

# Comparison of P and cation cycling in two contrasting seasonally dry forest ecosystems

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## Abstract

- **Context** Interactions of N and P cycles and those of other macro-elements in forests are scarcely known.
- **Aim** This study compares the P cycle in two very different forest ecosystems where soil P availability is low (tropical dry forest in Mexico and Mediterranean forest in Spain) in relation to Ca, K, and Mg cycles.
- **Methods** Compiled data belonging to these two forest sites are discussed, comparing the P and base cation budgets and exploring relationships among P and base cation cycles.
- **Results** Broad differences between input and output of base cations were observed. Analysis of the P budget indicates P retention inside both forest ecosystems. The tropical dry forest has higher nutrient contents than those found in the Mediterranean temperate forest. Chemical composition of forest leaves and litters, and base cation–P ratios varied according to soil P availability and cation concentrations. However, P resorption is higher in the tropical dry forest than in the temperate one.
- **Conclusion** This study reveals the existence of P retention at the ecosystem level in both forests, but suggested P limitation at the Mediterranean forest seems to be stronger than that occurring at the tropical forest.

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**Contribution of the co-authors** Julio Campo: designing the study, and writing the paper.

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## 1 Introduction

Phosphorus (P) is an essential nutrient to a variety of plant functions and plays an important role in photosynthesis (Lambers et al. 2008); its restricted availability often acts limiting plant carbon acquisition and growth (Elser et al. 2007; Reich et al. 2009). There is evidence that some tropical forests are P-limited because of the age and pedogenetic stage of the soils (Vitousek 1984); i.e., warm and wet tropical climate enhances rock weathering and P mineralization and tropical soils become depleted in available P with progressing pedogenesis (Walker and Syers 1976). In contrast, the rates of geochemical and biological processes in cold and dry climates are reduced, and P and other rock-derived elements are still present in the soil matrix because of limited weathering degree (Turrión et al. 2002). These global trends are supported by data of the P contents in green- and senesced-leaves (McGroddy et al. 2004; Ordoñez et al. 2009; Reich and Oleksyn 2004; Yuan and Chen 2009). Specifically, foliar P concentration is lower in warmer and wetter climates; consequently, a negative correlation between P concentration and mean annual temperature is usually found (Elser et al. 2010). McGroddy et al. (2004) informed about other factors that may govern these global trends; as an example, they showed that, on average, P resorption by plants is generally higher in tropical forests than in temperate forests.

Different biotic and geochemical mechanisms control the P availability in soils (Vitousek et al. 2010). The well-known cause of P limitation to terrestrial ecosystem

productivity is the progressive P depletion during long-term ecosystem development; this available-P loss is produced by both P leaching (Hedin et al. 2003) and P occlusion, increasing the P fraction that is not accessible to organisms (Crews et al. 1995; Walker and Syers 1976). This hypothesis involves a pattern including soil substrate variations at biome scale (Reich and Oleksyn 2004) and this is consistent with the empirical evidence. When N is a non-limiting factor for plant growth in an ecosystem, the availability of elements derived from rock materials (mainly P, but also Ca, K, and Mg) becomes to be limiting (Vitousek and Howarth 1991); little attention has been paid to this last subject, particularly interactions among the cycles of these elements (Castle and Neff 2009; Ladanai et al. 2010). Of these nutrients, Ca and K have generally the higher concentrations in plant tissues, often close to those of N (Lambers et al. 2008). Each cation performs a different physiological function in plants (Lambers et al. 2008). For example, K is required to proteins construction, photosynthesis, osmotic regulation, and ion transport; Ca for cell wall construction, permeability of membranes, and root growth, and Mg is component of chlorophyll and activate enzymes. Despite the importance of these rock-derived elements to ecosystem function, none of these previous studies comprehensively tested if the relationship base cation–P cycling varies among biomes, as the indicated hypothesis concerning the age of soil substrate predicts. Then, the general hypothesis is that the weathering intensity of primary minerals can control the nutrient availability for plants (e.g., the “final” low pH reduces the availability of soil P; Rengel 2003).

The concept of limiting nutrients can be misleading in the context of regulating the primary production of ecosystems. Plants require a variety of relative specific proportions of mineral nutrients in soils (stoichiometric ratios; Sterner and Elser 2002); i.e., a proper balance of nutrients is required for plant production (Knecht and Göransson 2004). Measurements of foliar chemical composition and stoichiometry are often used as an indicator of soil nutrient availability and plant nutrition condition (Aerts and Chapin 2000). Limiting elements are expected to be utilized for growth and transferred within ecosystem with high efficiency, while non-limiting elements (by definition present in excess) must be abundant, and they may be recycled or lost. On the other hand, ecological stoichiometry is a tool for analyzing how the balance of the multiple elements required by organisms creates fundamental differences between ecosystems in relation to the capture and sequestration of C, or other ecosystem processes (Sterner and Elser 2002). Thus, the concept of stoichiometric regulation should not be restricted to the application to individual organisms. The literature on the nutrient limitations points out that the general limitations in terrestrial ecosystems are related to N (LeBauer and Treseder 2008) or P (Vitousek et al. 2010).

There are several analyses in bibliography relating interactions among C–N–P cycles because N and P commonly limit terrestrial primary production (Elser et al. 2007). However, interactions with other elements (e.g., P with other macronutrients) are less well investigated (Knecht and Göransson 2004; Watanabe et al. 2007) and these studies have been focused on plant investments and did not include an integral ecosystem view, such as interactions of elements in the inputs to, and in the outputs from the ecosystem, and their relationships with the intra-system cycling. The lack of this information constrains the understanding of global P dynamics. As contribution to replenish this gap, the present study compares the cycle of P in two very different forest ecosystems but with similar net primary productivity and where P availability in the soil is low: a tropical dry forest in Mexico and a Mediterranean forest in Spain. To this end, we also focus on the essential (but typically non-limiting) base cations cycles, such as Ca, K, and Mg, because they are closely controlled by primary minerals (related to the weathering intensity, varying significantly with parent material and soil aging, as occur with P). We approached this task using published data relating these two forest sites in two ways. Firstly, comparing the P and base cation budgets and their intra-system cycles in these. And secondly, these data were also used to explore the relationships between P and base cation cycles in each ecosystem. We address two fundamental questions: (1) Are both forests characterized by a P conservation at ecosystem-level? (2) Do P–base cation relationships at forest scale differ in response to predicted variations in nutrient availabilities?

## 2 Materials and methods

### 2.1 Selected forest sites

The tropical dry forest (TDF) site is located in the Chamela Biological Station, located at Western Mexico (19° 1' N, 105° 0' W). It is about 5 km far from the Pacific Ocean; the site has a mean annual temperature of ~24°C, that varies by <5.0°C annually, receiving a mean annual precipitation of ~700 mm year<sup>-1</sup>. Most of the rain falls during the wet season, from June to October (summer). The landscape consists of low hills (50 m asl). The predominant parent material includes Tertiary volcanic rocks, constituted by rhyolitic and rhyodacitic sediments (Campo et al. 2001b). Soils are poorly developed (soil type FAO: *Lithosol*), shallow (0.5–1.0 m depth), and with neutral pH reaction (from 6.5 to 7.0). This mature forest is conformed by deciduous trees, mainly belonging to the *Leguminosae* family; these comprising a 15 % of the species (Lott 1985).

The Mediterranean temperate forest (MTF) is located at east of the town of Navafrias, on the south-west corner of

the Salamanca Province (Western Spain; 40° 2' N, 3° 0' W). The climate in the MTF site is temperate, subhumid Mediterranean, with a mean annual temperature of 11.0°C and mean annual precipitation about 1,580 mm year<sup>-1</sup>. A dry season typically occurs between June and September (summer) of each year. The landscape is hilly (*Sierra de Gata* Mountains, 960 m asl). The predominant parent material includes acid schists and slates, deeply weathered. This weathered material favors pedogenesis (*Ortic umbrisol*), being deeper (<1.0 m depth) and more acid (pH 4.2 to 5.0) soils than its tropical counterpart. Forests (80 years old) are dominated by the deciduous Atlantic oak (*Quercus pyrenaica* Willd., *Fagaceae*); this MTF vegetation shows a relatively lower diversity, including grasses, shrubs, forbs, and the deciduous oak indicated.

In the particular case of the two forests studied, available information indicates that both forest ecosystems have similar net primary productivity (Table 1). Soil organic C and total N concentrations in the MTF soil are three and two times higher than those found in the TDF, respectively. Apparently, soil organic matter in TDF has better quality than in MTF, as indicated by the C–N ratio.

The C pools of these two forests were well documented by García-Oliva et al. (2006). Although aboveground and total biomass values in the TDF are close to those in the MTF (Table 1), the TDF has less soil organic C content than its MTF counterpart (soil organic C pool is 35.2 Mg Cha<sup>-1</sup>

in TDF vs. 103 Mg Cha<sup>-1</sup> in MTF); then, the total C pool in the tropical system is 45 % lower than in the MTF (82.6 Mg Cha<sup>-1</sup> vs. 149 Mg Cha<sup>-1</sup>). The mean residence time value of soil organic matter is 5.1 times higher in MTF than its TDF counterpart (86 years vs. 16.8 years).

Leaf-nutrient concentration values are lower in MTF (by a factor of 4 and 3 in the cases of Ca and P, respectively, and by a factor of 2 in the cases of K and Mg) in relation to those found in TDF (Table 1).

## 2.2 Methods

The methodology used is based on a nutrient-balance approach and measurements of leaf nutrients, aboveground litterfall nutrients, and forest floor litter nutrients, as well as nutrients concentrations in soils. These fundamental data in nutrient cycling referred to these two P-poor forest ecosystems are compared between.

Published data on P, Ca, K, and Mg contents in bulk deposition and runoff water, as well as in foliage, litterfall, forest floor litter, and mineral soil of both mature forests (i.e., TDF and MTF), were collected from literature. Although data have been previously published elsewhere, but they have never been compared.

A detailed description of nutrient sampling and analysis for the TDF can be found in Campo et al. (2000, 2001a), and for the MTF in Gallardo et al. (1998), Moreno-Marcos and

**Table 1** Characteristics of the two forest sites studied

	Tropical dry forest (TDF) <sup>a,b,c,d</sup>	Mediterranean temperate forest (MTF) <sup>e,f</sup>
Soils (0–20 cm depth)		
Bulk density (Mg m <sup>-3</sup> )	0.9	0.8
Texture (sands:silts:clays, %)	60:14:26	27:47:26
pH (H <sub>2</sub> O)	6.5–7.0	4.2–5.1
Organic C (mg C g <sup>-1</sup> )	18.9	70.1
Total N (mg N g <sup>-1</sup> )	2.3	4.0
C:N ratio	8.2	17.5
Available P (mg P kg <sup>-1</sup> )	6.4	4.9
Resin P (mg P kg <sup>-1</sup> )	1.73	0.40
Total P (mg P kg <sup>-1</sup> )	290	420
Exchangeable Ca (mg Ca kg <sup>-1</sup> )	1744	280
Exchangeable Mg (mg Mg kg <sup>-1</sup> )	453	85
Exchangeable K (mg K kg <sup>-1</sup> )	163	195
Vegetation		
Aboveground biomass (Mg Cha <sup>-1</sup> )	36.2	33.6
Roots (0–20 cm depth; Mg Cha <sup>-1</sup> )	6.7	10.9
Total biomass (Mg Cha <sup>-1</sup> )	42.9	44.5
Leaf P concentration (mg P g <sup>-1</sup> )	2.8	0.9
Leaf Ca concentration (mg Ca g <sup>-1</sup> )	19.1	4.6
Leaf Mg concentration (mg Mg g <sup>-1</sup> )	4.8	2.1
Leaf K concentration (mg K g <sup>-1</sup> )	15.2	7.3

<sup>a</sup>Campo et al. 2000

<sup>b</sup>Campo et al. 2001a

<sup>c</sup>García-Oliva et al. 2006

<sup>d</sup>Jaramillo and Sanford 1995

<sup>e</sup>Moreno-Marcos and Gallardo-Lancho 2002b

<sup>f</sup>Turrión et al. 2008

**Table 2** Nutrient inputs (via bulk deposition) and outputs by runoff in the two forest sites studied

	Tropical dry forest (TDF) <sup>a,b</sup>					Mediterranean temperate forest (MTF) <sup>c,d</sup>				
	Rainfall/Runoff mm year <sup>-1</sup>	P kg ha <sup>-1</sup> year <sup>-1</sup>	Ca kg ha <sup>-1</sup> year <sup>-1</sup>	K	Mg	Rainfall/Runoff mm year <sup>-1</sup>	P kg ha <sup>-1</sup> year <sup>-1</sup>	Ca	K	Mg
Inputs	752	0.16	3.0	1.3	0.8	1572	0.16	7.6	2.2	1.6
Outputs	86	0.06	5.2	2.8	1.8	155	0.16	6.2	3.2	2.6
Net gain or loss (-)		0.09	-2.2	-1.5	-1.0		~0	1.4	-1.0	-1.0

<sup>a</sup> Campo et al. 2000<sup>b</sup> Campo et al. 2001a<sup>c</sup> Moreno-Marcos and Gallardo-Lancho 2002a<sup>d</sup> Vicente et al. 2003

Gallardo-Lancho (2002b), and Vicente et al. (2003). In the TDF, all the measures were done at a mature forest in five contiguous small watersheds (12–28 ha), established for long-term ecosystem research (Sarukhán and Maass 1990). In Navafrias (MTF) data come from papers derived from the study of a deciduous oak forest (Gallardo-Lancho 2000) located in a catchment (20 ha). Nutrient entering by bulk deposition to ecosystem and dissolved nutrient exported from the ecosystem were measured during a 6-year period, and internal nutrient cycling for a 1-year period. Litterfall data come from monthly collections, and forest floor litter data from quarterly collections. Both, data sets of litterfall and of litter used come from samples collected in the same year at each site, and include leaf fall and leaf litter. Data sets of inputs and outputs per year were used for calculated annual means with  $n=6$  years per forest. Means of annual litterfall and of annual forest floor litter of five plots were calculated ( $n=5$  plots) per forest. We calculated mean nutrient ratios for each forest. We considered flux average nutrient contents across all dominant species and individual within each forest. For soil nutrients, we only used studies where collections were done from upper soil profile.

### 3 Results

Phosphorus inputs from the atmosphere do not differ between forests, but base cation inputs by bulk deposition in the MTF doubled approximately those of the TDF (Table 2). Despite of similar P inputs, P outputs differed between forests (by a factor of 2.7 times), observing high nutrient losses in MTF. Also, base cation outputs by runoff were higher in MTF in relation to TDF (by 19 % in the case of Ca, by 14 % in the case of K, and by 44 % in the case of Mg). A comparison between P losses from the ecosystem and P inputs from the atmosphere in the TDF showed that the latter were higher than runoff ones, mean while the balance between P inputs and outputs in the MTF is close to zero (i.e., there are no net gains or losses). In contrast, base cation losses by leaching were generally higher than inputs in both forests, only differing less than  $1.0 \text{ kg ha}^{-1} \text{ year}^{-1}$  for Ca.

As expected, TDF had a 1.6 times higher litterfall amounts than MTF, but both forests had similar forest floor litter in spite of the contrasting productivities and climatic conditions (Table 3). Nutrient fluxes in the litterfall differed considerably between forests (by a factor of 2.4 in the case of P, and in a range of 3.2 to 6.3 times in the cases of the base cations) favorable to TDF. In addition, TDF had 1.5

**Table 3** Nutrients fluxes by litterfall, and pools in the stand litter and their mean residence time (years) of the two forest sites studied

	Tropical dry forest (TDF) <sup>a,b</sup>					Mediterranean temperate forest (MTF) <sup>c</sup>				
	Dry Matter Mg ha <sup>-1</sup> year <sup>-1</sup> or Mg ha <sup>-1</sup>	P kg ha <sup>-1</sup> year <sup>-1</sup> or kg ha <sup>-1</sup>	Ca	K	Mg	Dry Matter Mg ha <sup>-1</sup> year <sup>-1</sup> or Mg ha <sup>-1</sup>	P kg ha <sup>-1</sup> year <sup>-1</sup> or kg ha <sup>-1</sup>	Ca	K	Mg
Litterfall	3.39	3.8	114.0	23.1	15.9	2.09	1.6	18.1	6.0	5.0
Stand litter	5.11	4.1	202.0	19.8	18.6	5.25	2.8	36.0	4.6	7.2
Mean residence time	1.3	1.2	1.8	0.9	1.2	2.0	1.8	2.0	0.8	1.4

<sup>a</sup> Campo et al. 2000<sup>b</sup> Campo et al. 2001a<sup>c</sup> Gallardo et al. 1998

times greater P pool, and between 2.6 and 5.6 times greater base cation pools in the forest floor than those in the MTF. Turnover of organic matter and P (expressed as mean residence time, in years) in the forest stand litter of the TDF was 50 % faster than those of the MTF, while the mean residence time of each base cation were similar between forests.

The MTF had approximately two times higher values of base cation–P ratios in bulk deposition than those found in TDF (expressed in molar basis; Table 4). However, TDF generally had two times higher values of base cation–P ratios in runoff water than those in MTF. Furthermore, TDF had higher values of leaf–Ca–P ratios than those in MTF; but the former forest had lower values of leaf K–P and Mg–P ratios in relation to the values found in MTF (by 33 % in the case of the K–P ratio and by 27 % in the case of the Mg–P ratio). In contrast, there is a similar pattern concerning the base cation–P ratios in both litterfall and litter; all values of base cation–P ratios in litterfall and in litter were higher in TDF than in MTF.

#### 4 Discussion

The studied TDF and MTF have been developed on different bedrock types, and they have soils that ranged from relatively nutrient-rich (such as the tropical *Lithosol*) in the former site, to nutrient-poor (such as the Mediterranean *Umbrisol*) in the last site. The difference in parent material chemistry (including variation in nutrients such as P, Ca, K, and Mg) may influence ecosystem dynamics through soil nutrient availability (Table 1).

Although the low soil moisture and relatively rapid drying, conditioning slow rates of mineral weathering in

seasonal semi-arid ecosystem environments (especially during dry summers), the well drained soil of MTF in a climate with a mean annual precipitation of 1,580 mm and moderate temperature (11°C of mean annual temperature), or the exchange Ca and Mg in the TDF soil, do not point to low weathering rates in both ecosystems.

#### 4.1 Mineral balance

In seasonally dry ecosystems is expected that the dry deposition is very important at times. Thus, the P input from the atmosphere by bulk precipitation in both forest ecosystems (i.e., TDF and MTF) is 60 % greater than the estimated average of the global atmospheric P deposition (~0.1 kg P ha<sup>-1</sup> year<sup>-1</sup>, Mahowald et al. 2008). Comparison of P flux in the throughfall in both forest sites (0.30 kg P ha<sup>-1</sup> year<sup>-1</sup> in TDF and 0.60 kg P ha<sup>-1</sup> year<sup>-1</sup> in MTF; Gallardo et al. 1998; Campo et al. 2001a, b) with bulk precipitation values suggest that deposition of P from the atmosphere could be underestimated. We cannot determine whether such increase in amounts of P as rainfall moved through the canopy only resulted from the washoff of leaves by throughfall water (i.e., a direct consequence of washoff of the P deposition in leaves between rainfall events) or whether it reflects also the leaching of some P content in leaves (cf. Parker 1983). Aside from this potential increase in P deposition from the atmosphere, our study allows us to conclude that the annual P input amounts in both forest ecosystems are lower than the values of the P mobilized by the internal cycle in litterfall.

The comparison of nutrient losses from the ecosystem with input rates from the atmosphere showed that P is the most conserved nutrient in both forests studied (total dissolved P output generally did not exceed ~0.2 kg P ha<sup>-1</sup> year<sup>-1</sup>, meanwhile dissolved Ca, Mg, and K losses

**Table 4** Base cation–P ratios (in moles per moles) in the two forest sites studied

	Tropical dry forest (TDF)			Mediterranean temperate forest (MTF)		
	Ca–P	K–P	Mg–P	Ca–P	K–P	Mg–P
Inputs–outputs						
Ratios in bulk deposition	14.5	6.4	6.4	36.7	10.9	12.7
Ratios in runoff waters	67.0	37.0	38.2	30.0	15.8	20.7
Ratios outputs–inputs	4.6	5.7	6.0	0.8	1.5	1.6
Intra-system cycling						
Ratios in leaves	5.3	4.3	2.2	3.9	6.4	3.0
Ratios in litterfalls	23.2	4.8	5.3	8.7	3.0	4.0
Ratio litterfall–leaf	4.4	1.1	2.4	2.2	0.5	1.3
Ratios in forest stand litter	38.1	3.8	5.8	9.9	1.3	3.3
Ratios litter–litterfall	1.6	0.8	1.1	1.1	0.4	0.8
Ratios in soils (base cation–available P)	211	20.2	90.2	44.2	31.5	22.1



ranged from  $\sim 2.0$  to  $\sim 6.0$  kg ha<sup>-1</sup> year<sup>-1</sup>). This pattern is consistent with the existence of a strong P retention by biotic and geochemical mechanisms in both ecosystems (Campo et al. 1998; Gallardo-Lancho 2000). Despite the differences in climate and parent material between these two forests, generally TDF and MTF had similar balance of rock-derived elements. Moreover, when results of ecosystem-level mass balance of base cations in TDF and MTF are considered, our study also suggests that both forests have strong releases of K and Mg via rock weathering.

#### 4.2 Intra-system cycling

Mediterranean temperate forest soils are comparatively deeply weathered in relation to TDF, as well as more acid and with lower amounts of plant-available forms of nutrients, probably because of leaching of nutrient by heavy and frequent rains during winter over time (Moreno-Marcos and Gallardo-Lancho 2002a). In contrast, TDF soils tend to have much higher concentrations of essential nutrients (P and basic cations) because of the intense weathering of fresh rock materials (Campo et al. 2001b). The loss by leaching of mobile cations (Ca, K, Mg, and also Na) in MTF soils (increasing the exchangeable H<sup>+</sup> in the soil, as indicated by the decline of the value in soil pH) produces a shift to Fe and Al as dominant cations (Moreno-Marcos and Gallardo-Lancho 2002b; Turrión et al. 2002). This low pH reduces further the availability of P in the MTF soil (as a consequence of a decrease of phosphate solubility to low levels below a pH of 5.0; Turrión et al. 2008). Thus, the nutrient deficiencies of MTF soils relative to TDF soils are an inevitable consequence of the climatic conditions, in addition to the age and nature of the parent material.

Several factors complicate the evaluation of plant nutrient concentration and their relation with soil nutrient content. Different plant species have different leaf characteristics that result in large differences in foliar nutrient content. However, the data in our study are consistent with findings that variation in soil P, as well as soil Ca and Mg availabilities can regulate foliar chemistry (Aerts and Chapin 2000). Trees growing on more weathered and P-poor soils (as in MTF) have a lower foliar P and base cation concentrations. Thus, our study suggests that the imprint of soil nutrient availability on foliar nutrient concentrations in the TDF occurs, despite of the substantial biogeochemical variability in the tropics (Townsend et al. 2008).

In contrast to green leaves (where nutrient concentrations are subject to the specific soil nutrient availability), nutrient concentrations in senescent leaves should be better controlled by the plant (Lambers et al. 2008) and therefore may still provide a more representative picture of the relative nutrient requirements. A large proportion of leaf tissue is made up of cell walls in which Ca is an important

structural and insoluble nutrient. This physiological constraint limits the amount of Ca that can be resorbed during senescence. In contrast, P is not as highly constrained as Ca, and P resorption may be more flexible in plants (Ågren 2008). Our data showed that, in general, P resorption exaggerated differences between base cation–P ratios in green leaves of tropical and temperate forest sites. For example, the relatively high Ca–P ratio found in the foliage of the tropical forest increased further in litterfall, giving an index of P deficiency when comparing the litterfall Ca–P ratio in relation to the MTF one. Not only climate and soil differences affect foliar chemistry, differences could be reflect of variation at species level in foliar nutrient usages. Particularly, legumes, consist 15 % at TDF, exhibit specific characteristics for P acquisition (Houlton et al. 2008) and resorption (Inagaki et al. 2011).

Because plants control more effectively the P resorption (Lambers et al. 2008), it is expected that the concentration of this element in litterfall show less difference between forests than base cations. Our results on plant nutrient use (calculated by the ratio of the dry mass loss in the litterfall to the element loss in the litterfall, sensu Vitousek 1984; Table 3) are consistent with this expected pattern. Differences between forests are approximately 1.5 times for P, meanwhile ranged from 2 to 4 for base cations. Because of the characteristics of forest litter is determined by the interaction of many organisms and climate, biologically controlled P should be more different between ecosystems in the forest floor litter than in the litterfall (Neff et al. 2006). However, we observed that differences between forests in P concentration in the forest litter floor (calculated by the ratio of the litter element mass to the litter dry mass; Table 3) were similar in magnitude to differences in the plant nutrient use (i.e., approximately 1.5 times higher in TDF than in MTF). Moreover, differences between forests concerning P concentrations in green leaves doubled those found in both plant P use and concentrations in forest floor litter (values were approximately 3 times higher in TDF than in MTF), suggesting that P content is more strongly controlled in the green-leaves than in the stand litter.

#### 4.3 Stoichiometric ratios

Despite of a similar pattern of loss of elements derived from rocks and atmospheric inputs between forests, we found differences between base cation–P ratio values in TDF and MTF. TDF showed high base cation–P ratios in runoff water; we cannot determine either if such high value in the ratio resulted from the observed efficient P recycling in the tropical ecosystem (Campo et al. 1998), or if it reflects higher base cation outputs (a direct consequence of strong weathering release of base cations at the TDF; Campo et al. 2001b) than in the temperate counterpart, or both.

We found considerable variation in ratios for K–P, Ca–P, and Mg–P in leaves between the two forests studied. Values of these ratios (with the exception of K) were usually above what was considered as optimum values for deciduous plants (Ca–P ranged from 0.4 to 0.5, K–P ranged from 3.5 to 4.4, and Mg–P ranged from 0.2 to 0.6, according to Knecht and Göransson 2004). Such noticeable differences in these two forests from the optimal set of elements suggest that P may be limiting for plant growth in both forest ecosystems. Although, Turrión et al. (2000) did not find any response from the oak trees to P fertilization in the Navasfrías site at short-term (three years); this hypothesis need to be verified with a long-term study on primary production at the ecosystem level, analyzing the way in which P-limited forests respond to a surpassing of such limitation.

By comparing nutrient ratios found in litterfall (i.e., abscised leaves) with ratios in green leaves, we can infer that plants reabsorb higher amounts of P (relative to base cations) in TDF compared with MTF. Such resorption is consistent with the idea that plants conserve nutrients that are in short supply before leaves are abscised and lost as litterfall (Aerts and Chapin 2000). On the other hand, the trend of a high P resorption in TDF is consistent with observed differences between stoichiometric ratios in the available soil pools and estimated plant demand (i.e., stoichiometric ratios in green-leaves): for example, the differences in Ca–P and Mg–P ratios are higher in TDF (ranged from 40 to 45 times) than in MTF (ranged from 7 to 10 times), that indicates a stronger uncoupled P supply by soil against plant demand in the tropical site.

These findings point out that other factors may control the intra-system cycling. First of all, the comparison of base cation–P ratios between outputs and inputs increase from 4.2 to 5.5 in the case of the TDF (Table 4), but varied only from 0.8 to 1.6 in the case of the MTF. Such increase indicates that P is the most conserved nutrient in the tropical ecosystem, in more intensity than in the MTF. Secondly, the turnover time of P in the stand litter of the TDF is 0.6 years, faster than in the temperate forest (Table 3). In contrast, mean residence time of nutrients that are not limiting (i.e., Ca, K, and Mg) are similar between forests. Nevertheless, we cannot determine whether such faster P turnover in TDF is a consequence of the warm climate (that favors microbial activity in the forest floor), if it reflects differences in soil P supply, or both.

## 5 Conclusions

In summary, our study reveals the existence of P retention at ecosystem level in both seasonally dry forests. Despite this similitude, in general, a probable P limitation at MTF seems

stronger than that at TDF due to its deeply weathered, Fe and Al saturated acidic soils and results of resin P. In addition, the two forest sites studied differed in foliar nutrient concentrations according to their specific soil nutrient levels (regardless of the similarity of ecosystem productivities). Results of stoichiometric ratios in litterfall and leaves are opposite to these patterns (the ratio between the base cation–P in litterfall and leaves suggest a greater P resorption in the tropical site relative to its temperate counterpart). This opposite trend probably points out a stronger effect of difference in the species compositions of the two forest ecosystems rather than climate and soil P availability. Nevertheless, taking into account that plant species can adjust their foliar concentrations to face limiting factors (including shortage of water), sometimes conclusions should be restricted to the environmental conditions during the experimental study. Then, a generalization to other dry areas should be avoided. In spite of these restrictions, the estimation of values of P cycling and stoichiometric ratios is a very useful tool for global biogeochemical coupling assessments, especially when referring to seasonal dry areas.

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