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Variation in tissue element concentrations in *Quercus ilex* L. over a range of different soils

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Abstract

In order to study the variability in nutrient concentrations in four tissues of *Q. ilex* in relation to soil properties, we selected fifteen stands in both *Quercus ilex* forests and *Q. ilex-Pinus halepensis* mixed forests. These stands had developed on soils derived from eight different parent materials. Three soil groups were differentiated according to their chemical properties: calcareous soils, siliceous soils, and volcanic soils. Across sites, nutrient concentrations were generally less variable in current-year tissues than in older tissues. Nitrogen and potassium showed the lowest variability among sites, their concentrations in current-year leaves ranging from 1.17% to 1.39% for N and from 0.53% to 0.68% for K. There were few statistically significant correlations between tissue element concentrations, the most frequent being the antagonistic relationship between calcium and magnesium. Nitrogen concentration in current-year leaves was negatively correlated with soil chemical fertility (nitrogen, phosphorus and potassium). This may reflect a nutritional imbalance between nitrogen and other nutrients, some of which may be more limiting than nitrogen to *Q. ilex* growth in Catalonia forests. Negative correlations were also found between plant magnesium and soil calcium, and positive correlations between plant calcium and soil calcium.

Introduction

Population studies on the patterns of variation in many plant species have revealed the existence of intraspecific differences in various aspects of morphological and physiological traits (Harper 1977; Gottlieb 1984; Karlsson & Nordell 1988). These differences can be on a very broad spatial scale (over hundreds of km) or on a very local scale (over just a few meters). In either case, patterns of population differentiation tend to closely follow patterns of environmental variation (Bradshaw 1984).

There are two basic ways of responding to spatial environmental heterogeneity: firstly, plants may adjust phenotypically through plasticity in individual development, and secondly, they may evolve locally-adapted ecotypes. As a result of the latter, a significant amount of genetic variation is found both within and between plant populations

(Jain & Bradshaw 1966; Kuiper & Kuiper 1988).

Aspects of physiological performance show greater differences than those of morphological ones (Bradshaw 1965; Schlichting 1986). For relative nutrient use efficiency of one species over a range of different environmental conditions – climatic and edaphic – differences could evolve concerning nutrient uptake from soil, nutrient utilization and internal nutrient redistribution (Clark 1983; Ericksen & Nordal 1989; Turner & Lambert 1986).

The principal aim of the present study was to examine the variability in nutrient concentrations of different plant tissues among fifteen holm oak (*Quercus ilex* L.) populations. Holm oak is a long-lived, perennial, angiosperm tree with a wide edaphic tolerance. It is distributed primarily in the Mediterranean region. The sampled stands were developed on soils derived from eight different parent materials. Because of heterogeneity among soils, the possibility of adaptative differentiation among the populations was high. The other two aims of this paper were to report on the varying concentrations of elements in the fifteen soils and to quantify the relationships between element concentrations in plant tissues and those in the soil.

Methods

Site selection and sampling

We conducted our study in forests in Catalonia (NE Spain) where we selected fifteen stands from both *Q. ilex* forests and *Q. ilex* – *Pinus halepensis* mixed forests. The stands had developed on soils derived from eight different parent materials: limestone, marl, conglomerate, sandstone, granodiorite, granite, schist and volcanic rock. Two stands were chosen on each parent material except for granite on which only one was chosen. As a result, a wide variation in soil properties was obtained. The stands were located in a semi-circle within a 90 km radius of Barcelona. A description of the sampled stands is shown in Table 1.

We selected a 30 × 30 m plot in each stand from which plant and soil samples were collected. Because various factors can affect plant nutrient concentrations (Wells & Metz 1963; van den Driessche 1974), the following factors were taken into account in the sampling process: position within the crown, type of tissue, age of foliage, and time of year. The samples were taken from the top of the canopy of dominant and co-dominant trees, in order to avoid differences in

Table 1. Major characteristics of the fifteen stands selected in *Quercus ilex* forests and *Q. ilex-Pinus halepensis* mixed forests.

Stand no.	Parent rock	Aspect	Slope (°)	Altitude (m)	Type of forest	Locality
1	Limestone	W	19	280	mixed	Olesa de Bonesvalls
2	Limestone	E	24	320	mixed	Olesa de Bonesvalls
3	Marl	SE	8	700	holm oak	Tona
4	Marl	S	13	730	holm oak	Tona
5	Conglomerate	SW	11	760	mixed	St. Llorenç del Munt
6	Conglomerate	SE	24	780	mixed	St. Llorenç del Munt
7	Sandstone	N	6	500	mixed	Aiguafreda
8	Sandstone	NW	5	500	mixed	Aiguafreda
9	Granodiorite	NW	16	375	mixed	La Garriga
10	Granodiorite	E	20	450	mixed	Lliçà
11	Granite	W	25	620	mixed	La Garriga
12	Schist	SW	27	600	mixed	La Garriga
13	schist	E	32	330	mixed	Aiguafreda
14	Volcanic rock	W	25	740	holm oak	Olot
15	Volcanic rock	SW	29	690	holm oak	Olot

light intensity. Four different tissues of fifteen randomly selected trees were sampled and then mixed for each stand: current-year leaves, older leaves, current-year shoots, and branches < 1 cm in diameter. A composite soil sample of each stand was obtained by mixing 10 separate soil samples taken from the first 10 cm depth of mineral soil. All samples were taken in August 1984.

Chemical and statistical analyses

Plant material was dried at 70 °C for 72 h before chemical analyses. We determined nitrogen by the Kjeldahl method in a Kjeltec Auto 1030 Analyzer. Plant samples were subjected to conventional wet digestion in a mixture of perchloric and nitric acids (2:5) to analyze for phosphorus, potassium, magnesium and calcium concentrations. Phosphorus was complexed with vanadomolybdate and read colorimetrically in a spectophotometer at 420 nm, while potassium, magnesium and calcium were determined by atomic absorption.

Soil samples were air dried in the laboratory and sieved to pass through a 2 mm mesh prior to analysis. They were analyzed for organic matter, total nitrogen, extractable phosphorus, exchangeable potassium, magnesium, calcium and sodium, cation exchange capacity, and pH. Total nitrogen was analyzed by the Kjeldahl method. Sodium bicarbonate extraction (0.5 M) was used to determine extractable phosphorus, while ammonium acetate (1 N) was used for cation exchange capacity and for exchangeable potassium, magnesium, calcium and sodium (MAP 1981). Distilled water (2:1, water:soil by weight) was used to measure pH. The soil analyses were carried out by the Laboratorio Agrario del Estado in Cabrils (Barcelona). We analyzed available nitrogen (ammonium and nitrate) by spectophotometry after extraction with potassium chloride (1 M), but not all soil samples could be analyzed due to improper storage. For this reason, we only analyzed ten soils for available nitrogen. These are discussed in the text but they were not incorporated in tables and statistical analyses.

Simple regression models were used to assess correlations between plant and soil variables. Principal components analysis (PCA) was carried out on the soil data (SAS Institute 1988). Logarithmic transformations were used to normalize the data for all plant and soil variables, except for pH.

Results

Soil analysis

For all soils, the mean available nutrient concentrations decreased in the order Ca > Mg > Na > K > P (Table 2). Remarkably low concentrations of phosphorus were found in all sampled soils, ranging from 1.2 μg/g to 5.2 μg/g. Variability of nitrogen (C.V. = 62.0%) and potassium (C.V. = 94.3%) among the sampled soils, as measured by the number of times the maximum value is higher than the minimum one, was eight and seventeen-fold, respectively. The highest variability was found in K (C.V. = 94.3%), while P showed the lowest variability (C.V. = 51.0%). There was a wide range of pH from 5.3 to 7.9, reflecting a wide range of calcium concentrations.

Three soil groups could be distinguished along the first two axes of the PCA (Fig. 1). The first axis was correlated with organic matter (r = 0.44), total nitrogen (r = 0.44), extractable phosphorus (r = 0.35) and exchangeable potassium (r = 0.44), reflecting a gradient of chemical fertility. The second axis was correlated with calcium (r = 0.59) and pH (r = 0.58), reflecting a gradient of base status. Together these axes explain 77% of the variance. The three soil groups obtained were:

1. Calcareous soils (Stands No 1, 2, 3, 4, 5, 6).
2. Siliceous soils (Stands No 7, 8, 9, 10, 11, 12, 13).
3. Volcanic soils (Stands No 14, 15).

Stand numbers are shown in Table 1. Summary information of the chemical properties of the three soil groups is shown in Table 2. The first group was characterized by neutral and moderately high pH, and was associated with good chemical fer-

Table 2. Mean and range of soil chemical properties for the three soil groups obtained in the principal components analysis, and mean and coefficient of variation (C.V.) for all soils. Analyses were made on the first 10 cm depth of mineral soil.

Soil parameter	Calcareous soils		Siliceous soils		Volcanic soils		All soils	
	Mean	Range	Mean	Range	Mean	Range	Mean	C.V. (%)
Organic matter (%)	4.77	2.46–8.70	2.28	1.32–3.02	6.74	6.66–6.83	3.87	55.97
Total nitrogen (%)	0.20	0.12–0.39	0.08	0.05–0.12	0.28	0.28–0.29	0.16	62.02
C/N	13.3	11.9–15.8	15.7	13.2–18.3	13.5	13.1–14.0	14.5	13.3
Extractable phosphorus (μg/g)	3.37	1.60–5.20	1.57	1.20–2.20	2.00	2.00–2.00	2.35	51.08
Exchangeable cations								
Potassium (μeq/g)	5.6	2.2–14.2	1.6	0.8–2.9	3.6	3.6–3.7	3.5	94.3
Magnesium (μeq/g)	36.0	12.7–77.8	21.1	6.8–35.8	34.5	24.5–44.5	28.9	65.8
Calcium (μeq/g)	393.3	150.0–579.0	140.0	50–268.0	88.0	57.0–119.0	234.4	78.3
Sodium (μeq/g)	27.8	20.9–35.6	10.5	1.1–30.4	2.6	1.3–3.9	16.4	79.5
C.E.C.* (μeq/g)	215.1	124.5–362.0	146.0	123.0–162.0	412.3	396.7–428.0	209.2	53.8
pH	7.54	6.9–7.9	6.15	5.3–7.0	5.87	5.85–5.90	6.67	13.7

* Cation excange capacity.

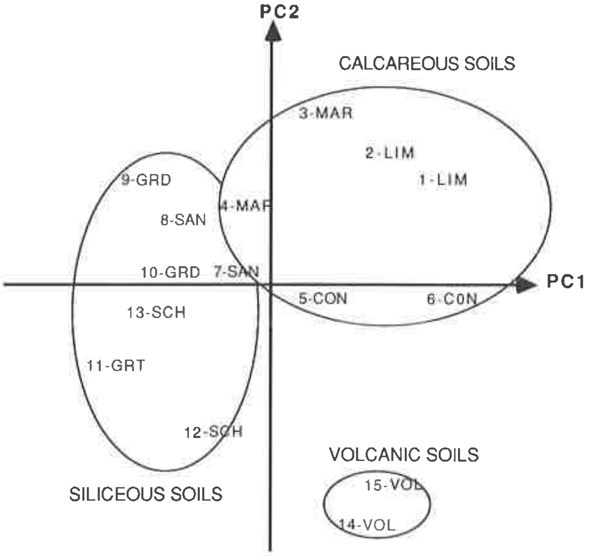

Fig. 1. Principal component analysis of the soil data for the fifteen soils derived from eight parent materials. Abbreviations: LIM-limestone, MAR-marl, CON-conglomerate, SAN-sandstone, GRD-granodiorite, GRT-granite, SCH-schiste, VOL-volcanic rock. The corresponding stand numbers are shown in Table 1.

tility (o.m., N, P, K). The second group was characterized by lower pH and fertility, while the third showed low pH, and high chemical fertility.

The siliceous soils showed lower fertility than the other two soil groups, especially those soils derived from granodiorite and granite (sites No 9, 10 and 11, Table 1). They had less than 0.08% total nitrogen, less than 1.6 μg/g extractable phosphorus, and between 0.8 and 1.5 μg/g exchangeable potassium, which are the lowest concentrations in the fifteen soils studied. In addition, these soils showed the highest C/N ratio and the lowest C.E.C., which is also correlated with low fertility. Calcareous soils showed the highest concentrations of extractable phosphorus and a remarkably high C.E.C. was found in volcanic soils.

There was a close correlation between total nitrogen and pH ($r = 0.78$, $P = 0.002$, $n = 13$) when volcanic soils were excluded. Chemical properties of the latter were very different from those of the other soils. A good correlation was found between total nitrogen and ammonium + nitrate ($r = 0.83$, $P = 0.003$, $n = 10$).

Table 3. Concentrations (mg/g) of live mineral elements -N, P, K, Mg, Ca- in current-year leaves (C.L.), older leaves (O.L.), current-year shoots (C.S.) and branches < 1 cm in diameter (B.) for *Quercus ilex* in the fifteen stands selected. Maximum and minimum concentrations in bold.

Stand No	Nitrogen				Phosphorus				Potassium				Magnesium				Calcium			
	C.L.	O.L.	C.S.	B.	C.L.	O.L.	C.S.	B.	C.L.	O.L.	C.S.	B.	C.L.	O.L.	C.S.	B.	C.L.	O.L.	C.S.	B.
1	11.80	10.11	**6.71**	7.11	**1.09**	**1.12**	**1.34**	0.94	6.15	**5.42**	8.94	**3.09**	**0.96**	**0.78**	**1.04**	**0.41**	5.68	8.52	7.25	8.99
2	**11.70**	11.25	6.88	**5.25**	**0.69**	0.56	**0.84**	**0.60**	6.69	4.81	9.40	4.50	1.29	0.92	1.38	0.64	5.94	**9.47**	**8.16**	**11.16**
3	13.10	10.98	**7.99**	6.69	0.98	0.63	1.30	0.97	**5.35**	3.80	8.84	4.52	1.36	1.09	1.85	0.85	4.24	6.86	7.64	7.33
4	13.70	11.30	6.92	7.49	0.74	0.56	0.92	0.79	6.02	3.63	8.03	4.33	1.40	0.99	1.77	0.84	5.56	8.02	7.21	8.32
5	12.50	10.40	7.45	6.39	0.96	0.59	1.11	0.87	5.94	3.59	8.48	4.61	1.53	1.30	1.90	0.97	4.24	6.42	**5.70**	7.25
6	11.90	10.69	7.22	5.73	0.80	**0.53**	0.94	0.72	6.43	3.57	8.41	4.33	1.58	1.36	1.98	0.93	4.48	**6.12**	6.55	7.18
7	12.30	9.90	6.97	5.47	0.99	0.69	1.14	0.85	**6.84**	3.88	**10.91**	**4.91**	1.45	1.03	1.90	0.79	5.39	7.62	7.07	8.40
8	12.10	10.11	6.90	6.11	0.94	0.66	1.16	1.05	6.58	4.40	9.62	4.84	1.25	0.87	1.63	0.72	**6.40**	8.86	8.00	9.33
9	13.70	10.36	7.30	6.02	0.87	0.70	1.04	0.80	6.78	3.69	8.24	4.30	1.55	1.13	1.67	0.76	6.21	8.92	7.84	8.63
10	13.80	10.80	7.40	6.18	0.89	0.59	0.99	0.77	6.63	4.40	**7.91**	4.40	1.34	1.07	1.80	0.79	4.94	8.63	7.56	7.82
11	13.10	**11.68**	7.70	6.50	1.06	0.92	1.18	1.08	5.53	4.34	8.20	4.33	1.40	1.32	1.85	0.89	4.27	7.10	6.23	6.14
12	12.57	11.42	7.93	7.22	0.97	0.69	1.13	1.08	6.74	4.82	10.09	4.72	1.46	1.26	1.97	0.92	**3.80**	7.29	6.19	7.48
13	**13.87**	**9.57**	7.35	6.96	0.87	0.57	1.09	1.15	6.11	**3.48**	8.78	4.57	1.60	1.37	2.05	0.91	4.00	7.02	6.79	6.32
14	12.17	11.06	7.13	6.97	0.87	0.78	1.28	1.05	6.22	4.50	9.97	4.75	**2.28**	**1.86**	2.39	**1.28**	5.23	7.27	6.47	6.20
15	11.90	10.72	7.21	**8.34**	1.06	0.84	1.19	**1.22**	5.60	4.25	8.40	4.53	1.90	1.72	**2.52**	1.26	4.65	6.78	6.28	**5.96**
Mean	12.68	10.69	7.27	6.56	0.92	0.70	1.11	0.93	6.24	4.17	8.88	4.45	1.49	1.20	1.85	0.86	5.00	7.66	7.00	7.77
C.V. %	6.27	5.69	5.25	12.45	12.60	23.35	13.00	18.89	7.75	13.70	9.30	9.50	20.03	24.97	19.31	24.94	16.75	13.27	10.71	18.28

Plant analysis

There were differences among plant tissues with respect to the concentrations of all elements (Table 3). The mean element concentrations in current-year leaves decreased in the following order: N > K > Ca > Mg > P. The same pattern was shown in current-year shoots, whereas calcium was quantitatively more important than potassium in old leaves and branches < 1 cm in diameter. Current-year leaves had the highest nitrogen concentrations while the highest levels of phosphorus, potassium and magnesium were found in current-year shoots. Magnesium concentrations in plant tissues were much higher in stands on volcanic soils, and for current-year leaves were as much as 50% higher than the mean concentrations over all soils. The N/P ratio was 14.0 ± 0.6 (mean ± std. error) in current-year leaves from all stands.

Generally, the coefficient of variation was lower in current-year tissues over the range of the fifteen stands studied, while a wider range of concentrations was found in the tissues of both old leaves and branches < 1 cm in diameter (Table 3). Nitrogen and potassium concentrations in current-year leaves showed the lowest variability among sites, ranging from 1.17% to 1.39% (C.V. = 6.27%) and from 0.53% to 0.68% (C.V. = 7.75%), respectively. The coefficient of variation for nitrogen in current-year leaves was 6.27%, but the lowest variability was in current-year shoot (C.V. = 5.25%). Otherwise, the highest variations were found in magnesium concentrations, mainly as a result of the high concentration of magnesium in stands on volcanic soils (C.V. = 19.3% to 25.0%, depending on the tissue).

There were few statistically significant correlations between tissue element concentrations. Calcium and magnesium were negatively correlated in old leaves (r = − 0.68, P = 0.005) and branches < 1 cm in diameter (r = − 0.75, P = 0.001). A positive correlation was found between phosphorus and nitrogen (r = 0.71, P = 0.003) in branches < 1 cm in diameter.

Plant-soil relationships

There were several significant correlations between plant nutrient concentrations and soil parameters for *Q. ilex* over the fifteen soils. Two basic groups of correlations were found: first, those related to soil chemical fertility and, second, those related to the antagonistic relationship between calcium and magnesium.

The first group of correlations was between nitrogen concentration in current-year leaves and the following soil parameters: organic matter,

Table 4. Statistically significant correlations between plant nutrient concentrations and soil nutrient concentrations over all stands studied (c.-y. = current year, o. = old).

No	Plant		Soil parameter	Statistics	
	Element	Tissue		r	P
1	Nitrogen	C.-y. leaves	Organic matter	− 0.79	0.0005
2	Nitrogen	C.-y. leaves	Total nitrogen	− 0.77	0.0008
3	Nitrogen	C.-y. leaves	Phosphorus	− 0.52	0.0461
4	Nitrogen	C.-y. leaves	Potassium	− 0.77	0.0008
5	Magnesium	C.-y. leaves	Calcium	− 0.55	0.0348
6	Magnesium	O. leaves	Calcium	− 0.57	0.0126
7	Magnesium	C.-y. shoots	Calcium	− 0.57	0.0318
8	Magnesium	Branches < 1 cm ∅	Calcium	− 0.62	0.0141
9	Calcium	C.-y. shoots	Calcium	0.58	0.0302
10	Calcium	Branches < 1 cm ∅	Calcium	0.56	0.0317

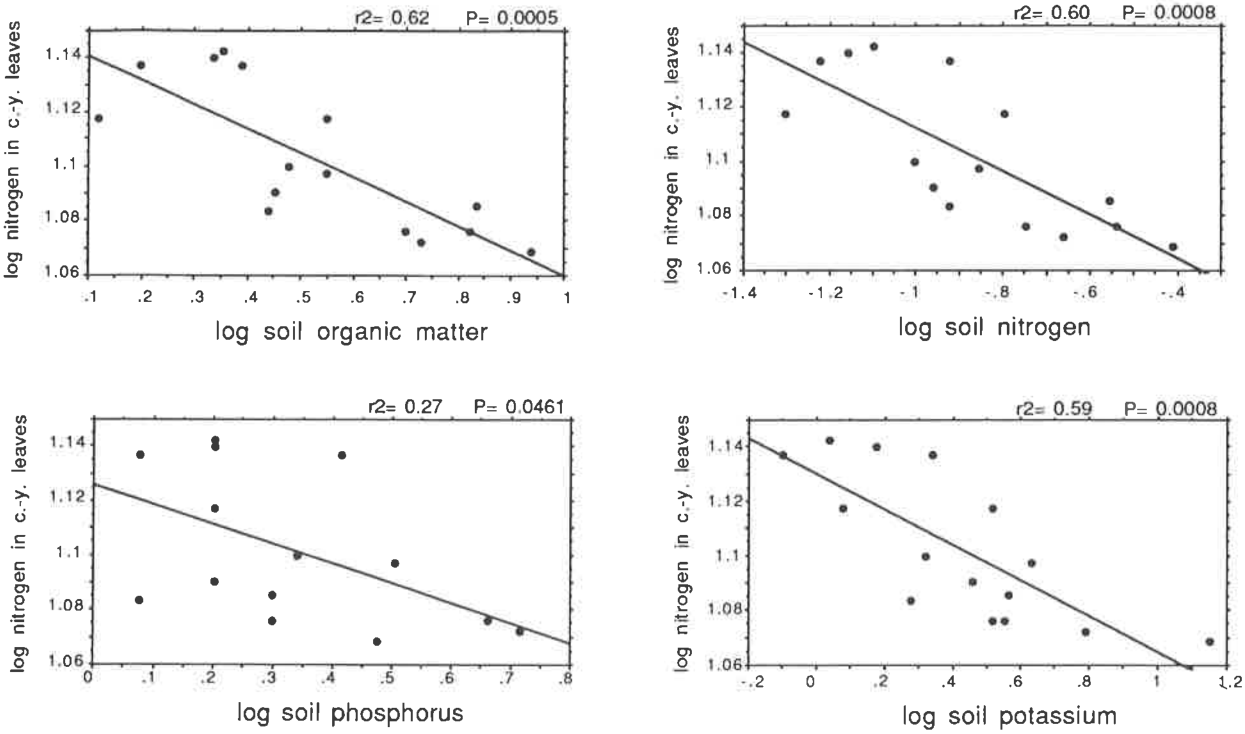

Fig. 2. Linear relationship between nitrogen concentration in current-year leaves (mg/g) and soil chemical fertility – organic matter (%), total nitrogen (%), extractable phosphorus (μg/g) and exchangeable potassium (μeg/g) –, based on linear regression.

total nitrogen, extractable phosphorus and exchangeable potassium. All the correlations were negative and statistically significant (Table 4, Fig. 2). No correlations were found between nitrogen concentration in old leaves, current-year shoot or branches < 1 cm in diameter, and soil parameters. The second group of correlations was between soil calcium concentration and plant calcium concentration for woody tissues (current-year shoots and branches < 1 cm in diameter, positive correlations). Also, soil calcium concentrations were negatively correlated with magnesium concentrations in the four tissues (Table 4).

Discussion

Soil parent material contributed, to a great extent, to the chemical variation found among the fifteen soils. Principal components analysis gave three soil groups, which were closely related to different types of rocks. Calcium content and pH, both tightly influenced by bedrock type, accounted for an important percentage of the variance. But other soil and environmental factors such as microclimate, topography, and forest stand characteristics can also be very important in explaining total variation in soil properties (Gauch & Stone 1979). The low fertility found in siliceous soils, especially the low levels of nitrogen, phosphorus and potassium, could be important in limiting plant growth. Total soil nitrogen concentration may be used as an adequate index of nitrogen availability at a regional scale (Binkley & Hart 1989) and, for our soils, was closely related to ammonium plus nitrate concentrations (r = 0.83).

The tissue concentrations of different elements for *Q. ilex* showed in general a close agreement with those presented by Brun *et al.* (1975), Lossaint & Rapp (1978), Leonardi & Rapp (1980), Clemente (1983), Ferrés (1984), and Mayor (1990). Our results do however emphasize the variability in tissue element concentration over a range of sites. The three mineral elements most likely to be limiting growth – nitrogen, phosphorus and potassium – varied less in the current-year leaves than did concentrations of other nutrients. Plant tissues other than current-year leaves had a higher variability for these nutrients, except for nitrogen in older leaves and current-year shoots. The concentrations of nitrogen, phosphorus and potassium seem to be more closely controlled than other nutrients, which could reflect the specific amounts needed for biochemical function. The higher coefficients of variation generally found in tissues other than current-year leaves may due to a nutrient redistribution process (i.e., retranslocation) of varying intensity and for a longer period of time than current-year leaves. In addition, varying accumulation and dilution rates during growth can be as important as the retranslocation process.

The highest variability in nutrient concentrations was found for magnesium, which varied between two- and three-fold depending on the type of plant tissue. This was probably not a consequence of selective uptake of magnesium but rather due to the moderately high magnesium concentrations in volcanic soils (luxury consumption, Chapin 1980). As our results for magnesium illustrate, a high concentration of a given element in a plant tissue need not necessarily be accompanied by high concentrations of other elements (Marschner 1986).

The nutrient concentrations in foliage and woody tissues reflect the roles of these nutrients in plant biochemistry, as illustrated by concentration in metabolically active tissues (e.g., current-year leaves) and tissues whose main function is support and solution transport (e.g., branches). Concentrations of nitrogen, phosphorus, potassium and magnesium in foliage and in woody tissues decreased with age. Contrary to this pattern, the concentration of calcium increased with tissue age, because calcium is an immobile nutrient which tends to accumulate when tissues age, and is an important structural element as part of the cell wall and other components (Garten 1976).

It is worth noting that potassium concentrations were higher in current-year shoots than in other plant tissues, and relatively low in branches < 1 cm in diameter. This suggests that current-year shoots accumulate potassium, a highly mobile nutrient, which can be used in new growth. Similar, but less clear, patterns were exhibited for magnesium and phosphorus.

A few significant correlations were found between nutrient concentrations in plant tissues. Despite the close relationship between N and P in plant biochemistry, particularly in protein synthesis (Marschner 1986), we only found a significant correlation between nitrogen and phosphorus in branches < 1 cm in diameter. The negative correlation between calcium and magnesium in plant tissues probably results from competition for their absorption since both have the same chemical valence.

Several studies have reported nutrient contents in evergreen sclerophyllous leaves for species in Mediterrean ecosystems, which show important interspecific differences (Kruger *et al.* 1983; Spech 1988). The N/P ratio is expected to be less variable than the absolute concentrations of both elements, due to their close metabolic association. Nitrogen and phosphorus are considered to be most limiting to plant growth (Tamm 1975; Lee *et al.* 1983; Schulze & Chapin 1987). Therefore, important differences in the N/P ratio may reflect adaptations to a particular nutritional environment. Data collected by Margaris *et al.* (1984) showed N/P ratios of 15.2 in leaves of chaparral species in California, 8,2 for matorral species in Chile, a figure as high as 45 for Australian mallee, 10 for South Africa ecosystems, and 16.9 for evergreen in Greek ecosystems. The mean N/P ratio calculated in our study for current-year leaves was 14.0, which is close to that for chaparal and Greek ecosystems. The extreme differences between ratios for matorral and mallee seem to reflect an important basic difference in soil phosphorus availability, which is extremely low in mallee ecosystems (Beadle 1954; Specht 1963). The other figures show good agreement with those reported for vascular plants by Garten (1976).

Simple correlations between plant and soil nutrient concentrations do not exist in certain cases, because plants can selectively take up as well as exclude elements from the soil solution (Gerloff *et al.* 1966; McColl 1969; Imper & Zobel 1983; Vermeer & Verhoeven 1987; Ohlson 1988; Marion *et al.* 1989). In addition, factors other than soil nutrient content determine plant nutritional status (Tilton 1978; Bunderson & Weber 1986). In our study, negative correlations were found between nitrogen concentrations in current-year leaves and soil element concentrations related to chemical fertility. So, higher concentrations of nitrogen in leaves were found as soil nutrient availability decreased. This pattern is contrary to that found in many studies, in which soil nitrogen, leaf nitrogen and plant production are positively correlated (Alban 1974; Lamb 1977; Madgwick *et al.* 1983; Powers 1984; Johnson *et al.* 1987; Hansen *et al.* 1988). Our results could thus reflect a nutritional imbalance between nitrogen and another nutrient more limiting than nitrogen. Alternatively, sites with higher total soil nitrogen could be those sites where nitrogen mineralization rates are lower and nitrogen accumulates in the soil. Hence, higher total soil N could result from lower instead of higher nitrogen availability, and be associated with lower foliar nitrogen concentrations, as found in our study. This interpretation is not necessarily contradicted by the positive correlation we found between total nitrogen and mineral nitrogen in the soil, since mineral nitrogen contents typically show large temporal variations, and a single measurement can be a poor indicator of nitrogen availability at a given site. It is also possible that the negative correlation between foliar nitrogen and total soil nitrogen arises from an unidentified factor having opposite effects on the two variales.

The antagonistic relationship between calcium and magnesium could be due to their similar mechanisms of uptake across cell membranes, because both elements share common valence states (Garten 1976). So, the amount of magnesium absorbed on the exchange sites can be inhibited by calcium in those soils from calcareous environments in which large amounts of calcium are present.

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