

Nutrient efficiency and resorption in *Quercus pyrenaica* oak coppices under different rainfall regimes of the Sierra de Gata mountains (central western Spain)

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Abstract – Nutrient uptake, nutrient resorption and nutrient use efficiency (NUE) were estimated in four *Quercus pyrenaica* oak coppices situated in the Sierra de Gata mountains (province of Salamanca, central-western Spain). The efficiency (NUE) with which a given nutrient is used depends on several factors. In the oak coppices studied, availability of P, Ca and Mg in the soil was one of the factors governing efficiency. On the other hand, there was a certain independence between soil N and K availability and their plant efficiency; in the case of N this occurred possibly because it is a limiting factor. There was a plant nutritional Ca–Mg imbalance due to soil acidity. Leaf absorption and/or leaching at canopy level would also influence the N and K efficiency. The stand with the most dystrophic soil was the least efficient regarding Mg, and the plot with the most eutrophic soil regarding Ca. All the oak coppices had low N efficiency. Bioelement resorption did not affect the NUE decisively but it seemed to be influenced by leaf absorption and leaching occurring at the canopy level. Higher aboveground production suggested that the stands on granite absorbed greater yearly amounts of N, K and P than those on schist. (© Inra/Elsevier, Paris.)

nutrient use efficiency / resorption / root uptake / oak coppice / *Quercus pyrenaica* / biogeochemical cycles

Résumé – Efficacité et réabsorption d'éléments nutritifs dans quatre taillis à *Quercus pyrenaica* suivant un transect pluviométrique dans la Sierra de Gata (ouest de l'Espagne). L'absorption d'éléments nutritifs, la réabsorption et l'efficacité d'utilisation d'éléments nutritifs (NUE) ont été étudiés dans quatre chênaies (*Quercus pyrenaica*) de la Sierra de Gata (province de Salamanque, ouest de l'Espagne). L'efficacité d'utilisation de bioéléments (NUE) est dépendante de différents facteurs. Dans les chênaies étudiées la disponibilité édaphique des éléments nutritifs influe sur l'efficacité d'utilisation de P, Ca et Mg. Au contraire, il n'y a pas de relation entre l'efficacité de N et K, et la disponibilité édaphique de ces éléments, peut être en raison des réserves édaphiques importantes de N total et de l'acidité du sol qui entraîne une insuffisance pour Ca. L'absorption et le lessivage des feuilles des arbres peuvent aussi influencer l'efficacité de N et K. La station avec le sol le plus dystrophe correspond à la chênaie la moins efficace pour Mg, tandis que la station la moins dystrophe est la chênaie la moins efficace pour le Ca. En ce qui concerne N, toutes les chênaies ont une efficacité très basse. La réabsorption d'éléments biogènes n'affecte pas la NUE des taillis étudiés, parce qu'elle est influencée par les processus d'absorption et le lessivage des bioéléments au niveau de la canopée forestière. Les peuplements sur granit absorbent plus d'N, K et P et produisent plus de litière que les peuplements sur schistes. (© Inra/Elsevier, Paris.)

efficacité d'utilisation des bioéléments / réabsorption / absorption des racines / taillis de chêne / *Quercus pyrenaica* / cycles de bioéléments

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1. Introduction

Nutrient use efficiency (NUE) has been defined by Ferrés et al. [17] as the biomass production by plants (in terms of fixed C) per unit of nutrient uptake.

NUE appears mostly in the literature with reference to infertile habitats, such as marshes [12], peatlands [7], heathlands [2] or semi-deserts [33]. The efficiency of nutrient use by plants to produce biomass may be an important adaptation to infertile habitats [7]; an increase in NUE in a plant species should be a response to the decreasing soil nutrient availability, but this is not found in general [1]. Furthermore, it is not clear whether the greater NUE observed in oligotrophic soils is a characteristic of the species inhabiting them or whether it is a phenotypical response of individual specimens to low nutrient availability [4].

In short-lived plants, biomass production per unit of absorbed nutrient is simply the inverse of the concentration of the nutrient in question in the tissues of the plant. However, in long-lived plants some bioelements suffer resorption (i.e. reabsorption by young tissues of nutrients retranslocated from senescent tissues as mature leaves), which allows the plants to use the same unit of absorbed nutrient to produce several vegetative organs [38], increasing the NUE. Resorption is the repeated use of the same nutrient units and could therefore be a good means of estimating the efficiency of nutrient use; nevertheless resorption has not been found for all the bioelements, but is frequent for N and P. Apart from the probable adaptive value of efficient resorption, important interspecific differences in resorption indices have been observed.

Therefore nutrient concentrations only afford a very approximate idea of the efficiency of nutrient use by forest species. In these cases, it seems more appropriate to estimate efficiency by measuring net primary production (aerial and underground) per unit of nutrient uptake during the year. Under controlled conditions, such measurements are possible; however, they are not very practical under field conditions [4].

As an alternative, Vitousek [38] defined NUE (see equation later) as the total amount of organic matter return (as litterfall and root return) plus that stored permanently in the plant (in the wood), divided by the amount of nutrients lost (as litterfall, canopy leaching or by root return) plus the nutrients remaining stored owing to the growth of the vegetation (uptake according to Cole and Rapp [10]).

An easier method of calculating the NUE (specifically for forests) was proposed by Vitousek [38, 39] as the inverse of the concentration of the nutrient (that is, amount of dry matter in litterfall per unit of the nutrient

contained in it). Later, Bridgham et al. [7] used the ratio of 'litterfall production/litterfall nutrient' as an index of nutrient efficiency (NUE; production per unit of resource uptake), distinguishing it from the resource response efficiency (RRE), defined as the production per unit of available resource. In forests an additional problem is the exact measurement of the availability of the resource [24, 25].

Carceller et al. [8] reported that under nutrient stress conditions (either due to soil oligotrophy and/or to low water availability, giving rise to deficiency symptoms) some plants respond with increased efficiency. Nevertheless, parameters of both total and available soil nutrients are sometimes not correlated to plant nutrient uptake (in both fertile and very unfertile soils), probably because many factors affect nutrient efficiency in the field.

Vitousek [38] has pointed out that the literature contains many references to litterfall and to the amounts of N, P, Ca, Mg and K returned through litterfall, but little information concerning the amount of nutrients stored in wood [14, 31] and even less about root return [8, 30]. Furthermore, Cole and Rapp [10] and Gallardo et al. [20] have shown that N-, P- and Ca-return to the soil is mostly achieved through litterfall, while K-return is mainly due to canopy leaching; Mg is intermediate between these two possibilities and varies according to the ecosystem studied. Consequently, it is difficult to compare the results on NUE from different studies because the data are obtained from different calculations, depending on previous definitions of NUE and the ecosystems. Blair [5] affirmed that the definition of NUE depends on the ecosystem in question (annual, deciduous, evergreen plants, etc.).

Aerts [3] stated that efficiency is also related to nutrient resorption by plants; reviewing the literature he found that nutrient resorption is close to 50 % for N and P in some tree species. Del Arco et al. [11] reported that N resorption is a key process through which plants reach maximum efficiency in their use of N.

Among the factors assumed to exert some effect on the above-mentioned differences in resorption [16] are soil fertility, soil dryness and those affecting leaf demography (leaf shedding period, time of residence of nutrient in leaves). When requirements are greater than uptake, the plant must meet the rest of its needs for nutrients by retranslocating them from old organs to new ones. Following this line of thought, Carceller et al. [8] calculated bioelement resorption as the difference between the leaf mineral mass at the end of August minus the potential return of nutrients to the soil through the leaf litter [20].

Significant relationships between leaf nutrient concentration and soil nutrient availability are reported frequently, but Aerts [3] did not find any link between leaf nutrient resorption and leaf nutrient concentration, or soil nutrient availability and leaf nutrient resorption.

Regarding the effect of soil fertility on NUE, several theories have been advanced; it seems logical that species found on the sites most impoverished in soil P or N would have higher resorption indices because they would be obliged to retain these elements and reuse them as much as possible, thus favouring more efficient internal recycling [34] and affording the plants a certain independence from the supply coming from the soil. Paradoxically, species living in highly fertile areas may have very high nutritional requirements, leading them to use nutrients more efficiently too [36].

However, in general, the majority of autochthonous European forests are restricted to areas with poor soils. For example, Gallardo et al. [18] have carried out research on deciduous oak (*Quercus pyrenaica* Willd.) coppices developed on acid soils with low base and available P contents [37]. Other aspects related with the biogeochemical cycles of these forests [23, 26, 27, 37] and their water balance [28, 29] have also been studied.

It could thus be of interest to know the NUE and resorption values in four well-studied, oak-forest ecosystems of the Sierra de Gata mountains following a rainfall gradient [19] and to see whether it is possible to find differences between those values in relation to soil characteristics, especially soil pH and biochemical properties.

The aim of the present work was first to estimate the NUE (according to Vitousek [38]) and resorption of macronutrients on plots of these deciduous oak (*Q. pyrenaica*) coppices and then to elucidate which factors govern these processes, taking into account the soil availability of each macronutrient.

2. Materials and methods

2.1. Site description and stand characteristics

The study area is located in the El Rebollar district (Sierra de Gata mountains, province of Salamanca, western Spain). The co-ordinates of the area are 40° 19' N and 6° 43' W.

Four experimental plots of *Quercus pyrenaica* Willd. coppices were selected (*table I*) with areas ranging from 0.6 to 1 ha. They were named Fuenteguinaldo (FG), Villasrubias (VR), El Payo (EP) and Navasfrías (NF). Stand ages range from 60 to about 80 years (*table I*). These coppices were thinned for pasturing (cattle).

The climate of the area is classified as warm Mediterranean, characterised by wet winters and hot, dry summers [28], with an average rainfall and temperature (*table I*) of approximately 1 580 L m⁻² year⁻¹ and 10.4 °C for NF, and 720 L m⁻² year⁻¹ and 12.9 °C for FG.

The dominant soils are *humic Cambisols* developed over schist and greywackes at NF and VR, and over Ca-alkaline granite at EP and FG [26]. The physical, physicochemical, and biochemical properties of the four forest soils are shown in *table II*; soil samples were taken from the selected modal soil profile at each plot [37].

Tree density (*table I*) ranges between 1 043 trees ha⁻¹ at the VR plot and 406 trees ha⁻¹ at the EP plot [22, 28]. The plot with the lowest tree density (EP) has the highest mean trunk diameter (25 cm), the greatest height (17 m) and biomass (131 Mg ha⁻¹); the lowest values of these parameters correspond to the VR plot (11 cm, 8.5 m and 63.8 Mg ha⁻¹, respectively). Aboveground production ranged from 4.1 to 2.6 Mg ha⁻¹ year⁻¹ in FG and NF, respectively [20].

Methodological aspects and data of soil analysis, aboveground biomass, litterfall production (from February 1990 to February 1993), foliar analysis, rainfall distribution, throughfall, water concentrations of bioelements, canopy N absorption, annual potential return of bioelements (total nutrients returned to the soil through the litterfall, assuming complete mineralization), etc., have been given by Gallego et al. [22, 23], Martín et al. [26], Moreno et al. [28, 29] and Gallardo et al. [19, 20]. Owing to methodological difficulties, no data on root biomass and below ground production of oak coppices have been obtained. Annual nutrient immobilisation in wood has also been estimated [18]. Exchangeable cations were determined following the neutral ammonium-acetate method [26]; available Ca and K using 1 N ammonium acetate as extracting solution [37]; and available P using the Bray-Kurtz [6] procedure.

Some of the important soil characteristics of the stands are shown in *table II*.

2.2. Methods

Each plot was divided into three parts, and in each of the three subplots the same experiments were performed. As a result, data refer in general to a mean of three replicates. Standard deviations were only calculated where data are directly determined by chemical determinations.

Table I. Characteristics of the four experimental plots (from Gallego et al. [22] and Moreno et al. [29]).

Stands	Fuenteguinaldo (FG)	Villasrubias (VR)	El Payo (EP)	Navasfrias (NF)
Altitude (m a.s.l.)	870	900	940	960
Long-term mean precipitation (L m ⁻² year ⁻¹)	720	872	1245	1580
Mean annual temperature (°C)	12.9	N.d.	8.1	10.4
Geology	Ca-alkaline granite	schist and greywackes	Ca-alkaline granite	schist and greywackes
Soil [15]	<i>Humic Cambisol</i>	<i>Humic Cambisol</i>	<i>Humic Cambisol</i>	<i>Humic Cambisol</i>
Age of oak coppice (years)	80	60	80	60
Last thinning (years ago)	35	25	50	35
Density (tree ha ⁻¹)	738	1 043	406	820
Mean D.B.H. (cm at 1.3 m)	16.5	11.0	25.4	15.2
Mean height (m)	12.0	8.5	17.0	13.0
Total biomass (Mg ha ⁻¹)	98.0	63.8	131	64.5
L.A.I. (m ² m ⁻²)	2.6	2.0	1.9	1.8
Basal area (m ² ha ⁻¹)	21.2	13.5	19.9	15.6
Stem growth (Mg ha ⁻¹ year ⁻¹)	4.69	1.98	3.65	7.40
Litter production (Mg ha ⁻¹ year ⁻¹)	4.1 ± 0.3	2.8 ± 0.2	3.5 ± 0.3	2.6 ± 0.2
Leaf production (Mg ha ⁻¹ year ⁻¹)	2.8 ± 0.1	2.2 ± 0.2	2.4 ± 0.1	2.1 ± 0.1

D.B.H.: Mean diameter at breast height (1.3 m); L.A.I.: leaf area index. (± standard deviation); N.d.: no data available.

2.2.1. Estimation of tree uptake (TU)

An estimation of the annual, soil nutrient uptake by plants was made. The tree nutrient uptake from the soil was calculated according to the following equation (units in kg ha⁻¹ year⁻¹):

$$TU = LF + SG + TF$$

where TU is tree uptake of the nutrient considered; LF, litterfall; SG, stem growth; and TF, throughfall (nutrients retained in small branches and bark are difficult to determine).

2.2.2. Calculation of efficiency indices

Two efficiency indices, involving different factors, were determined.

The first was defined by Vitousek [38] as dry matter of litterfall per unit of nutrient content in litterfall; this index is frequently used for N and P (we also use it for K, for comparative purposes) and is shown in *table III* as NEI (nutrient efficiency index).

The second index determined, GEI (general efficiency index), contains all the terms given by Vitousek [38] except the contribution from roots (not determined in this study) and can therefore be defined by the following formula:

$$GEI = \frac{LF + SG}{NR + NI + TF}$$

where LF is litterfall (referred to as kg dry matter ha⁻¹); SG, stem growth (referred to as kg dry matter ha⁻¹); NR, nutrient returned by litterfall (in kg ha⁻¹); NI, nutrient immobilised by stems (in kg ha⁻¹); and TF, throughfall of the nutrient considered (in kg ha⁻¹).

The amount of nutrients absorbed by the leaves at the canopy level [29] is subtracted since these nutrients are of external origin and are not absorbed directly by the roots.

2.2.3. Estimation of the resorption index (Re)

Taking into account the theoretical considerations expressed above, and in an attempt to overcome the drawbacks involved in the calculation of resorption, the resorption index (Re) was estimated using the following expression (units in kg ha⁻¹):

$$Re (\%) = \frac{MM - (NR + CL)}{MM} \times 100$$

where MM is leaf mineral mass (sum of the masses of the nutrient considered) calculated by harvesting trees of different diameter classes; NR is nutrient return by leaf litter; and CL is nutrient canopy leaching (*sensu stricto*). In this estimation only the soil losses brought about by root absorption (without considering the increase in root biomass) and the soil gains through leaf litter and throughfall are considered [19]. Thus, the nutrient leaching has also been taken into account in this resorption index, as proposed by Ferrés et al. [17].

Table II. Physico-chemical and biochemical properties (referring to < 2 mm fraction) of four forest soils with *Quercus pyrenaica* coppices.

Stands horizons	Soil Depth (cm)	pH (water)	Organic C (Mg ha ⁻¹)	Total N (Mg ha ⁻¹)	Available P (kg ha ⁻¹)	Available Ca (kg ha ⁻¹)	Available K (kg ha ⁻¹)	Exchangeable cations (cmolc kg ⁻¹)			Sum of bases	V (%)		
								CEC	Ca ²⁺	Mg ²⁺			K ⁺	Na ⁺
Navasfrias (NF)	Ah/ 0-20	4.9	103	4.88	6.2	295	135	36.1	1.4	0.7	0.5	0.1	2.7	7.5
	Ah2 20-40	4.8	55	3.20	2.0	95	42	25.8	0.1	0.3	0.2	0.0	0.6	2.3
	Bw 40-65	5.0	12	1.11	7.6	235	28	14.4	0.2	0.1	0.1	0.0	0.4	2.8
El Payo (EP)	Ah 0-20	4.7	98	5.97	12	1 020	195	29.1	0.6	0.4	0.5	0.0	1.5	5.2
	ABw 20-40	5.2	39	2.73	9.6	2 620	45	16.3	0.4	0.0	0.3	0.2	0.9	5.5
	BC 40-60	5.0	8.2	0.74	5.5	2 365	32	12.4	0.4	0.0	0.2	0.1	0.8	6.5
	C > 60	4.8	12	1.26	7.1	2 380	38	16.4	0.5	0.1	0.1	0.1	0.8	4.9
Villasrubias (VR)	Ah 0-20	4.6	66	3.91	7.5	295	16	25.1	0.1	0.5	0.4	0.3	1.3	5.2
	Bw 20-40	5.1	15	1.58	1.8	255	20	9.4	0.0	0.1	0.1	0.2	0.4	4.3
	C > 40	5.2	20	3.00	9.1	650	91	6.6	0.0	0.0	0.0	0.1	0.1	1.5
Fuenteginaldo (FG)	Ah 0-20	5.4	47	3.63	49	675	90	23.7	8.2	1.3	0.7	0.0	10.2	43
	ABw 20-40	5.1	31	2.56	80	5660	375	16.3	0.8	0.4	0.4	0.0	1.6	9.8
	Bw 40-60	5.3	15	1.66	27	1 480	30	12.4	0.0	0.0	0.1	0.0	0.1	8.1
C > 60	5.3	10	0.89	91	1 830	150	15.8	0.3	0.1	0.0	0.0	0.4	2.5	

CEC: cation exchange capacity; V: base saturation). Adapted from Martín et al. [27] and Turrión et al. [37].

Table III. Mean leaf and litter concentration of bioelements, estimated root uptake of nutrients, and calculated indices of resorption and efficiency (NEI and GEI, respectively).

Stands	Bioelements	N	P	Ca	Mg	K
Navasfrías	Mean leaf concentration (mg g ⁻¹)	17.0 (± 0.8)	1.1 (± 0.7)	7.0 (± 0.2)	1.65 (± 0.06)	3.6 (± 0.3)
	Mean litter concentration (mg g ⁻¹)	14.0 (± 0.9)	0.6 (± 0.1)	6.9 (± 0.3)	2.1 (± 0.1)	2.2 (± 0.2)
	Root uptake (kg ha ⁻¹ year ⁻¹)	46	3.4	68	9.6	20
	Resorption					
	Absolute (kg ha ⁻¹ year ⁻¹)	27.0	1.8	N.d.	N.d.	1.8
	Relative (%)	58	58	N.d.	N.d.	18
(NF)	NEI	76	1 620	144	N.d.	433
	GEI	158	2 124	108	762	362
El Payo	Mean leaf concentration (mg g ⁻¹)	13.7 (± 0.2)	1.22 (± 0.04)	5.1 (± 0.5)	1.76 (± 0.06)	7.4 (± 0.3)
	Mean litter concentration (mg g ⁻¹)	15.0 (± 0.8)	0.9 (± 0.1)	5.7 (± 0.2)	1.9 (± 0.1)	2.7 (± 0.3)
	Root uptake (kg ha ⁻¹ year ⁻¹)	52	4.2	36	8.7	23
	Resorption					
	Absolute (kg ha ⁻¹ year ⁻¹)	7.0	0.5	N.d.	N.d.	3.6
	Relative (%)	23	18	N.d.	N.d.	22
(EP)	NEI	71	1 168	176	N.d.	370
	GEI	106	1 304	154	626	234
Villasrubias	Mean leaf concentration (mg g ⁻¹)	14.9 (± 0.1)	1.64 (± 0.04)	4.9 (± 0.2)	2.14 (± 0.04)	8.1 (± 0.3)
	Mean litter concentration (mg g ⁻¹)	10.1 (± 0.5)	0.7 (± 0.1)	5.2 (± 0.2)	2.4 (± 0.2)	2.2 (± 0.2)
	Root uptake (kg ha ⁻¹ year ⁻¹)	32	3.0	45	12	21
	Resorption:					
	Absolute (kg ha ⁻¹ year ⁻¹)	9.4	1.6	N.d.	N.d.	5.3
	Relative (%)	32	49	N.d.	N.d.	33
(VR)	NEI	98	1 529	196	N.d.	445
	GEI	203	2 129	143	539	306
Fuenteguinaldo	Mean leaf concentration (mg g ⁻¹)	12.6 (± 0.2)	1.58 (± 0.03)	7.7 (± 0.3)	1.96 (± 0.03)	5.4 (± 0.2)
	Mean litter concentration (mg g ⁻¹)	13.1 (± 0.7)	1.2 (± 0.1)	8.3 (± 0.5)	2.2 (0.1)	2.6 (± 0.3)
	Root uptake (kg ha ⁻¹ year ⁻¹)	72	8.2	139	13	33
	Resorption:					
	Absolute (kg ha ⁻¹ year ⁻¹)	11.5	1.1	N.d.	N.d.	4.7
	Relative (%)	27	20	N.d.	N.d.	26
(FG)	NEI	80	898	124	N.d.	344
	GEI	160	1 398	83	889	348

Relative resorption related to mineral mass (see text). N.d.: not determined (± standard deviation).

The greatest problem involved in calculating the resorption index for N is the leaf absorption of N at the canopy level [29]. Escudero et al. [16] have shown that the maximum N contents of leaves of *Q. pyrenaica* are reached only 2 or 3 months after sprouting, the stabilisation phase being prolonged until leaf fall [23]. Since it is not possible to know the exact moment at which leaf N absorption at the canopy level takes place, it has been assumed that leaf absorption of N would occur during the initial stages of leaf growth and development owing to the greater demand for N during this stage (afterwards rainfall decreases [28]).

Accordingly, it is assumed that the amount of leaf absorbed N would already be included in the mineral-mass value (values estimated during the phase when concentrations become stabilised [23]). Thus, to estimate the

resorption of N (ReN), the following expression is used in this case:

$$ReN(\%) = \frac{NR - TU}{MM} \times 100$$

where NR, TU, and MM are as above.

3. Results and discussion

The results are given in *table III*.

3.1. Leaf and leaf-litter composition

Table III gives the mean nutrient composition of tree leaves and leaf-litter. Granite plots (EP and FG) had

lower values of N and P concentrations in leaves than those found in the schist plots (NF and VR); knowing that leaf and litter production (*table I*) are higher in the first two plots than in the latter two stands, these lower N and P concentrations may reflect a dilution effect [19]. The poorest soil (VR) had the highest values of Mg and K concentrations and the lowest of Ca, demonstrating a nutrient imbalance [27].

Theoretically, the Ca and Mg composition of leaf litter is increased compared to leaf contents because of the loss of organic C during the decomposition process; but for elements undergoing leaching (K) or resorption (N and P), the nutrient concentration is lower in the leaf-litter than in the tree leaf [27]. Thus, Gallego et al. [23] stated that the chemical composition of the tree leaf changes during the year in these coppices.

3.2. Tree nutrient uptake (TU)

Root nutrient uptake is shown in *table III*.

The sum of return ($LF + TF$) was previously determined by Gallardo et al. [19] and the annual retention in the trunk and branch biomass by Gallego et al. [23]. Net foliar absorption of N from atmospheric contributions [19, 29] was estimated to be 5.4, 6.6, 10.2 and 5.4 kg ha⁻¹ year⁻¹ at NF, EP, VR and FG, respectively; note the high leaf absorption of the stand (VR) with more dystrophic soil.

3.2.1. Nitrogen

The total tree N uptake (root uptake plus leaf absorption) was 51, 59, 42 and 78 kg ha⁻¹ year⁻¹ at NF, EP, VR and FG, respectively. The stands developed on granite (FG and EP) take up more total N (they also have a higher N root uptake; *table III*) and the highest aboveground production (*table I*). The supply of N throughout the mineralisation of abundant soil humus does not seem to be limited [27] except by summer soil dryness [37].

3.2.2. Phosphorus

The stands developed on granite (FG and EP) also take up more P (*table III*) than those on schist (NF and VR). They require more available soil P to maintain the higher aboveground production (*table I*). In this case, soil P is not a limiting factor [37].

3.2.3. Calcium

The greater amount of soil Ca at FG (*table II*) leads to a much higher root uptake (139 kg ha⁻¹ year⁻¹) than that observed in the other plots.

3.2.4. Magnesium

The plots at VR and FG displayed the most intense Mg uptake (*table III*). This higher Mg root uptake in VR is possibly due to Ca/Mg nutritional imbalance [27]. In any case, Mg reserves in soil should contribute to tree nutrition [29].

3.2.5. Potassium

FG also has the highest K root uptake (*table III*). Owing to the solubility and ease of K leaching [29], a high quantity of K must be supplied by the soil K pool.

3.3. Resorption

It is assumed that the leaves shed before the normal period of abscission have not undergone resorption of nutrients, according to Carceller et al. [8]; this assumption is difficult to accept if severe defoliation has occurred (e.g. EP). As a result, the inclusion of damaged leaves in the calculation would lead to an underestimation of the resorption index.

3.3.1. N resorption

The absolute values of N resorption (*table III*) are similar for all the stands, except NF (the stand with the highest rainfall; *table I*), where the N resorption is much higher than for other stands. Since the lengths of the abscission periods are very similar because all the plots contain the same species and are subject to almost identical climatic conditions (except rainfall), the calculated values of the resorption index were similar (except for NF with highest precipitation, implying a higher leaf N leaching and more resorption). There seems to be no relation between resorption indices and soil characteristics.

The relative values of the three drier stands (EP, VR, FG) are lower than those reported by Escudero et al. [16] for *Q. pyrenaica* (46 %) and for most deciduous species (values between 69 % for *Betula pubescens* and 37 % for *Crataegus monogyna*); the value of NF is also lower than those reported by Carceller et al. [8] for *Fagus sylvatica* (63 %) and by Chapin and Moilanen [9] for *B. papyrifera* (between 58 and 65 %). Our results can be considered to be moderate or even low compared with

those appearing in the literature; this could be a consequence of the different methods used to calculate the indices considered, but the same trend is observed when our results are compared with those of Carceller et al. [8], who used identical calculations. This could indicate that there is not a severe limitation of N in the coppices studied. The low N resorption might also be due to leaf absorption of N by the canopy [29] and it can be assumed that the energy cost for the tree is lower than for high resorption. One can speculate about the idea that the species only display resorption when they are able to derive additional benefits from the use of their strategy and do not become involved in excessive costs (as, for example, when nutrients stored in old leaves can be used more efficiently in other parts of the plant). In view of the low production of fruits [20], this does not seem to occur in the forests studied.

3.3.2. P resorption

Concerning the relative values of P resorption (*table III*), stands on schist (NF and VR) with low available P-reserves show values around 50 % and those developed on granitic substrates (FG and EP) with higher available P-reserves have values close to 20 %. Turrión et al. [37] also observed differences in available P depending on the nature of the parent material. However, within each group, the differences between P resorption values are minimal in spite of the fact that there is four times as much available soil P at FG than at EP (*table II*). The usual clear relationship between available soil P (in *Ah* horizon) and P resorption does not exist any more when threshold values of soil availability or plant organs are exceeded; therefore, the nature of the underlying substrate does seem to have some effect on the P resorption. Furthermore, it is necessary to take the general abundance of micorrhizal fungi into account (Schneider, pers. comm.) in these oak coppices.

The levels of P resorption vary considerably, being greater overall in deciduous species [35] than in evergreen species. For a single species, in most cases these levels remain almost constant, regardless of the different habitats occupied. The P resorption values recorded are similar to those reported by Sanz [32] for *Q. pyrenaica* (between 33 and 65 %), for *Betula pubescens* (76 %) and *Fraxinus angustifolia* (27 %); by Carceller et al. [8] for *Fagus sylvatica* (50 %); and by Chapin, Moilanen [9] for *B. papyrifera* (between 27 and 45 %).

Stands with high N resorption efficiency also showed greater efficiency in P resorption (*table III*). Sanz [32] reported a significant relationship between both indices for different deciduous species and she found the following expression:

$$\text{ReP} = 5.49 + 0.98 \times \text{ReN} \quad r = 0.70 \quad (P < 0.01)$$

where ReP and ReN are the resorption indices of P and N, respectively. The slope of the straight line is almost equal to unity, demonstrating the proportionality between both variables.

Obviously, availability of N and P are dependent on the mineralisation rate of soil organic matter (and mycorrhizal fungi; Duchaufour [13]); but using the decomposition constants obtained by Martín et al. [27] a non-significant relationship was obtained between these constants and the resorption indices.

3.3.3. K resorption

The highest K resorption is obtained at VR (*table III*), which is precisely the plot with the lowest soil available K concentration. However, this factor does not seem to affect the resorption of this element to any considerable extent, because the other plot developed over schist (NF) has a lower content of soil available K than EP (*table II*) and, in contrast, it has the lowest resorption. Therefore, the differences between plots are masked by the participation of two factors (leaf litter return and throughfall) of similar importance.

The relative K resorption indices (*table III*) are much lower than the 59 % obtained by Carceller et al. [8] for *Fagus sylvatica* forests; it should be stressed that these authors did not consider throughfall, which is very important [29]. It is therefore difficult to establish a comparison between these values.

3.4. Efficiency indices

3.4.1. Nitrogen

Based on the efficiency indices described, the stands at EP, NF and FG used N in the least efficient way (*table III*), VR being the most efficient one.

Calculated NEI values (between 71 and 98) were lower than those determined by Ferrés et al. [17] for *Quercus ilex* (152), *Abies* sp. (157) and *Fagus sylvatica* (179), and by Núñez et al. [30] for *Cistus laudaniferus* (225), but similar to those determined by Carceller et al. [8] for *F. sylvatica* (99) and those reported by Vitousek [38] for temperate deciduous forests (ranging from 30 to 92).

In the case of N, Birk and Vitousek [4] found that efficiency decreased with the increase in available N. Likewise, Ferrés et al. [17] attributed greater efficiency to reduced N availability in the soil, caused by delayed decomposition of organic matter due to persistent

drought in Mediterranean areas. In our work, the soils (EP and NF) with the highest percentage of total N (*table II*) appear to make less efficient use of this nutrient. Turrión et al. [37] found that, theoretically, soil N is not a limiting factor, because of the high amount of total soil N and the relatively high decomposition rate of soil organic matter [27], but they also pointed out that summer drought can hamper the nitrification and nitrate transport towards the roots [37]. Accordingly, the moderate or even low efficiency values of N in the forests studied can be said to correspond to moderate or high total soil N levels, respectively.

It could be expected that the leaf N resorption does not affect the efficiency of the overall use of this nutrient decisively, because leaf N leaching and drought also have an influence on N efficiency.

In summary, there are favourable conditions for the loss of N in these forests (litterfall coincides with the period of maximum rainfall, as pointed out by Moreno et al. [29], a rapid colonisation of floor litter by micro-organisms that slow down the release of N [27] and leaf absorption of this nutrient by the canopy [29]; these factors lead to a low efficiency of this element.

3.4.2. Phosphorus

P was used more efficiently in oak coppices located on schist (NF and VR) than in those developed on granites (*table III*). Turrión et al. [37] found more available P in soils on granite (FG and EP) than in soils on schist. The efficiency indices at VR and NF are very similar; in fact there are no differences in available soil P contents in these two oak coppices (*table II*), in contrast to the values found in the other two stands.

FG had the lowest efficiency index, corresponding to a higher content of available P in the epipedon (*table II*).

The calculated efficiency indices are lower than those reported by Ferrés et al. [17] for *Fagus sylvatica* (2 416) but similar to those estimated by the same authors for *Abies* sp. (1 518) or *Quercus ilex* (1 246), and similar to the values reported by Carceller et al. [8] for *F. sylvatica* (1 438) and those found by Vitousek [38] for temperate deciduous forests or Mediterranean ecosystems. However, if only the NEI is considered, the FG plot (which has a high content of soil available P; *table II*) would be less efficient in the utilization of P than the other oak stands and, also, less efficient than a *jaral* (*Cistus laudaniferus*) ecosystem of western Spain [30].

3.4.3. Calcium

The highest NEI for Ca occurs in the stand with the lowest concentration of soil-exchangeable Ca^{2+} and a

relatively acid soil (VR; *table III*), while the FG stand has the lowest indices (NEI and GEI) and a higher content of both exchangeable and available Ca (higher pH of the epipedon) in the soil.

For this nutrient, GEI seems to be more related to the soil exchangeable Ca than to available Ca (*Ah* horizon).

The efficiency of Ca for the four oak stands studied here lies within the values given by Vitousek [38] for temperate deciduous forests and is slightly higher than those given by Ferrés et al. [17] for *F. sylvatica* (113) or *Q. ilex* (111).

Because no deep drainage was observed at FG [28] there is no loss of bases from the soil profile and this explains the much higher pH and base saturation values of the superficial horizon (*Ah*), compared the other sites (*table II*; [20, 26]) with the highest aboveground productivity (*table I*).

3.4.4. Magnesium

In the case of this element, only the GEI was estimated since the return of this nutrient to the soil is governed to a large extent by throughfall [29]. Application of this index shows that in the plots studied the order of efficiency for Mg is directly the opposite to that observed for Ca (*table III*); i.e. VR would be the least efficient plot for Mg utilization, perhaps because of a possible nutrient imbalance between Ca and Mg [26]; i.e. an increase in Mg uptake in Ca-deficient forest soils. The lowest leaf Ca/Mg ratio occurs in VR (2.3) and this ratio is close to 4 in NF and FG. FG showed the highest Mg efficiency and litter production (*table I*).

3.4.5. Potassium

The plot at NF had the highest GEI for K (*table III*); there is obviously an inverse relationship between this index and leaf leaching (the quantitative importance of throughfall differs considerably among the stands [19]. The plot at VR has the highest NEI and the lowest K leaching; this index has a limited value in the other plots in this case owing to the intense K leaching (high solubility of K).

4. Conclusions

As a result of the present findings, we can conclude that: stands developed on granite annually absorbed greater amounts of N, K and P annually than stands developed on schist, related to their higher aboveground production.

Bioelement resorption does not affect the NUE of these oak coppices decisively, but is influenced by processes of leaf absorption and leaching occurring in the canopy.

Rainfall differences between sites do not seem to influence the NUE nor the resorption of the stands (except N resorption in NF). Obviously other factors (besides pluviometry) also influence the NUE, as deduced from the definition of GEI.

In the oak stands studied, the soil nutrient availability governs efficiency in the case of P and Ca, but not in the case of N and K. Concerning N this occurred possibly because the nitrate supply was limited by drought. Leaf absorption and/or leaching at the canopy level would also influence the N and K efficiency. Nevertheless, all the oak coppices showed low N efficiency, indicating that there was no severe N deficiency.

FG (with the highest litter production and the least dystrophic soil) is the least efficient coppice regarding Ca.

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