**REGULAR ARTICLE** 

# Changes in leaf nutrient traits in a wildfire chronosequence

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Abstract The effect of wildfire on ecosystem function is gaining interest since climate change is expected to increase fire frequency and intensity in many forest systems. Fire alters the nutritional status of forest ecosystems, affecting ecosystem function and productivity, but further studies evaluating changes in leaf nutrient traits induced by forest wildfires are still needed. We used a 17-year-old Pinus canariensis wildfire chronosequence to elucidate the nature of nutrient limitations in natural and unmanaged pine forest in the Canary Islands. Pine needles were sampled in winter and spring and analysed for N and P concentrations. As expected, we found the lowest leaf N and leaf P in recently burned plots. However, the leaf N:P ratio was higher in burned versus unburned plots, suggesting that the decrease in P availability due to the fire is larger than that of N. For all leaf traits and sampling dates, leaf trait values in burned plots matched those observed in unburned plots 17 years after a fire. The N:P ratio

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J. M. Fernández-Palacios Departamento de Ecología, Universidad de La Laguna, 38206 La Laguna, Tenerife, Spain found in *P. canariensis* needles was one of the lowest values reported in the literature for woody species, and suggests that all pine trees in the chronosequence are unambiguously limited by low N availability. Our results show that these N-limited pine forests retained N more efficiently than P 4 years after a wildfire; however, leaf N recovery is slower than P recovery, suggesting that the mechanisms responsible for pine N limitation operate continuously in these forests.

**Keywords** Nitrogen · Phosphorus · Forest fire · *Pinus canariensis* · Nutrient limitation

# Introduction

Climate change may increase wildfire frequency and intensity, and has already increased interest in the effect of wildfire on ecosystem function (Scholze et al. 2006; Westerling et al. 2006). Fire can affect plant nutritional status by altering soil nutrient availability (Wan et al. 2001; Huang and Boerner 2007), and previous studies have shown that leaf nutrient concentrations may reach high levels immediately after a fire, but that a decrease in nutrient concentration and the emergence or exacerbation of nutrient limitation may be observed a few years later (Reich et al. 1990; Van de Vijver et al. 1999; Huang and Boerner 2007). However, although some authors have tried to study the long-term effects of fire on vegetation nutrient dynamics, further studies evaluating long-term

changes in plant nutritional status after a wildfire are still needed (Bond-Lamberty et al. 2006; Wirth et al. 2002). Several studies have shown that leaf nutrients reflect soil nutrient availability (e.g. Aerts and Chapin 2000; Vitousek 2004; Townsend et al. 2007). Other published studies have proposed that low foliar N:P values should reflect N limitation, while high N:P values likely reflect P limitation. Colimitation of N and P should exist at foliar N:P ratios of 14-16 (e.g. Koerselman and Meuleman 1996; Reich and Oleksyn 2004). Although N:P mass ratios vary throughout the world for different vegetation types (e.g. 13.7 and 14.9 for woody and herbaceous species, respectively), N:P ratios less than 10 and greater than 20 often correspond to N- and P-limited biomass production, respectively, as shown by shortterm fertilisation experiments (Güsewell 2004). Thus, leaf N:P ratio can be used as a fast, reliable and simple alternative to labourious fertilisation experiments to predict the nature of the nutrient limitation of plant communities (Koerselman and Meuleman 1996; Tessier and Raynal 2003).

Most nutrient cycling studies have been conducted in areas with relatively high anthropogenic atmospheric N deposition rates (but see Nardoto et al. 2006), which alter ecosystem nutrient cycling by alleviating the N losses expected under any disturbance regime (Vitousek and Howarth 1991; Galloway 1998). Thus, the full extent of the effect of fires on nutrient cycling would be better understood in areas of low anthropogenic input (Rodríguez et al. 2009a). Furthermore, although critical N:P values are appealing in their simplicity, further work will be required to determine if these indices indeed reflect soil nutritional status in different types of ecosystems with different disturbance regimes (Drenovsky and Richards 2004).

The unmanaged *Pinus canariensis* forests on La Palma Island (Canary Islands) are not exposed to the increasing atmospheric deposition rates detected in Continental European forests, and wildfires are the only significant disturbance in these forests (Klein et al. 2007; Durán et al. 2008; Galloway et al. 2008). Some previously published research papers on these pine forests showed a significant long-term reduction in soil N pools and N mineralisation rates due to wildfires (Durán et al. 2008, 2009a, b). To determine the extent to which those changes in soil availability were reflected in plant nutritional status was our next

challenge. Grime et al. (1997) argued that mineral nutrients should be considered the fundamental currency of vegetation processes, but changes in nutrient availability are not always reflected in leaf nutrient status due to genotypic and phenotypic responses at the individual level, and to species replacements at the community level (Aerts and Chapin 2000). Here, we explore if wildfire effects on forest soil N and P are reflected in the nutritional status of the dominant plant species in these forests. We expected that wildfire should have a significant long-term effect on plant nutrition, which would have important consequences for ecosystem function and productivity. Due to leaf nutrient concentration changes as a consequence of nutrient resorption and retranslocation, seasonal changes were also taken into account.

We first hypothesised that, in recently burned areas (4 years after a fire), the pine population should exhibit the lowest leaf N and P concentrations, reflecting high losses of these nutrients from the ecosystem. Pines should then increase their leaf N and P concentrations as time elapses after a fire, eventually recovering to unburned nutrient levels. Because N is more susceptible to disturbance losses than P (Vitousek and Howarth 1991), we would expect to find the minimal N:P ratio in recently burned areas, but N retention mechanisms should lead to an increase in this ratio until it matches the unburned values.

#### Methods

# Study area

The study was carried out in *Pinus canariensis* forests located on La Palma Island (Canary Islands, latitude: 28°41′ N; longitude: 17°45′ W). These forests are among the last natural and unmanaged pine forests of Europe. Like most of the Canary Islands, La Palma is one of the inhabited areas with the lowest anthropogenic atmospheric N deposition in the world (Galloway et al. 2008). Therefore, these forests are usually N-limited, and syndromes of N deficiencies are frequently observed in pine needles (Tausz et al. 2004; Durán et al. 2008). These forests are occasionally affected by severe wildfires that completely eliminate the undergrowth. Although these fires usually reach the pine

canopies (crown fires), they rarely kill the trees, and surviving individuals that exceed 100 cm diameter at breast height (DBH) are commonly found. The survival of adult individuals of P. canariensis after a fire makes pine stands with different fire histories comparable in terms of pine age and structure.

The pine stands lie between 1,200 and 1,800 m above sea level, with a mean annual rainfall of 600 mm and a mean annual temperature of 16°C (Climent et al. 2004). Soils are of volcanic origin and are classified as leptosols, vertisols, and andosols. The organic matter content of the sampled areas ranged from 4% to 4.5%, with total N ranging from 0.3% to 0.4% and pH from 6.6 to 6.9 (Table 1). Vegetation is dominated by large individuals of Pinus canariensis Chr. Sm. ex DC. with an average canopy cover of 80%. The pine population is comprised of adult trees (20-30 m height), some of which are very old (up to 700 years). The understory vegetation is very scarce, with a few individuals (up to 10-20 individuals per hectare) of Adenocarpus viscosus (Wild.) Webb and Berthel, Erica arborea L., or Cistus symphytifolius Lam (Rodríguez et al. 2009b).

Experimental design and chronosequence plot selection

The selected fire chronosequence was composed of unburned plots (control) and plots burned in 1987, 1990, 1994, 1998, and 2000 (17, 14, 10, 6 and 4 years since wildfire, respectively). For each year and for the control plot, we selected four 25 m $\times$ 25 m replicate plots, except for the 1987 forest stand, where only two replicates with homogeneous characteristics were found. Although each plot does not correspond to an 71

independent fire event, they were chosen in separated areas (never less than 100 m between plots) and were therefore considered as spatially independent plots. Criteria for plot selection were that half of the replicate plots were low-slope plots (4-8%), while the other half were high-slope plots (20-25%). Similarly, north and south aspect plots were selected in all sites. For the 1987 stands, one plot was lowslope, and the other was high-slope, both northfacing. Soil physical and chemical characteristics were similar across the chronosequence, with a narrow range of organic matter and pH levels (Table 1). Fire intensity and severity was assessed by the amount and height of the fire scars. Based on these signals and on the information given by a local environmental agency, all fires were classified as crown fires. Previous fire history was also provided by the local environmental agency, and the selected plots had not burned since 1967. Fuel conditions were similar in all the plots, which were also fairly comparable in terms of stand structure (Table 1).

We performed two samplings, one in the spring (April 2004) during the growing season, and a second in the winter (February 2005), when growth is usually limited by low temperature. Ten individuals were selected randomly from each plot, and first order lateral green twigs were pruned on light exposed crown positions at three different heights (ca. 15, 13 and 11 m) to form a unique composite sample. Wherever possible we selected fully developed, mature needles of P. canariensis. However, these needles probably grow during the whole season so it was inevitable to sample some needles that were not fully elongated. Needle samples were placed inside polyethylene bags, sent to the laboratory in coolers and kept at 4°C until analysis.

Table 1 Altitude, stand structure (mean  $\pm$  SE) and soil properties (sampling of the first top 10 cm of the soil profile) of the plots burned in different years and the unburned plots

(Durán et al. 2009a). DBH Mean diameter at breast height, OM organic matter, N total nitrogen, C/N carbon to nitrogen ratio

Time since fire (years)	Altitude (m)	DBH (m)	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	OM (%)	N (%)	C/N	Olsen-P (g kg <sup>-1</sup> )	pН
Unburned	1,201	27.16±2.9	30.06±3.8	3.98	0.29	7.98	39.79	6.55
17	1,603	$34.38 {\pm} 8.2$	66.66±18.6	4.17	0.41	5.91	39.15	6.6
14	1,217	$35.44 \pm 5.6$	33.16±5.3	3.97	0.26	8.88	23.70	6.85
10	1,894	$46.89 {\pm} 2.8$	35.94±4.9	4.5	0.35	7.48	30.81	6.63
6	1,364	33.82±4.4	37.53±11.9	4.08	0.28	8.47	13.12	6.87
4	1,218	$35.86{\pm}7.4$	26.85±1.3	4.03	0.41	5.71	4.53	6.68

#### Laboratory analysis

Prior to chemical analysis, the needle samples were oven-dried at 80°C for 48 h, then milled and acid digested, following Allen et al. (1986). Diluted aliquots of the digestion were analysed for N and P by colorimetry using a microplate reader [indophenol blue method (Sims et al. 1995) and molybdenum blue method (Allen et al. 1986), respectively). Leaf N and P concentrations were expressed as milligrams of nutrient per gram of leaf dry weight.

#### Data analysis

We used repeated measures ANOVA to check the overall effect of wildfire and sampling date on the studied variables. Either untransformed or logtransformed variables satisfied the normality and variance homogeneity assumptions (Shapiro-Wilk and Levene tests, respectively). Asymptotic permutation tests were performed to compare leaf variable levels among different fire years, burned and unburned plots, and sampling dates. Significant levels were corrected by the Bonferroni procedure. To test for significant trends as time elapsed after a fire, the average values of the variables were compared to a linear regression line with the fire year as an independent variable. Statistical analysis was performed using the R 2.7.2 statistical package (R Development Core Team 2008).

#### Results

Leaf N and P concentrations and the leaf N:P ratio were significantly affected by fire year and the sampling date, with no significant interaction between these two factors (Table 2). Leaf N and P concentrations tended to be lower in burned than unburned plots for both sampling dates, but significant differences were found only for leaf P (Table 3). The N:P ratio was highest in the burned plots, but differences were significant only for the winter sampling. We observed a significant decrease of the leaf N and P concentrations four years after the last wildfire as compared with unburned plots for both the spring and winter sampling dates (Fig. 1). Leaf P concentration decreased by 58% and 53% in the spring and winter samplings, respectively, while leaf N decreased by 45% and 18% for the same time points. For both sampling dates, the leaf nutrient concentration tended to increase as time elapsed after a wildfire (Fig. 1). The slope of this trend was significantly different from zero for the winter sampling date for both N  $(df=3, R^2=0.87, F=19.84, P<0.05)$  and P  $(df=3, R^2=0.87, F=19.84, P<0.05)$  $R^2=0.83$ , F=14.18, P<0.05), but not for the spring sampling date either for N (df=3,  $R^2=0.52$ , F=3.30, P=0.17) or P (df=3,  $R^2=0.76$ , F=9.49, P=0.054). The N:P ratio tended to be highest at 4 years after the wildfire and then showed decreasing levels as time elapsed after the fire (Fig. 1), although this trend was not significant either for spring ( $df=3, R^2=0.56, F=$ 3.89, P=0.14) or winter (df=3,  $R^2=0.67$ , F=6.23, P=0.088) sampling dates. For all leaf traits and sampling dates, leaf trait values from burned plots matched the values of unburned plots after 17 years.

Leaf N and P concentrations were consistently higher in needles collected in the winter. For leaf N concentration, these differences were significant in all plots, whereas for leaf P concentration, differences were significant in the unburned plots and in plots sampled 4, 14 and 17 years after wildfire (P<0.05). The same differences were found for the N:P ratio, but they were less consistent and were significant

**Table 2** Results of repeated measures ANOVA comparing the effects of fire years and sampling dates on foliar N and P concentrations (mg g leaf<sup>-1</sup>) and on foliar N:P ratio

	Leaf N		Leaf P	Leaf P			Leaf N:P ratio		
	df	F	Р	df	F	Р	df	F	Р
Fire year	5	6.57	***	5	11.14	***	5	4.54	**
Sampling date	1	135.27	***	1	28.69	***	1	26.55	***
Fire x sampling	5	0.48	NS	5	0.45	NS	5	2.26	NS

\*P<0.05, \*\* P<0.01, \*\*\*P<0.001, NS non significant

**Table 3** Means and standard errors of leaf N and P concentrations (mg g leaf<sup>-1</sup>) and of leaf N:P ratios registered in unburned and burned plots in spring and winter samplings

		Spring	;		Winter			
		Mean	SE	Р	Mean	SE	Р	
Leaf N	Unburned Burned	6.89 5.84	0.64 0.33	NS	11.52 10.83	0.91 0.35	NS	
Leaf P	Unburned Burned	1.61 1.22	0.11 0.09	*	2.47 1.75	0.06 0.13	*	
Leaf N:P ratio	Unburned Burned	4.38 4.98	0.63 0.23	NS	4.7 6.46	0.48 0.38	*	

\*P<0.05, NS non significant

only in plots sampled 4 and 10 years after fire (P < 0.05).

# Discussion

As we hypothesized, leaf N and P concentrations tended to be lower in the burned than unburned plots, with the lowest values in the most recently burned plots. Although the differences were not always statistically significant for individual comparisons, the overall results showed a consistent pattern. These low values in the burned plots most likely reflect nutrient losses that wildfires cause through processes like volatilisation, post-fire leaching and soil erosion (Certini 2005). In another study on the same chronosequence, we observed the lowest values of the different soil N and P pools 4 years after the fire (Durán et al. 2009a, b). Thus, leaf nutrient concentrations seems to reflect changes in soil nutrient availability after the wildfire. However, the unambiguous temporal linear trend observed for leaf N and P in the fire chronosequence (although statistically significant only for the winter sampling) contrasted with the noisier trend found by Durán et al. (2008, 2009a, b) for soil nutrient availability indices, suggesting that leaf nutrients are a more precise method of detecting changes in nutrient availability in secondary succession than soil measurements. The main advantage of leaf nutrient measurements is that nutrient availability is integrated along the growing season. The main disadvantage is that nutrient availability is not represented for the whole plant community (and even less for soil microorganisms), but only for the analysed plant species. However, in our study, *P. canariensis* is the dominant species in the plant community and thus likely reflects the nutritional status of the whole plant community (Grime 1998; Tessier and Raynal 2003).

In consistent with results obtained in previous work on edaphic N and P availability (Durán et al. 2008, 2009a), and as compared with the unburned plots, the wildfire produced a larger reduction of P than N availability for plants, as suggested by the observed decrease in leaf P and N concentrations. As proposed by Vitousek and Howarth (1991), any disturbance should affect N more than P retention mechanisms because N is retained in the ecosystem mainly by biological processes, while P is retained by both biological and geochemical retention mechanisms. Thus, P should be less mobile than N in burned soils and much less prone to leaching losses, so we expected the lowest N:P ratios in recently burned plots as compared with older burned and unburned plots (Schlesinger 1997). However, the highest N:P ratio in the wildfire chronosequence was found in recently burned plots. This high N:P ratio, rather than indicating greater P losses from the ecosystem, may show a restructuring of the soil biogeochemical P fractions because of increased sorption and decreased bioavailability produced by the wildfire (García-Montiel et al. 2000, Rodríguez et al. 2009a). Interestingly, leaf P concentration recovered faster than leaf N as time elapsed after the fire. Both leaf N and P showed a linear recovery along the chronosequence, reaching values in the 17-year-old burned plots similar to those found in the unburned plots. Recovery of ecosystem N levels from a disturbance happens via both atmospheric deposition and biological fixation (Vitousek and Howarth 1991). In contrast, P recovery relies on the weathering of soil minerals. These mechanisms can recover pre-fire levels on a long-term basis, but they may have less influence on changes in N and P availability in our chronosequence time scale. The increase in N availability as time elapses after a wildfire has been explained as a consequence of the accumulation of soil organic matter following a fire (MacKenzie et al. 2004; Yermakov and Rothstein 2006). Because wildfires on La Palma Island are not stand-replacing fires, post-fire soil organic accumulation from pine litter should be relatively fast, which may explain the rapid recovery of pre-fire leaf N and P concentrations found



Fig. 1 Regression plot and mean and standard error for leaf N and P concentrations (mg g leaf<sup>-1</sup>) and for leaf N:P ratio in burned and unburned plots of *Pinus canariensis* forests. Same

in our chronosequence. However, the faster recovery of leaf P than leaf N concentration was unexpected, suggesting that specific recovery mechanisms for P should be operating. For example, fire-induced changes in the biogeochemistry of P could result in the gradual release of non-occluded forms of P from occluded forms, accelerating the recovery of the soil P levels (García-Montiel et al. 2000; Durán et al. 2008). Additionally, the external inputs of P-rich dust from the Saharan desert may help to explain the faster recovery of P compared to N availability after wildfires (Crews et al. 1995; Moreno et al. 2006).

lower case letter indicates no significant difference between plots (P<0.05, permutation test)

The parallel trends for the spring and winter samplings, both for the leaf N and P concentrations and the leaf N:P ratio, reinforce the effect of wildfire on the nutritional status of *P. canariensis* forests. Differences were higher for the winter than for the spring sampling, but we are aware that these differences likely reflect the winter end of the growing season versus the resorption and retranslocation dynamics from old to new needles during spring (Wang et al. 2003; Covelo et al. 2008). On the other hand, while leaf N and P concentrations tended to be higher in the winter sampling than in the spring sampling, fewer differences were observed in the leaf N:P ratio, supporting the idea that leaf N:P ratio is more reliable for the study of forest nutritional status than the nutrient concentrations alone (Koerselman and Meuleman 1996; Verhoeven et al. 1996; Tessier and Raynal 2003). However, seasonal sampling (especially in evergreen species) is recommended to corroborate N or P limitation in forest stands with known seasonality (Townsend et al. 2007).

The N:P ratio found in P. canariensis needles is one of the lowest values reported in the literature for woody species (Tessier and Raynal 2003; Güsewell 2004), and suggests that all pine trees in the chronosequence are unambiguously limited by low N availability (Verhoeven et al. 1996). Furthermore, leaf N concentrations in the fire chronosequence were always below 13-14 mg g<sup>-1</sup>, an additional indication for N limitation proposed by Wassen et al. (1995). As a direct consequence of the different dynamics of leaf N and P concentrations, the leaf N:P ratio tended to decrease (negative slope very close to the level of significance for both winter and spring samplings) from recently burned plots to unburned plots, suggesting a deviation from the critical (or optimal) N:P ratios and that wildfire may cause a temporary relief of the system N limitation. Compared to the most closely related continental pine species (P. halepensis and P. pinaster), it seems that N limitation is due to the low N availability in the ecosystem, as the ranges of leaf P values do not differ from normal levels in continental species (e.g. Fürst 1997; Tausz et al. 2004). The ultimate cause of N limitation may lie in the low N atmospheric deposition found in this area of the Atlantic Ocean (see Galloway et al. 2008). Biological N fixation also seems to be low as judged by the scarce presence of leguminous plants. In contrast, most of the pine communities on the European continent have been exposed for decades to high atmospheric N inputs, probably explaining why N is less limiting for plant growth than was previously assumed in terrestrial ecosystems (Elser et al. 2007).

# Conclusions

The *P. canariensis* forest on La Palma Island is one of the last European unmanaged pine forests under low atmospheric deposition. Therefore, these systems can provide a unique opportunity to study the long-term effects of wildfire on the nutritional status of natural pine forests without any major interference, and with fire being the only significant disturbance, they can serve to some extent as control sites for polluted coniferous forests.

Our results show that the leaf N and P concentrations and the leaf N:P ratio may be useful tools with which to describe temporal trends of nutrient status after forest disturbance. These N-limited pine forests retained N more efficiently than P 4 years after a wildfire, but leaf N recovery is slower than P recovery, suggesting that the mechanisms responsible for pine N limitation (as low atmospheric N deposition, low rates of N fixation or sustained P inputs) are continuously operating in these forests, and that fire caused only a temporary relief to their inherent N limitation.

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## References

- Aerts R, Chapin FSIII (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv Ecol Res 30:1–68
- Allen SE, Grimshaw HM, Rowland AP (1986) Chemical Analysis. In: Moore PD, Chapman SB (eds) Methods in plant ecology. Blackwell Scientific, Oxford, pp 285–344
- Bond-Lamberty B, Gower ST, Wang C, Cyr P, Beldhuis H (2006) Nitrogen dynamics of a boreal black spruce wildfire chronosecuence. Biogeochemistry 81:1–16
- Certini G (2005) Effects of fire on properties of forest soils: a review. Oecologia 143:1–10
- Climent J, Tapias R, Pardos JA, Gil L (2004) Fire adaptations in the Canary Islands pine (*Pinus canariensis*). Plant Ecol 171:185–196
- Covelo R, Rodríguez A, Gallardo A (2008) Spatial pattern and scale of leaf N and P resorption efficiency and proficiency in a *Quercus robur* population. Plant Soil 311:109–119
- Crews TE, Kitayama K, Fownes JH, Riley RH, Herbert DA, Mueller-Dombois D, Vitousek PM (1995) Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. Ecology 76:1407–1424

- Drenovsky RE, Richards JH (2004) Critical N:P values: predicting nutrient deficiencies in desert shrublands. Plant Soil 259:59–69
- Durán J, Rodríguez A, Fernández-Palacios JM, Gallardo A (2008) Changes in soil N and P availability in a *Pinus canariensis* fire chronosequence. For Ecol Manage 256:384–387
- Durán J, Rodríguez A, Fernández-Palacios JM, Gallardo A (2009a) Long-term decrease of organic and inorganic nitrogen concentrations due to pine forest wildfire. Ann For Sci (in press)
- Durán J, Rodríguez A, Fernández-Palacios JM, Gallardo A (2009b) Changes in net N mineralization rates and soil N and P pools in a pine forest wildfire chronosequence. Biol Fert Soils 45:781–788
- Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, Smith JE (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol Lett 10:1135–1142
- Fürst A (1997) Literaturübersicht: Nährstoffdaten Koniferen. Austrian Federal Forest Research Centre, Vienna
- Galloway JN (1998) The global nitrogen cycle: changes and consequences. Environ Pollut 102:15–24
- Galloway JN, Townsend AR, Erisman JW, Bekunda M, Cai Z, Freney JR, Martinelli LA, Seitzinger SP, Sutton MA (2008) Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. Science 320:889–892
- García-Montiel DC, Neill C, Melillo J, Thomas S, Steudler PA, Cerri CC (2000) Soil phosphorus transformations following forest clearing for pasture in the Brazilian Amazon. Soil Sci Soc Am J 64:1792–1804
- Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecol 86:902–910
- Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, Rorison IH, Hendry GAF, Ashendent TW, Askew AP, Band SR, Booth RE, Bossard CC, Campbell BD, Cooper JEL, Davison AW, Gupta PL, Hall W, Hands DW, Hannah MA, Hillier SH, Hodkinson DJ, Jalilia A, Liu Z, Mackey JML, Matthews N, Mowforth MA, Neal AM, Reader RJ, Reiling K, Ross-Fraser W, Spencer RE, Sutton F, Tasker DE, Thorpe PC, Whitehouse J (1997) Integrated screening validates primary axes of specialisation in plants. Oikos 79:259–281
- Güsewell S (2004) N:P Ratios in terrestrial plants: variation and functional significance. New Phytol 164:243–266
- Huang J, Boerner R (2007) Effects of fire alone or combined with thinning on tissue nutrient concentrations and nutrient resorption in *Desmodium nudiflorum*. Oecologia 153:233– 243
- Klein H, Benedictow A, Fagerli H (2007) Transboundary air pollution by main pollutants (S, N, O3) and PM. The European Community. Norwegian Meterological Institute, Oslo
- Koerselman W, Meuleman AFM (1996) The vegetation N: P ratio: a new tool to detect the nature of nutrient limitation. J Appl Ecol 33:1441–1450
- MacKenzie MD, DeLuca TH, Sala A (2004) Forest structure and organic horizon analysis along a fire chronosequence in the low elevation forests of western Montana. For Ecol Manage 203:331–343

- Moreno T, Querol X, Castillo S, Alastuey A, Cuevas E, Herrmann L, Mounkalia M, Elvira J, Gibbons W (2006) Geochemical variations in aeolian mineral particles from the Sahara-Sahel dust Corridor. Chemosphere 65:261–270
- Nardoto GB, Silva S, Kendall C, Ehleringer JR, Chesson LA, Ferraz ESB, Moreira MZ, Ometto JPHB, Martinelli LA (2006) Geographical patterns of human diet derived from stable-isotope analysis of fingernails. Am J Phys Anthropol 131:137–146
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. Proc Natl Acad Sci USA 101:11001–11006
- Reich PB, Abrams MD, Ellsworth DS, Kruger EL, Tabone TJ (1990) Fire affects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. Ecology 71:2179–2190
- Rodríguez A, Durán J, Fernández-Palacios JM, Gallardo A (2009a) Wildfire changes the spatial pattern of soil nutrient availability in *Pinus canariensis* forests. Ann For Sci 66:1–7
- Rodríguez A, Durán J, Fernández-Palacios JM, Gallardo A (2009b) Spatial variability of soil properties under *Pinus canariensis* canopy in two contrasting soil textures. Plant Soil 322:139–150
- Scholze M, Knorr W, Arnell NW, Prentice IC (2006) A climatechange risk analysis for world ecosystems. Proc Natl Acad Sci USA 103:13116–13120
- Sims GK, Ellsworth TR, Mulvaney RL (1995) Microscale determination of inorganic nitrogen in water and soil extracts. Commun Soil Sci Plant Anal 26:303–316
- Schlesinger WH (1997) Biogeochemistry: an analysis of global change. Academic, San Diego
- Tausz M, Trummer W, Wonisch A, Goessler W, Grill D, Jiménez MS, Morales D (2004) A survey of foliar mineral nutrient concentrations of *Pinus canariensis* at field plots in Tenerife. For Ecol Manage 189:49–55
- Tessier JT, Raynal DJ (2003) Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation. J Appl Ecol 40:523–534
- Townsend AR, Cleveland CC, Gregory PA, Bustamante MMC (2007) Controls over foliar N:P ratios in tropical rain forests. Ecology 88:107–18
- Van de Vijver CADM, Poot P, Prins HHT (1999) Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. Plant Soil 214:173–185
- Verhoeven JTA, Koerselman W, Meuleman AFM (1996) Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. Trends Ecol Evol 11:494–497
- Vitousek PM (2004) Nutrient cycling and limitation: Hawaii as a model system. Princeton University Press, Princeton
- Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13:87– 115
- Wan S, Hui D, Luo Y (2001) Fire-Effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecol Appl 11:1349–1365

- Wang W-Q, Wan M, Lin P (2003) Seasonal changes in element contents in mangrove element retranslocation during leaf senescene. Plant Soil 252:187–193
- Wassen MJ, Venterink HGMO, De Swart E (1995) Nutrient concentrations in mire vegetation as a measure of nutrient limitation in mire ecosystems. J Veg Sci 6:5–5
- Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western U.S. forest wildfire activity. Science 313:940–943
- Wirth C, Schulze ED, Lühker B, Grigoriev S, Siry M, Hardes G, Ziegler W, Backor M, Bauer G, Vygodskaya NN (2002) Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests. Plant Soil 242:41–63
- Yermakov Z, Rothstein D (2006) Changes in soil carbon and nitrogen cycling along a 72-year wildfire chronosequence in Michigan jack pine forests. Oecologia 149:690–700