
- Sterner, R.W. & Elser, J.J. (2002). *Ecological Stoichiometry*. Princeton University, Princeton, NJ.
- Tateno, M. (2003). Benefit to N₂-fixing alder of extending growth period at the cost of leaf nitrogen loss without resorption. *Oecologia*, 137, 338–343.
- Trott, L.A., McKinnon, A.D., Alongi, D.M., Davidson, A. & Burford, M.A. (2004). Carbon and nitrogen processes in a mangrove creek receiving shrimp farm effluent. *Estuar. Coast. Shelf Sci.*, 59, 197–207.
- Vitousek, P.M. (1984). Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology*, 65, 285–298.
- Vitousek, P.M. & Sanford, R.L. (1986). Nutrient cycling in moist tropical forest. *Ann. Rev. Ecol. Syst.*, 17, 137–167.
- Woods, H.A., Makino, W., Cotner, J.B., Hobbie, S.E., Harrison, J.F., Acharya, K. *et al.* (2003). Temperature and the chemical

composition of poikilothermic organisms. *Funct. Ecol.*, 17, 237–245.

Wright, I.J. & Westoby, M. (2003). Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species. *Funct. Ecol.*, 17, 10–19.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Locations and characteristics of sites, including climate, dominant species, tree stature and numbers of trees.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461.0248.2007.01112.x>.

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

Editor, Johannes Knops

Manuscript received 25 May 2007

First decision made 25 June 2007

Manuscript accepted 24 August 2007