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ORIGINAL PAPER

Comparing the use of leaf and soil analysis as N and P availability indices in a wildfire chronosequence

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Abstract Two types of measures have traditionally been used to monitor changes after disturbances in the nutrient availability of forest ecosystems: (1) soil nutrient pools and transformation rates and (2) foliar nutrient content. We used a wildfire chronosequence in natural and unmanaged Pinus canariensis forests to determine which kind of measure is more effective in discriminating between disturbed and undisturbed plots and to determine whether the different availability indices provide comparable and consistent results within the chronosequence and between different sampling dates. The results showed that (1) foliar N and P concentrations were the variables that best discriminated between the plots of the chronosequence, (2) the various soil N availability indices neither showed steady relationships nor predicted the plant nutrient availability, and (3) P availability indices showed steady relationships and predicted plant nutrient availability. Due to the changing nature of the soil N pools, repeated sampling over a long period of time could yield results different from those presented here. However, the large sampling effort required would favor the use of foliar nutrient

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concentrations as the most desirable first approach to the community's nutritional status, especially when time or budget constraints are relevant.

Keywords PCA \cdot Pine \cdot Nitrogen \cdot Phosphorus \cdot Nutrient status

Introduction

Two types of measures have been essentially used to monitor changes in nutrient availability in forest ecosystems caused by disturbances. First, nutrient availability measures obtained from soil pools or transformation rates have proven to be very sensitive to disturbances and may effectively define the nutrient availability for the entire community, including soil microorganisms (Neary et al. 1999; Hart et al. 2005; Huang and Boerner 2007). However, these measures are highly variable in time and space, are difficult to study independently (due to a high interaction rate between organic and inorganic compounds), and are very expensive in terms of time and resources. Moreover, the results obtained using these measures do not necessarily reflect the nutrient availability for a specific species or the entire plant community (Jenny 1980; Binkley and Hart 1989; Stark and Hart 1997). Second, nutrient availability estimates obtained from leaf nutrient concentrations may reflect the nutritional status of the vegetation (Vitousek and Farrington 1997; Aerts and Chapin 2000; Hobbie and Gough 2002; Vitousek 2004; Townsend et al. 2007) and integrate several environmental factors such as soil properties, climate, herbivory, and nutrient atmospheric deposition (Mengel and Kirby 2001; Tausz et al. 2004). Literature reviews have revealed that leaf N and P concentrations shape the productivity of the plant community (Koerselman and Verhoeven 1995), and the use of leaf N-to-P ratios has been recently proposed as a simple and easy alternative to laborious fertilization experiments to predict the nature of nutrient limitation in terrestrial ecosystems (Koerselman and Meuleman 1996; Tessier and Raynal 2003). Furthermore, while the leaf nutrient concentrations and ratios for an individual taxon do not necessarily represent the nutrient availability for the whole plant community, when a dominant species governs the local biogeochemical processes and supports most of the biomass production, foliar analysis of a single species may indeed reflect the nutritional status of the system (Valentine and Allen 1990; Grime 1998; Tessier and Raynal 2003).

Wildfires are, among others, a type of perturbation that may alter soil nutrient concentrations and transformation rates, and leaf N and P concentrations (Kutiel and Naveh 1987; Knoepp et al. 2004; Palese et al. 2004; Scheuner et al. 2004; Durán et al. 2008, 2010b). However, in comparison with the literature on edaphic approaches to evaluating the nutrient status of terrestrial ecosystems, the literature on leaf nutrient status is sparse, showing conflicting results and a clear lack of information about the long-term effects of perturbations on plant nutritional status (Christensen 1977; Adams and Rieske 2003; Huang and Boerner 2007). In addition, few studies have linked leaf indices with edaphic indices in order to show the degree of concordance between them (Bridham et al. 2001).

We used multivariate analysis as a tool to understand which measures are more effective at discriminating between unburned plots and plots burned in different years, in a fire chronosequence in natural and unmanaged *Pinus canariensis* forests. Also, we tried to determine whether the nutrient availability indices we used provide consistent and comparable results in our chronosequence and in different sampling dates, despite the fact that each index measures a different nutrient pool or a different transformation rate and that the temporal variability may be important (Binkley and Hart 1989). We hypothesized that foliar N and P concentrations should be the variables that best discriminate between disturbed and undisturbed plots, and that different soil N and P availability indices would not show steady relationships or predict plant nutrient availability.

Materials and 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 European pine forests. La Palma is one of the inhabited areas with the lowest level of anthropogenic atmospheric N deposition, so these forests are usually N-limited, and N deficiency syndromes are frequently observed in pine needles (Tausz et al. 2004; Durán et al. 2008; Luis et al. 2009; Galloway et al. 2008). These forests are occasionally affected by severe wildfires that completely eliminate the undergrowth, and although these fires usually reach the pine canopies (crown fires), they rarely kill the trees, and individuals that exceed 100 cm dbh are commonly found. The survival of adult individuals of P. canariensis after a fire makes these pine stands comparable in terms of pine age and structure (Otto et al. 2010).

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 (IUSS Working Group WRB 2006). The organic matter content of the sampled areas ranged from 2 to 4%, with total N ranging from 0.3 to 0.4% and pH ranging from 6.6 to 6.9 (Table 1). The 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), and the understory vegetation is very scarce, with only very few individuals of *Adenocarpus viscosus* (Wild.) Webb and Berthel, *Erica arborea* L., and *Cistus symphytifolius* Lam.

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 of the unburned plots (Durán et al. 2009)

| Time since fire (year) | Altitude (m) | DBH (m) | Basal area $(m^2 ha^{-1})$ | OM (%) | N (%) | C/N | Olsen-P (g kg ⁻¹) | 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 ± 8.2 | 66.66 ± 18.6 | 4.17 | 0.41 | 5.91 | 39.15 | 6.6 |
| 14 | 1,217 | 35.44 ± 5.6 | 33.16 ± 5.3 | 3.97 | 0.26 | 8.88 | 23.70 | 6.85 |
| 10 | 1,894 | 46.89 ± 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 ± 7.4 | 26.85 ± 1.3 | 4.03 | 0.41 | 5.71 | 4.53 | 6.68 |

DBH Mean diameter at breast height, OM organic matter, N total; C/N C-to-N ratio

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. 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. The physical and chemical characteristics of the soil 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 charcoal stains deposited on the pine bark. Based on these signals and on the information given by a local environmental agency, all fires were classified as crown fires. Fuel conditions were similar in the plots, which were also fairly comparable in terms of stand structure (Table 1). Previous fire history was also provided by the local environmental agency, and the selected burned plots had not burned since at least 1967, while control plots had not burned since at least 1900.

We performed two sampling campaigns: the first in the spring (April 2004) during the growing season and the second in the winter (February 2005), when growth is usually limited by low temperatures. Ten individuals were randomly selected from each plot, and green needles were sampled at three different heights (ca. 15, 13, and 11 m) to form a composite sample. Fifteen random soil samples were collected at each plot using a 15×5 cm metallic corer, which allowed us to sample the first top 10 cm of the soil profile. The litter layer was removed before sampling, and samples were carried to the laboratory in coolers inside polyethylene bags. Plant and soil samples were placed inside polyethylene bags, sent to the laboratory in coolers, and kept at 4°C before analysis.

Lab analysis

Prior to chemical analysis, the needle samples were ovendried at 80°C for 48 h, and then milled and acid digested following the protocol of Allen et al. (1986). Diluted aliquots of the digestion were analyzed for N and P concentrations 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 mg per g of dry leaf weight.

We sieved the collected soil samples using a 2-mm mesh, retaining the part of the sample that passed through the sieve. To calculate the soil properties on a dry weight basis, we measured the gravimetric water content by drying a subsample in a forced-air oven at 80° until a constant weight was reached. Carbon and organic matter contents

were estimated using a wet digestion method, and total N was estimated by Kjeldahl digestion with sulfuric acid and copper sulfate as a catalyst (Allen et al. 1986). We analyzed the NH₄-N and NO₃-N concentrations by extracting 5 g of fresh soil with 50 ml of 2 M KCl and calculating the amount of N present in the extracts using the blue indophenol colorimetric method and a microplate reader (Sims et al. 1995; D'Angelo et al. 2001). We measured PO₄-P using the method described by Nelson and Sommers (1996) by extracting 2 g of fresh soil with 40 ml of 0.5 N Na₂CO₃ and calculating the amount of PO₄-P present in the extracts using a Bran + Luebbe - AA3 colorimetric nutrient autoanalyzer. We measured net N mineralization rates using the procedure described by Eno (1960). For each soil sample, the top 10 cm of the soil was removed and placed in a polyethylene plastic bag, then reburied in the forest floor for a 30-day incubation. The net N mineralization rate (R-Mi) was defined as the net increase in NO₃-N and NH₄-N over the incubation interval, and the net increases in NO₃-N and NH₄-N were used to indicate the net nitrification (R-Ni) and ammonification (R-am) rates, respectively.

Microbial biomass N (MB-N) was determined using the fumigation-extraction method following the procedure of Brookes et al. (1982). We fumigated 5 g of fresh soil with chloroform for 5 days. Fumigated soils were extracted with 50 ml of 0.5 M K₂SO₄ and filtered through 0.45-µm Millipore filters. We used subsamples extracted with 50 ml of 0.5 M K₂SO₄ just before fumigation for the control. MB-N was calculated by subtracting the total N of the nonfumigated samples from the total N of the fumigated samples. Total N in these extracts was calculated using the persulfate oxidation technique (D'Elia et al. 1977) and the colorimetric blue indophenol method mentioned above. Finally, we estimated the dissolved organic nitrogen (DON) by subtracting the mineral N obtained in those samples from the total N in non-fumigated samples (Cabrera and Beare 1993; Doyle et al. 2004).

I-100 and I-200 Excellion (Electropure Inc., Laguna Hills, California) ion exchange membranes (IEMs) were also used to estimate the soil N and P availabilities (Durán et al. 2008; Cain et al. 1999). The membranes were positioned at a depth of 10 cm with a metal spatula, and the soil around them was compacted to ensure good contact between the membranes and the soil. A cation exchange membrane and an anion exchange membrane were incubated for 15 days at each sampling point (15 per plot). After removal, the membranes were taken individually to the lab and were dried at ambient temperature. The attached soil was removed, the plastic rod was cut, and an extraction was performed with 50 ml of 2 M KCl by orbital spinning for 1 h at 200 rpm in 125-ml flasks. These extracts were used to calculate the quantities of NH₄-N (NH₄-m) and NO₃-N (NO₃-m) by the indophenol blue

method (Sims et al. 1995) and the quantity of PO_4-P (PO_4-m) by the molybdenum blue method (Allen et al. 1986).

Data analysis

We used principal component analysis (PCA) based on all the studied variables to determine the degree of similarity between the plots of the chronosequence with respect to their biogeochemical characteristics. The validity of the analysis was tested using the Kaiser-Meyer-Olkin test (KMO) and the sphericity test, and only factors with eigenvalues over 1 were selected. The relationship between each component and the studied variables was determined by Pearson correlation analysis. We also conducted Pearson correlation analysis between the studied variables to determine the degree of interrelation between the different nutrient availability indices. We carried out linear regression analysis ('stepwise') to construct a predictive model of the leaf N and P concentrations and the leaf N-to-P ratio based on the other study variables. When required, we logarithmically transformed the data in order to meet the assumptions of the parametric statistical analysis. The analysis was performed using the statistical packages SPSS-17 and R-2.7.2 (R Development Core Team 2007).

Results

The principal components analysis (PCA) showed that soil and leaf N and P variables discriminated between the plots burned in different years, both in the spring and in the winter (Fig. 1). In the spring sampling, the four components obtained from the PCA explained 75% of the variation of the studied variables (Table 2). The first component (29%) had the greatest influence in discriminating between plots and was robustly and positively correlated with leaf N

Fig. 1 Biplot for the principal component analysis of the burned plots as a function of soil and leaf nutrient variables

and P concentrations, soil-extractable P, and membraneextractable P (Table 3). The second axis (17%) was correlated with microbial biomass N, membrane-extractable ammonium, and nitrification rate, with all correlations in the positive direction except for the nitrification rate. In the winter sampling, the four components extracted by the PCA explained more than 80% of the variation (Table 2). The first component (36%) was positively correlated with microbial biomass N, DON, extractable ammonium, nitrate and P, nitrification rate, and membrane-extractable P (Table 3). The second component (23%), which in this sample was the component that better discriminated between the burned plots, was significantly and positively correlated with leaf N and P, extractable P, and membraneextractable P. This second component was equivalent to the first component extracted by PCA for the spring sampling.

Multiple regression analysis showed that none of the studied soil N variables significantly predicted leaf N concentration in either sampling season (Table 4). However, for both sampling dates, soil-extractable P appears to be a robust and significant predictor of leaf P concentration $(R^2 = 0.671, P < 0.001, F = 40.76; R^2 = 0.29, P < 0.05, F = 7.77;$ spring and winter sampling, respectively). Extractable P was, again, the only significant predictor of leaf N-to-P ratio for the spring sampling date $(R^2 = 0.28, P < 0.02, F = 7.62)$. In the winter sampling, extractable P was also a good predictor of the leaf N-to-P ratio, but the best model selected extractable P together with membrane-extractable nitrate as predictors of the leaf N-to-P ratio $(R^2 = 0.55, P < 0.001, F = 11.42)$.

The correlation tests between the different N availability indices showed a clear inconsistency between sampling dates. For the spring sampling, the only significant correlations observed were those between DON and MB-N (r = 0.507, P < 0.05, n = 22), between DON and NO₃–N (r = -0.491, P < 0.05, n = 22), and between nitrification



Table 2 Matrix of factors (varimax rotation), eigenvalues, and cumulative variances (VarAc) of the principal component analysis for the soil and leaf variables for two sampling dates

| Spring | | | | | Winter | | | | |
|--------------------|--------|--------|--------|--------|--------------------|--------|--------|--------|--------|
| | PC1 | PC2 | PC3 | PC4 | | PC1 | PC2 | PC3 | PC4 |
| Leaf P | 0.918 | -0.009 | -0.041 | -0.162 | DON | 0.915 | 0.208 | 0.001 | -0.01 |
| PO ₄ –P | 0.894 | 0.143 | -0.119 | 0.044 | R–Ni | 0.902 | 0.101 | 0.152 | -0.125 |
| Leaf N | 0.835 | 0.123 | 0.161 | 0.009 | MB-N | 0.898 | -0.06 | 0.027 | 0.215 |
| PO ₄ -m | 0.807 | -0.044 | 0.158 | 0.141 | NH ₄ –N | 0.856 | 0.031 | 0.021 | 0.322 |
| MB-N | 0.202 | 0.857 | -0.003 | 0.182 | NO ₃ –N | 0.799 | 0.358 | -0.241 | -0.033 |
| DON | -0.088 | 0.787 | -0.066 | -0.435 | PO ₄ –P | 0.138 | 0.828 | -0.113 | 0.085 |
| R-ni | -0.133 | -0.085 | 0.803 | -0.056 | PO ₄ -m | 0.168 | 0.818 | 0.142 | -0.285 |
| R-am | 0.272 | 0.407 | 0.796 | 0.082 | Leaf N | 0.031 | 0.797 | -0.066 | -0.021 |
| NH ₄ -m | -0.195 | 0.498 | -0.688 | 0.131 | Leaf P | 0.078 | 0.619 | -0.611 | 0.209 |
| NO ₃ –N | 0.024 | -0.137 | 0.134 | 0.873 | NO ₃ -m | -0.202 | -0.003 | 0.867 | 0.134 |
| NH ₄ –N | 0.127 | 0.305 | -0.188 | 0.701 | R-am | 0.392 | -0.035 | 0.698 | -0.078 |
| NO ₃ -m | -0.264 | -0.35 | -0.157 | 0.477 | NH ₄ -m | 0.162 | -0.06 | 0.016 | 0.957 |
| Autovalue | 3.466 | 2.152 | 1.891 | 1.47 | Autovalue | 4.515 | 2.527 | 1.546 | 1.051 |
| CuVar (%) | 28.882 | 46.819 | 62.581 | 74.833 | CuVar (%) | 37.626 | 58.682 | 71.567 | 80.326 |

rate and membrane-extractable NH₄–N (r = -0.451, P < 0.05, n = 22). However, for the winter sampling date, we found significant and positive correlations between NBM and DON, NH₄–N, NO₃–N, and Ni-Rate; between DON and NH₄–N, NO₃–N, and Ni-Rate; between NH₄–N and NO₃–N, and Ni-Rate; and between NO₃–N, and Ni-Rate (Table 5). In contrast, the different P availability indices showed a strong correlation and a great consistency between sampling dates, with a significant and positive correlation between leaf P, P–PO₄, and PO₄–mi (Table 5) both for the spring and winter samplings.

Discussion

The foliar nutrient concentrations (both leaf N and P concentrations) were the variables with the greatest influence on grouping the unburned plots and the plots burned in different years. This trend was identical for the two sampling dates, which supports the robustness of the observed patterns (Durán et al. 2010b). While several examples found in the literature show a significant effect of this type of disturbance on both foliar nutrient concentrations and on the various soil nutrient availability indices (e.g., Christensen 1977; Neary et al. 1999; Huang and Boerner 2007; Durán et al. 2008, 2010b), each of the soil nutrient availability indices measures a different nutrient pool or transformation rate, which are subject to strong and complex spatial and temporal variability (Stevenson 1986; Binkley and Hart 1989; Bridham et al. 2001). The use of standard methods to measure soil nutrient availability, most of which do not account for important rhizospheric processes and/or cause important significant soil disturbance, may lead unrepresentative pictures of the system status and the processes occurring therein (Frank and Groffman 2009). In contrast, leaf nutrient concentrations integrate variations in nutrient availability during the growing season, as well as changes in climate, herbivory rates, or atmospheric nutrient deposition over long periods of time (Vitousek and Farrington 1997; Mengel and Kirby 2001; Townsend et al. 2007). Therefore, several authors argue that leaf nutrient concentrations could reflect the nutritional status of the system more accurately than the soil nutrient availability indices (Foulds 1993; Thompson et al. 1997; Marschner 1995; Hobbie and Gough 2002). Moreover, in our study, P. canariensis is the absolutely dominant species in the plots of our chronosequence, so its nutritional status probably reflects the nutritional status of the whole plant community (Valentine and Allen 1990; Grime 1998; Tessier and Raynal 2003).

Similarly, both PO₄–P and PO₄–mi also had a significant influence in separating plots according to the year of disturbance. This result was not unexpected given the significant correlation between these edaphic indices of P availability and the leaf P concentration in both samplings, suggesting that all of these indices effectively measure a common pool of available P (Bridham et al. 2001). In contrast, the N availability indices were inconsistently correlated. While for the winter sampling we found significant correlations between some of the soil N availability indices (but not between foliar and edaphic availability indices), the number of significant correlations was clearly

| | Leaf N | Leaf P | MB-N | DON | NH_4-N | NO ₃ -N | $PO_{4}-P$ | R-am | R-ni | $\rm NH_{4}-m$ | NO ₃ -m | PO ₄ -m |
|-----------|---------------|-------------|---------------|---------------|---------------|--------------------|--------------|--------------|---------------|----------------|--------------------|--------------------|
| Spring s | ampling | | | | | | | | | | | |
| CP 1 | 0.852^{***} | 0.853 * * * | 0.421 | 0.115 | 0.166 | 0.016 | 0.855*** | 0.529 | 0.016 | -0.189 | -0.374 | 0.780^{***} |
| CP 2 | -0.08 | -0.043 | 0.622^{**} | 0.74^{***} | 0.215 | -0.341 | 0.088 | -0.190 | -0.517* | 0.791^{***} | -0.240 | -0.230 |
| CP 3 | 0.036 | 0.035 | 0.029 | -0.482* | 0.639^{**} | 0.681^{***} | 0.214 | -0.369 | -0.462* | 0.339 | 0.495* | 0.172 |
| CP 4 | -0.71 | -0.375 | 0.493 | 0.169 | 0.391 | 0.468^{*} | -0.224 | 0.655^{**} | 0.438* | -0.018 | 0.052 | -0.082 |
| Winter s. | sampling | | | | | | | | | | | |
| CP 1 | 0.350 | 0.377 | 0.811^{***} | 0.914^{***} | 0.820^{***} | 0.881^{***} | 0.473* | 0.293 | 0.839^{***} | 0.214 | -0.225 | 0.445* |
| CP 2 | 0.642^{**} | 0.723 * * * | -0.416 | -0.167 | -0.343 | 0.115 | 0.634^{**} | -0.504 | -0.302 | -0.261 | -0.383 | 0.546^{**} |
| CP 3 | 0.257 | -0.353 | -0.163 | 0.028 | -0.184 | -0.087 | 0.173 | 0.547^{**} | 0.163 | -0.492* | 0.623^{**} | 0.548^{**} |
| CP 4 | 0.201 | 0.130 | -0.008 | -0.129 | 0.117 | -0.167 | 0.262 | 0.102 | -0.201 | 0.768^{***} | 0.475* | 0.033 |

lower for the spring sampling. This inconsistency suggests either that the different methods to determine the N availability are characterizing different soil N pools that change over different time scales or that many of these indices are not adequate, at least in systems with high seasonal variability (Bridham et al. 2001). Accordingly, the multiple regression analysis showed that, unlike the P indices, none of the individual soil N indices or any combination of them significantly predicted the foliar N concentration for either of the two sampling dates.

The lack of correlation between the edaphic and foliar N availability indices may suggest that N is not the most limiting nutrient in these pine forests. However, the low N-to-P ratio, as well as the low N concentration registered in P. canariensis needles, suggests a strong N limitation (Durán et al. 2010b; Wassen et al. 1995; Koerselman and Meuleman 1996; Tessier and Raynal 2003; Güsewell 2004; Verhoeven et al. 1996). More likely, the temporal and spatial variability observed in this chronosequence for all of the soil N variables, undoubtedly higher than that for P variables (Durán et al. 2008, 2009, 2010a), may help explain this discrepancy. The low P variability in relation to the N variability may be due to the simplicity of inorganic P-containing compounds compared with inorganic N-containing chemical forms. Nitrogen can appear in several inorganic forms (N₂, NO₂, NO, N₂O, NH₄, NO₃), some of which are gaseous, and the transformations between these compounds require the participation of diverse microbial groups. In contrast, although phosphorus may also be involved in different and sometimes complex interactions in the soil, it does not have a gaseous form under natural conditions, and only a single inorganic form (PO_4) exists in the soil. This lower variability and complexity of the biological reactions involving P may explain its greater power to predict the leaf P concentrations (Schlesinger 1997). Alternatively, other physiological causes could be behind the discrepancy found between soil and leaf N levels. Plants adapted to nutrient-poor soils, such as these P. canariensis forests that are adapted to low N levels, have an inherent physiological inability to respond quickly to changes in nutrient availability, and this fact could help to explain the failure of the edaphic measures to predict the leaf N concentrations (Chapin et al. 1986; Pastor and Bridgham 1999; Aerts and Chapin 2000). Also, if N is indeed limiting, then fast changes in soil N availability may have increased the net primary production (NPP), but not necessarily increased foliar nutrient concentrations within the same temporal scale. Unfortunately, NPP was not measured and we cannot confirm or discard this possible explanation. For both explanations, these effects would be less important for P due to the fact that this nutrient is not a limiting factor in these P. canariensis forests (Durán et al. 2008, 2010b).

| variables | | | | | | |
|-----------|--------------------|----------------------|----------|---------------|-------|----------|
| Sampling | Dependent variable | Independent variable | Constant | Beta (EE) | R^2 | Р |
| Spring | Leaf P | PO ₄ –P | 0.327 | 0.140 (0.02) | 0.67 | < 0.0001 |
| | Leaf N-to-P ratio | PO ₄ –P | 0.987 | -0.118 (0.04) | 0.28 | 0.012 |
| Winter | Leaf P | PO ₄ –P | 0.415 | 0.110 (0.04) | 0.28 | 0.011 |
| | Leaf N-to-P ratio | PO ₄ –P | -0.668 | -0.15 (0.04) | 0.55 | < 0.001 |
| | | NO ₃ -m | | 5.66 (2.47) | | |
| | | | | | | |

 Table 4
 Linear regressions using the soil nutrient availability indices as independent variables and the leaf nutrient concentrations as dependent variables

Only significant regressions (P < 0.05) are shown

| Table 5 | Pearson | correlation | coefficients | between | soil | nutrient | availability | indices |
|---------|---------|-------------|--------------|---------|------|----------|--------------|---------|
|---------|---------|-------------|--------------|---------|------|----------|--------------|---------|

| Spring sa | mpling | | | | | | | | | | |
|--------------------|----------------|---------|--------------------|--------------------|--------|---------|--------------------|--------------------|--------------------|--------------------|--------------------|
| N availab | oility indices | | | | | | | | P a. i. | | |
| | BM-N | DON | NH ₄ –N | NO ₃ –N | R-am | R-ni | NH ₄ -m | NO ₃ -m | | PO ₄ –P | PO ₄ -m |
| Leaf N | 0.205 | 0.047 | 0.125 | 0.022 | 0.352 | 0.117 | -0.101 | -0.224 | Leaf P | 0.819** | 0.628** |
| MB-N | | 0.507* | 0.345 | -0.043 | 0.362 | -0.032 | 0.42 | -0.112 | PO ₄ –P | | 0.580** |
| DON | | | -0.054 | -0.491* | 0.224 | -0.139 | 0.315 | -0.292 | | | |
| NH ₄ –N | | | | 0.409 | -0.028 | -0.179 | 0.188 | 0.091 | | | |
| NO ₃ –N | | | | | 0.213 | -0.036 | 0.004 | 0.28 | | | |
| R–NH ₄ | | | | | | 0.395 | -0.393 | -0.358 | | | |
| R-NO3 | | | | | | | -0.451* | 0.032 | | | |
| NH ₄ -m | | | | | | | | 0.047 | | | |
| Winter sa | mpling | | | | | | | | | | |
| N availab | oility indices | ; | | | | | | | P a. i. | | |
| | BM-N | DON | NH ₄ –N | NO ₃ –N | R-am | R-ni | NH ₄ -m | NO ₃ -m | | PO ₄ –P | PO ₄ -m |
| Leaf N | -0.114 | 0.224 | -0.017 | 0.401 | 0.006 | 0.171 | -0.037 | -0.068 | Leaf P | 0.529* | 0.297 |
| MB-N | | 0.743** | 0.853** | * 0.599** | 0.342 | 0.749** | 0.331 | -0.146 | PO ₄ –P | | 0.722** |
| DON | | | 0.744** | * 0.824** | 0.298 | 0.873** | 0.121 | -0.1 | | | |
| NH ₄ –N | | | | 0.652** | 0.194 | 0.702** | 0.387 | -0.066 | | | |
| NO ₃ –N | | | | | 0.167 | 0.655** | 0.121 | -0.384 | | | |
| R–NH ₄ | | | | | | 0.432* | 0.067 | 0.315 | | | |
| R-NO ₃ | | | | | | | 0.016 | -0.024 | | | |
| NH ₄ -m | | | | | | | | 0.837 | | | |

* (<0.05), ** (<0.005), *** (<0.0005)

Our results show that foliar N and P indices seem to have a greater ability to discriminate between changing nutritional conditions (such as those found in a wildfire chronosequence) than the edaphic indices. This conclusion is particularly true for the leaf N concentration (as the soil inorganic P concentration also showed ability to discriminate between plots with different nutritional states), and might be valid, at least in N-limited ecosystems such as the *P. canariensis* forests used in this study. However, such a conclusion might also be valid in P-limited or co-limited systems because the intrinsic differences in the N and P biogeochemical reactions may also explain their differing abilities to detect changes in nutrient availability. On the other hand, given the changing nature of the soil N forms, we assume that a more intensive and/or extended soil sampling could yield different results than those presented here, and these results could show a tighter relationship between the indices. However, that greater sampling effort and cost would favor, especially when time or budget constraints are relevant, the use of foliar nutrient concentrations as the most desirable first indicator of the community's nutritional status. Acknowledgments We thank the La Palma Government for enabling access and providing logistic support for the sampling expeditions, and Javier Méndez, Gustavo Morales, Felix Medina, Alfredo Bermúdez, Rocío Paramá, Rosana Estévez, Feliciano Martínez, and Jesús Rodríguez for their valuable help with the field sampling and laboratory analysis. We also thank Jen Morse for her valuable help in editing the manuscript. This work was financed by the Ministerio de Ciencia y Tecnología of the Spanish Government (REN 2003-08620-C0201; CGL 2006-13665-C02-01).

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