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Original article

Nutrient cycling in deciduous forest ecosystems of the Sierra de Gata mountains: aboveground litter production and potential nutrient return

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Abstract – The potential nutrient return in a chestnut coppice (*Castanea sativa* Miller) over a period of 3 years (1991–1994) has been established and compared with the returns found in four deciduous oak (*Quercus pyrenaica* Wild.) forests (1990–1993) located in the Sierra de Gata mountains (central Spanish system). A convergence of abscission phenology patterns was observed among the different ecosystems studied, together with a delay in leaf fall at the warmest plot. This similarity is logical since the plots harbour the same deciduous species which are, however, subjected to climatological variations. The chestnut coppice was found to be more productive than the oak forests, the amounts of leaves, branches, flowers and total litterfall being significantly greater. Statistical analysis showed a highly significant correlation between the chestnut coppice and the oak forest aboveground production, ranging between 0.82 and 0.96 for the leaves and between 0.72 and 0.89 for the total litter. In general, the leaf organs of the chestnut trees showed a higher concentration of bioelements than the oaks, with N and Ca predominant in the buds, Ca and Zn in the branches, K in the fruits, and above all Fe and Cu in the other plant remains. In all the forests studied, the potential nutrient supply fluctuated over the years and depended strongly on phenological factors; above all it was found to be governed by the leaves, which contributed most to the return of mineral nutrients to the soil. The most marked potential nutrient return through the oak aerial organs occurred on the plot with the lowest rainfall, particularly with respect to P and Ca. Considering all the forest plots, the general sequence of the amount of bioelements returning with the litterfall to the soil was as follows:

$$C > N > Ca > K > Mg > P > Mn > Na > Fe > Zn > Cu$$

with the exception of one oak plot (with an acid soil reaction and poor soil drainage), where the Mn return was higher than that of P owing to the high concentration of Mn in all the litter components. (© Inra /Elsevier, Paris.)

forest ecosystems / nutrient cycling / litterfall / *Castanea sativa* / *Quercus pyrenaica*

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Résumé – Cycle des bioéléments dans des écosystèmes forestiers de la Sierra de Gata : production de litière et retour potentiel des bioéléments. Le retour potentiel des éléments biogènes dans un taillis de châtaignier (*Castanea sativa* Miller) a été comparé pendant trois années avec les retours observés dans quatre chênaies caducifoliées (*Quercus pyrenaica* Wild.) localisées dans la Sierra de Gata (système montagneux central espagnol). L'abcission des feuilles coïncide dans le temps dans tous les écosystèmes forestiers car ils sont situés dans les mêmes conditions climatiques, excepté un petit décalage en ce qui concerne la station la plus chaude. La châtaigneraie est la forêt la plus productive. Il y a une corrélation entre production totale de litière (coefficients de corrélation variant de 0,72 à 0,89) et production des feuilles (coefficients de corrélation variant de 0,82 à 0,96) de la châtaigneraie et des chênaies. En général, les feuilles du châtaignier présentent une plus grande concentration de bioéléments que celles des chênes. Dans l'ensemble des forêts étudiées, il y a une variation interannuelle de la production de litière et aussi du retour potentiel des bioéléments. Ce retour potentiel est contrôlé par les feuilles, car celles-ci représentent environ 80 % de la production aérienne de biomasse totale. Le retour potentiel le plus important correspond à la châtaigneraie (sauf pour Ca) puis à la chênaie la plus sèche, pour ce qui concerne Ca et P.

La séquence générale d'abondance des bioéléments contenus dans la litière dans tous les peuplements est la suivante : C > N > Ca > K > Mg > P > Mn > Na > Fe > Zn > Cu, avec l'exception de Mn (plus abondant que P) dans la chênaie ayant le sol le plus acide et le moins perméable. (© Inra /Elsevier, Paris.)

écosystèmes forestiers / cycles des bioéléments / litière / *Castanea sativa* / *Quercus pyrenaica*

1. INTRODUCTION

The biogeochemical cycle of organic matter and mineral elements plays a key role in the relationships between the soil, the vegetation and the surrounding environment and is of vital importance to natural biocenosis and to forest ecosystems in particular [35].

The annual return of organic matter and bioelements (elements related to organic matter) to the soil associated with litterfall is an important factor in conditioning renewal within forest ecosystems in that it may be used as an indicator for characterizing the ecosystem. In this sense, annual nutrient return governs an important part of the biological activity of the consumer/degrader population of the organic horizons and the pedological development of the soil [24].

The distribution and transfer of mineral nutrients available to the soil through litterfall varies as a function of several parameters. Some of these are biological, such as the phenology of the organs and others are climatic, such as the effects of wind, frost, prolonged drought, etc. [19]. In this sense, Bray and Gorham [3] compiled the information then available on world ecosystem production in such a way that the data would reflect the effects of factors such as latitude, altitude, exposure, climate and soil fertility. These authors and William and Gray [46] estimated that total production values ranged between 1 Mg ha^{-1} $year^{-1}$ in forests located in cold regions (taiga or alpine meadows) and 25 Mg ha^{-1} $year^{-1}$ in rainy equatorial forests. Other factors also affecting production are the plant species [4], the age of the forest system [2, 32] and species density [3].

In view of the importance of this turnover phase in ecosystems, many works have aimed at making quantitative determinations of such contributions, particularly in forest ecosystems. In this sense, the review studies of the following authors could be mentioned: Bray and Gorham [3], Hernández et al. [18], Khannah and Ulrich [21], Ovington [33], Rapp [35], Rodin and Bazilevich [37], Santa Regina et al. [39, 40], Scott et al. [43], Son and Gower [44].

The aim of the present work was twofold: to quantify litter production in a chestnut (*Castanea sativa* Mill.) coppice and four oak (*Quercus pyrenaica* Willd.) stands, and to make a comparison between nutrient recycling in *C. sativa* and the species it replaces (*Q. pyrenaica*) in the same area of the Sierra de Gata mountains (central Spanish system).

Quercus pyrenaica is a deciduous oak which is very abundant in the Spanish mountains with an annual rainfall ranging from 800 to 1 600 mm year^{-1} [12]; because of their low productivity (in terms of both timber and acorns), these oak forests are progressively being replaced by coniferous plantations. When the annual rainfall is higher than 900 mm year^{-1} and the soil is deep, *Q. pyrenaica* oak coppices have historically been replaced by *C. sativa* chestnut groves [16], with a higher production of both nuts and/or wood. Nevertherless, chestnut orchards are also in decline as a result of fungal diseases [38].

2. MATERIALS AND METHODS

2.1. Site description

The study site is located in the El Rebollar district (Sierra de Gata mountains, western Spain). The coordinates of the study area are 40° 19' N and 6° 43' W [27].

The forested area is mostly composed of *Q. pyrenaica* Willd. (deciduous oak), *Pinus pinaster* Ait. (martime pine) and, on the southern border of the El Rebollar district, *C. sativa* Mill. (chestnut).

The selected coppice of *C. sativa* is situated at the San Martín de Trevejo site (SM; province of Cáceres), with a density of 3 970 trees ha^{-1}, a mean trunk diameter of 10 cm and a trunk height of 13 m (*table I*). The mean basal area is 28.6 m^2 ha^{-1} and the leaf area index (L.A.I.) is 3.7 m^2 m^{-2} (*table I*). This coppice is about 25 year old.

The deciduous *Q. pyrenaica* oak stands are situated at Navasfrías (NF), El Payo (EP), Villasrubias (VR) and Fuenteguinaldo (FG), sites which are all close to each other (in the southwest of the province of Salamanca) and with a density varying between 1 043 trees ha^{-1} (VR) and 406 trees ha^{-1} (EP; [30]). The plot with the lowest density (EP) has the greatest mean trunk diameter (25.4 cm), greatest trunk height (17 m) and biomass (130.8 Mg ha^{-1}); the lowest values of these parameters correspond to VR with 11 cm, 8.5 m and 63.8 Mg ha^{-1}, respectively (*table I*). Other characteristics of the selected chestnut and oak plots are given in Martín et al. [27] and Turrión et al. [45].

The climate of the area is characterized by rainy winters and hot dry summers [30], and may be classified as warm Mediterranean (temperate Mediterranean at NF, EP, VR and FG; and maritime Mediterranean at SM; [9]).

The soils are generally humic Cambisols (*table I*; [11]), developed over slate and graywackes at NF and VR, and over Ca-alkaline granite at SM, EP and FG [13]. Additional information relating to the soil characteristics of these forest ecosystems has been previously provided by Martín et al. [26], Menéndez et al. [29] and Moreno et al. [31]. The main characteristics of these soils are shown in *table I*; available nutrients were extracted with neutral ammonium acetate [26, 45].

2.2. Analytical procedures

In order to quantify the annual return of organic matter and bioelements to the soil through litterfall from the trees, three series of ten 0.24-m^2 litter traps 30 cm high, were placed on each plot following transects based on the topography of the soil. Samples were collected at variable time intervals (from once a month to once every 2 weeks during the period of most rapid leaf fall [18]) over a period of three consecutive years (1990–1993 for oak and 1991–1994 for chestnut).

In the laboratory, each of the individual components (leaves, buds, branches, flowers, burrs, chestnut fruits, etc.) was separated, dried at 80 °C, and weighed.

Table I. General characteristics of the five experimental forest plots.

Plot paramters	Fuenteguinaldo (FG)	Villasrubias (VR)	El Payo (EP)	Navasfrías (NF)	San Martín (SM)
Altitude (m a.s.l.)	870	900	940	960	940
Geology	Granite	Slate	Granite	Slate	Granite
Long-term mean P (mm year^{-1})	720	872	1 245	1 580	1 152
Mean annual t (°C)	12.9	N.d.	8.1	10.4	14.2
Density (trees ha^{-1})	738	1 043	406	820	3 970
Mean forest age (year)	60	60	80	60	25
DBH (cm)	16.5	11.0	25.4	15.2	10.0
Mean height (m)	12	8.5	17	13	13
Biomass (Mg ha^{-1})	98.0	63.8	131	64.5	122
L.A.I. (m^2 m^{-2})	2.6	2.0	1.9	1.8	3.7
Basal area (m^2 ha^{-1})	21.2	13.5	19.9	15.6	28.6
Soil (F.A.O., 1989)			Humic Cambisol		
Characteristics, A_h horizon:					
Depth (cm)	0–20	0–20	0–20	0–20	0–20
pH	5.8	4.6	4.7	4.88	4.9
C (Mg ha^{-1})	46.7	65.9	97.9	103	70.3
N (Mg ha^{-1})	3.63	3.91	5.97	4.98	3.94
C/N	13	17	16	21	18
Available P (kg ha^{-1})	49	7.5	12	6.2	75
Available Ca (kg ha^{-1})	675	290	1 020	295	470
Available K (kg ha^{-1})	90	16	1195	135	320
Base saturation (%)	43	5.2	4.2	7.5	15
Texture	Loamy	Silty clay	Loamy	Loamy	Sandy loam

DBH: mean diameter at breast height (1.3 m); L.A.I.: leaf area index; P: annual rainfall; t: temperaure; N.d.: no data available.

All obtained samples were ground prior to chemical analysis. The elements determined in all samples were: C, N, Ca, Mg, P, K, Na, Mn, Fe, Cu and Zn. Total C was determined by dry combustion with a Wösthoff carmhograph. Total N was quantified using a Heraeus Macro N-analyzer. P was determined by spectrophotometry using the vanadomolybdate yellow technique [6]. Ca, Mg, Fe, Cu, Zn and Mn were measured by atomic absorption spectroscopy (Varian 1475), while Na and K were analyzed by flame photometry.

3. RESULTS AND DISCUSSION

Results are expressed in *tables II* (litterfall production), *III* (chemical composition) and *IV* (potential nutrient return), and *figures 1* to *4* (variation with time of aboveground production). The following three aspects are discussed below: a) the aboveground production of the stands selected; b) its potential return; and c) a comparison of the results from the chestnut coppice and the oak stands.

3.1. Litter production

In the study forests, the length of the biological activity period is mainly affected by two factors: low winter temperatures and summer drought. In any case, the contribution of ground vegetation has not been considered because of its relative unimportance

Table II. Annual and mean litter production (kg ha^{-1} ± 95 % confidence intervals, dry weight) and annual rainfall (mm $year^{-1}$) in the five experimental forest plots. Lichens in oak stands; burs in the chestnut coppice.

Plots	Year*	Leaves	Branches	Lichens/Burrs	Buds	Flowers	Fruits	Other	Total	Annual	Spring
Fuenteguinaldo (FG)	1990–1991	2 940 ± 203	521 ± 144	49 ± 13	168 ± 23	58 ± 19	13 ± 7	444 ± 86	4 194 ± 359	646	108
	1991–1992	3 068 ± 198	883 ± 496	148 ± 38	269 ± 32	50 ± 8	97 ± 46	204 ± 34	4 720 ± 599	544	31
	1992–1993	2 480 ± 233	416 ± 120	75 ± 16	201 ± 22	53 ± 10	43 ± 9	84 ± 20	3 351 ± 303	422	138
	Mean	2 829 ± 131	607 ± 177	90 ± 17	213 ± 17	54 ± 8	51 ± 17	244 ± 44	4 088 ± 274	537	92
Villasrubias (VR)	1990–1991	2 259 ± 330	291 ± 93	30 ± 16	64 ± 11	9 ± 3	3 ± 3	189 ± 42	2 845 ± 424	865	140
	1991–1992	2 162 ± 264	258 ± 66	103 ± 33	98 ± 17	19 ± 6	27 ± 13	94 ± 24	2 761 ± 355	733	49
	1992–1993	2 204 ± 304	362 ± 129	149 ± 51	92 ± 13	5 ± 2	22 ± 13	53 ± 17	2 887 ± 437	585	178
	Mean	2 208 ± 169	303 ± 57	94 ± 23	85 ± 8	11 ± 3	17 ± 7	112 ± 21	2 831 ± 229	728	122
El Payo (EP)	1990–1991	2 559 ± 199	524 ± 140	115 ± 24	118 ± 14	1 ± 1	3 ± 3	198 ± 25	3 518 ± 308	1 006	150
	1991–1992	2 301 ± 179	699 ± 553	290 ± 51	101 ± 9	41 ± 6	14 ± 8	109 ± 19	3 556 ± 609	753	40
	1992–1993	2 177 ± 131	725 ± 429	275 ± 77	129 ± 11	6 ± 2	30 ± 17	50 ± 9	3 392 ± 552	710	193
	Mean	2 346 ± 102	649 ± 232	227 ± 35	116 ± 7	16 ± 4	16 ± 7	119 ± 17	3 489 ± 285	823	128
Navasfrías (NF)	1990–1991	2 388 ± 193	308 ± 80	36 ± 26	102 ± 13	16 ± 3	7 ± 4	130 ± 24	2 987 ± 286	1 078	165
	1991–1992	2 070 ± 153	303 ± 138	70 ± 28	70 ± 9	24 ± 7	6 ± 4	69 ± 16	2 611 ± 261	852	47
	1992–1993	1 807 ± 192	223 ± 67	47 ± 19	82 ± 12	2 ± 1	12 ± 4	33 ± 11	2 206 ± 246	858	255
	mean	2 088 ± 113	278 ± 57	51 ± 14	84 ± 7	14 ± 3	8 ± 2	77 ± 13	2 601 ± 163	929	156
San Martín (SM)	1991–1992	3 200 ± 101	592 ± 131	297 ± 94	22 ± 4	486 ± 50	84 ± 56	113 ± 16	4 793 ± 249	N.d.	N.d.
	1992–1993	3 136 ± 85	915 ± 309	67 ± 52	79 ± 5	275 ± 28	50 ± 30	27 ± 4	4 549 ± 345	890	250
	1993–1994	3 950 ± 266	1 436 ± 593	242 ± 87	79 ± 4	402 ± 53	266 ± 112	19 ± 3	6 394 ± 704	1 641	345
	Mean	3 429 ± 124	981 ± 233	202 ± 49	60 ± 6	388 ± 31	133 ± 46	53 ± 11	5 245 ± 317	1 115	2 980

*Years refer to the period February–January ; N.d.: no data available).

(except for FG) in comparison with the litter production of the trees.

The mean litterfall production measured varied between 5.25 Mg ha^{-1} year^{-1} at SM (referred to as dry matter; *table II*) and 2.60 Mg ha^{-1} year^{-1} at NF (*table II*); there was a significant delay in leaf fall at FG; this was a result of the higher mean temperatures recorded at that plot (*table I*) prolonging the growth

Table III. Weighted mean concentrations of bioelements of different litterfall components in the five experimental forest plots (dry weight). Lichens in oak stands; burs in the chestnut coppice.

		C	N	C/N	P	Ca	Mg	K	Na	Mn	Fe	Cu	Zn
Components	Plots	(mg g^{-1})			(mg g^{-1})					(mg kg^{-1})			
Leaves	Fuenteguinaldo	467	13.1	36	1.2	8.3	2.2	2.6	245	404	100	11	20
	El Payo	481	15.0	32	0.9	5.7	1.9	2.7	217	555	117	15	25
	Villasrubias	479	10.1	47	0.7	5.2	2.4	2.2	220	904	115	16	18
	Navasfrías	465	14.0	33	0.6	6.9	2.1	2.2	158	556	80	12	20
	San Martín	490	12.1	40	1.9	5.3	3.2	4.3	408	919	74	14	27
Branches	Fuenteguinaldo	468	8.9	53	0.9	10.0	1.6	2.9	251	240	66	8	30
	Villasrubias	481	8.5	57	0.5	5.7	1.5	2.0	225	504	108	7	32
	El Payo	474	10.3	46	0.6	6.3	1.2	2.3	197	341	108	8	32
	Navasfrías	477	8.2	59	0.5	7.9	1.3	2.5	253	322	92	9	31
	San Martín	484	7.6	64	0.4	5.7	1.0	1.1	395	413	136	7	40
Lichens	Fuenteguinaldo	456	10.0	46	0.9	3.7	0.9	2.4	193	108	167	10	21
	Villasrubias	441	10.8	41	0.6	3.9	0.8	2.0	235	240	330	10	27
	El Payo	430	13.8	31	0.9	4.6	0.9	2.6	219	167	355	11	33
	Navasfrías	436	11.4	38	0.6	6.9	0.9	1.8	254	145	258	11	29
	San Martín	457	8.2	56	0.9	2.3	1.7	6.2	410	307	32	10	14
Burs or Buds	Fuenteguinaldo	481	13.0	37	0.9	6.1	1.3	3.0	214	211	124	13	17
	Villasrubias	496	12.3	40	0.9	4.1	1.2	2.6	214	391	221	10	19
	El Payo	475	13.9	34	1.0	5.1	1.3	3.1	157	310	169	11	20
	Navasfrías	486	9.8	50	0.7	5.9	1.1	2.7	201	296	151	9	15
	San Martín	480	19.0	25	1.6	5.9	2.4	3.9	387	679	164	19	36
Flowers	Fuenteguinaldo	487	18.2	27	1.5	5.0	2.2	7.6	221	213	97	12	19
	Villasrubias	476	18.2	26	1.2	3.9	2.0	5.5	193	513	167	12	21
	El Payo	458	19.4	24	1.0	3.6	2.0	3.7	182	318	98	14	20
	Navasfrías	480	15.6	31	1.4	4.7	2.2	7.8	192	321	107	16	23
	San Martín	481	9.8	49	0.7	2.2	1.7	7.3	306	340	91	15	15
Fruits	Fuenteguinaldo	473	10.4	45	0.7	3.7	1.1	6.1	170	101	27	11	12
	Villasrubias	437	10.2	43	0.8	2.8	1.3	5.5	191	234	44	10	13
	El Payo	462	11.6	40	0.8	3.8	1.2	11.8	218	210	46	16	18
	Navasfrías	463	8.4	55	0.5	5.1	1.1	5.3	194	151	46	10	18
	San Martín	468	12.5	37	1.8	1.3	1.5	9.3	405	174	38	9	19
Other	Fuenteguinaldo	464	15.5	30	1.1	5.1	1.5	4.7	158	184	162	10	22
	Villasrubias	466	13.5	34	0.7	3.7	1.2	2.3	151	330	300	10	27
	El Payo	444	15.9	28	1.0	4.5	1.2	2.5	177	263	344	11	41
	Navasfrías	459	12.1	38	0.7	6.8	1.4	1.8	148	260	279	10	29
	San Martín	440	14.7	30	1.2	5.2	2.0	2.9	262	530	406	66	32
	Standard deviation (maximum ±)	± 9	± 2.5	± 0.7	± 0.3	± 0.2	± 0.2	± 1.8	± 66	± 46	± 35	± 2	± 3

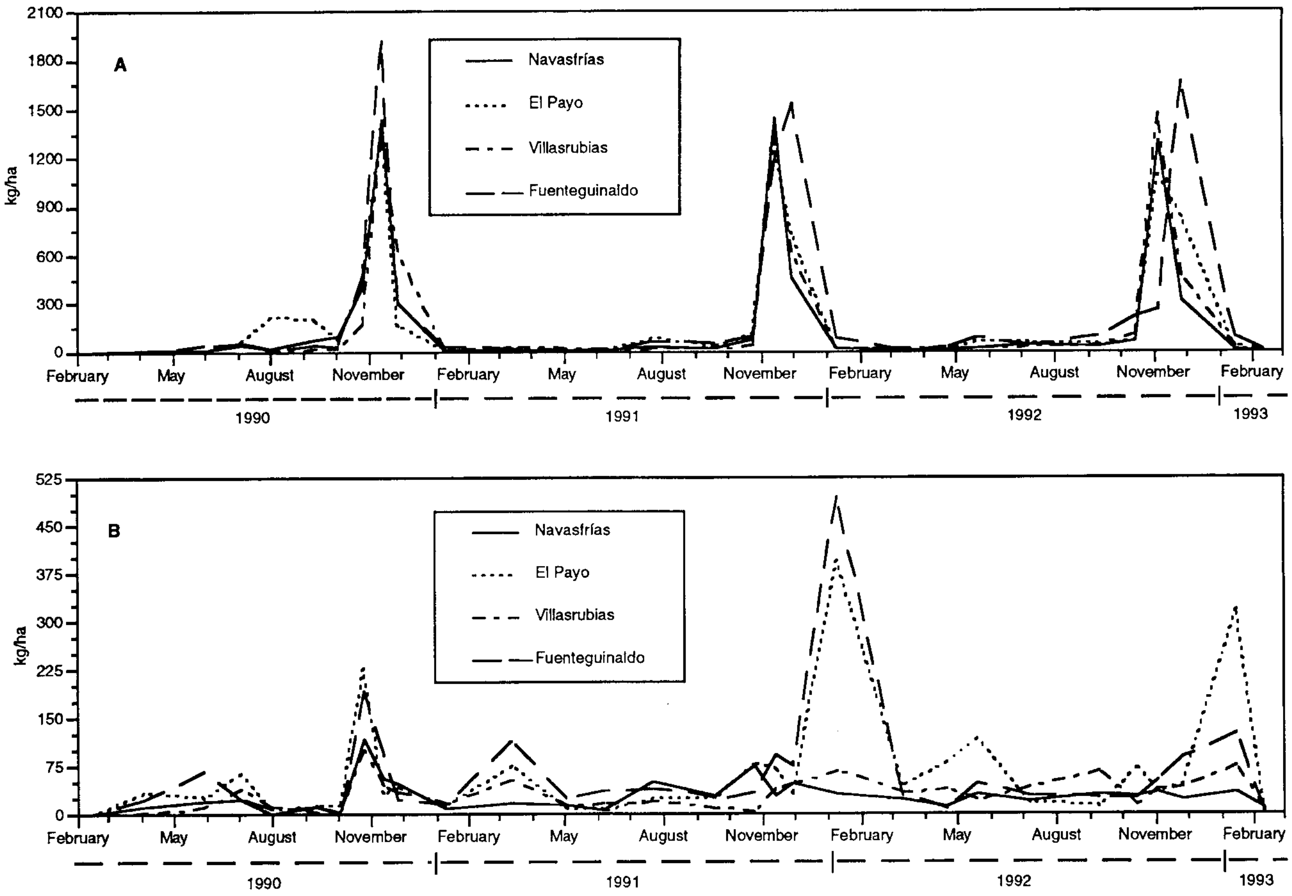

Figure 1. Variation with time of different litterfall fractions (leaves: A; branches: B) in the four experimental oak forest stands.

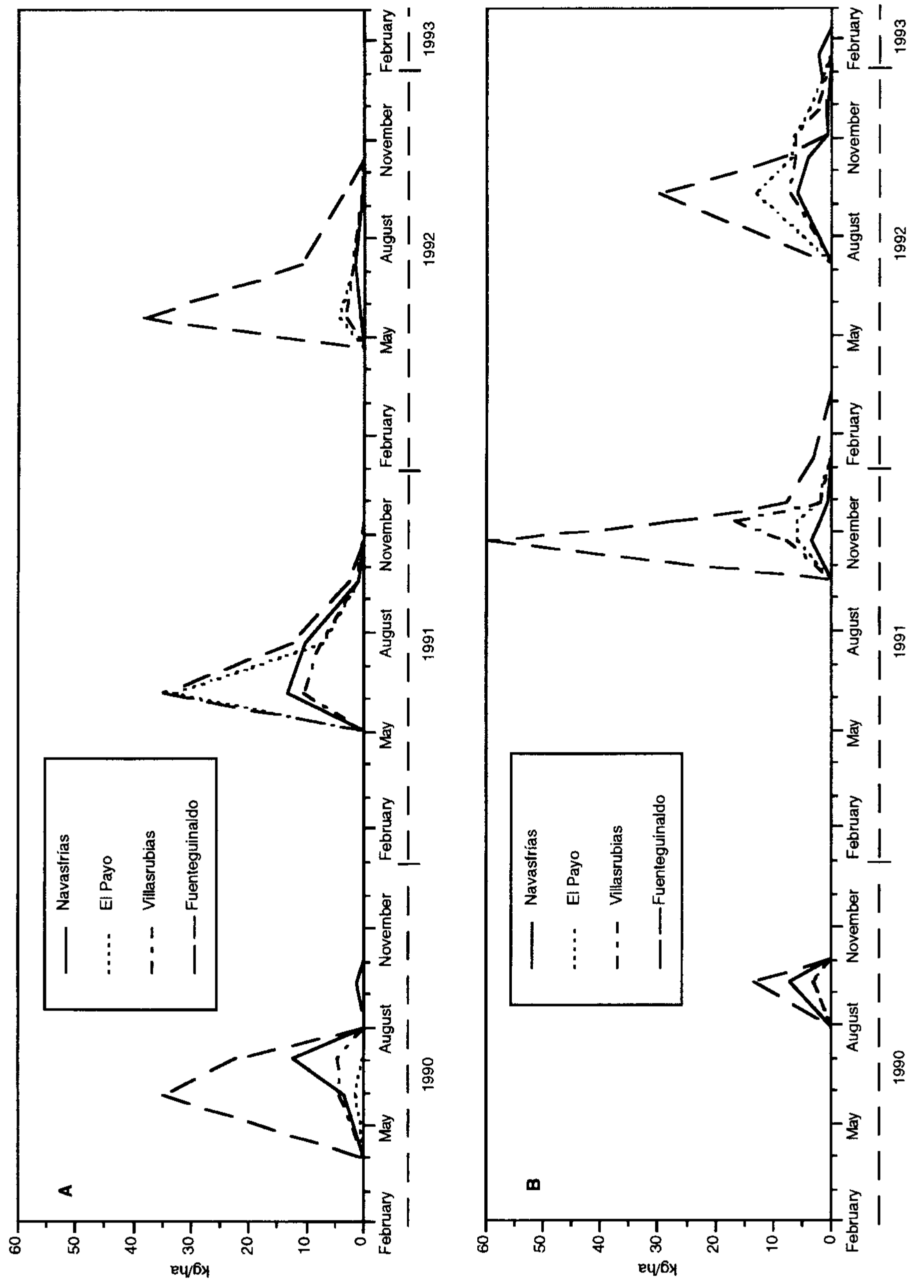

Figure 2. Variation with time of different litterfall fractions (flowers: A; fruits: B) in the four experimental oak forest stands.

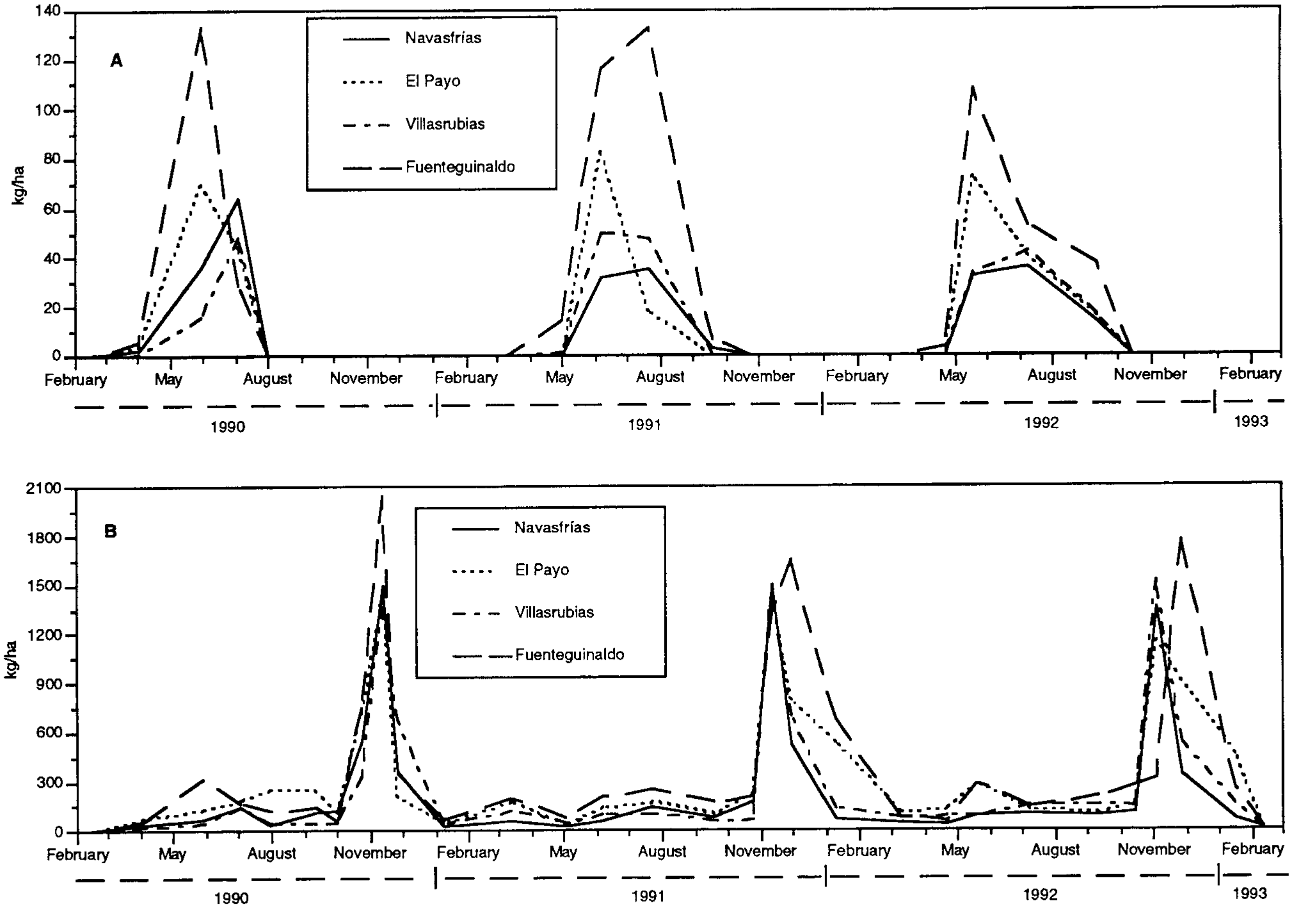

Figure 3. Variation with time of different litterfall fractions (buds: A; total litter: B) in the four experimental oak forest stands.

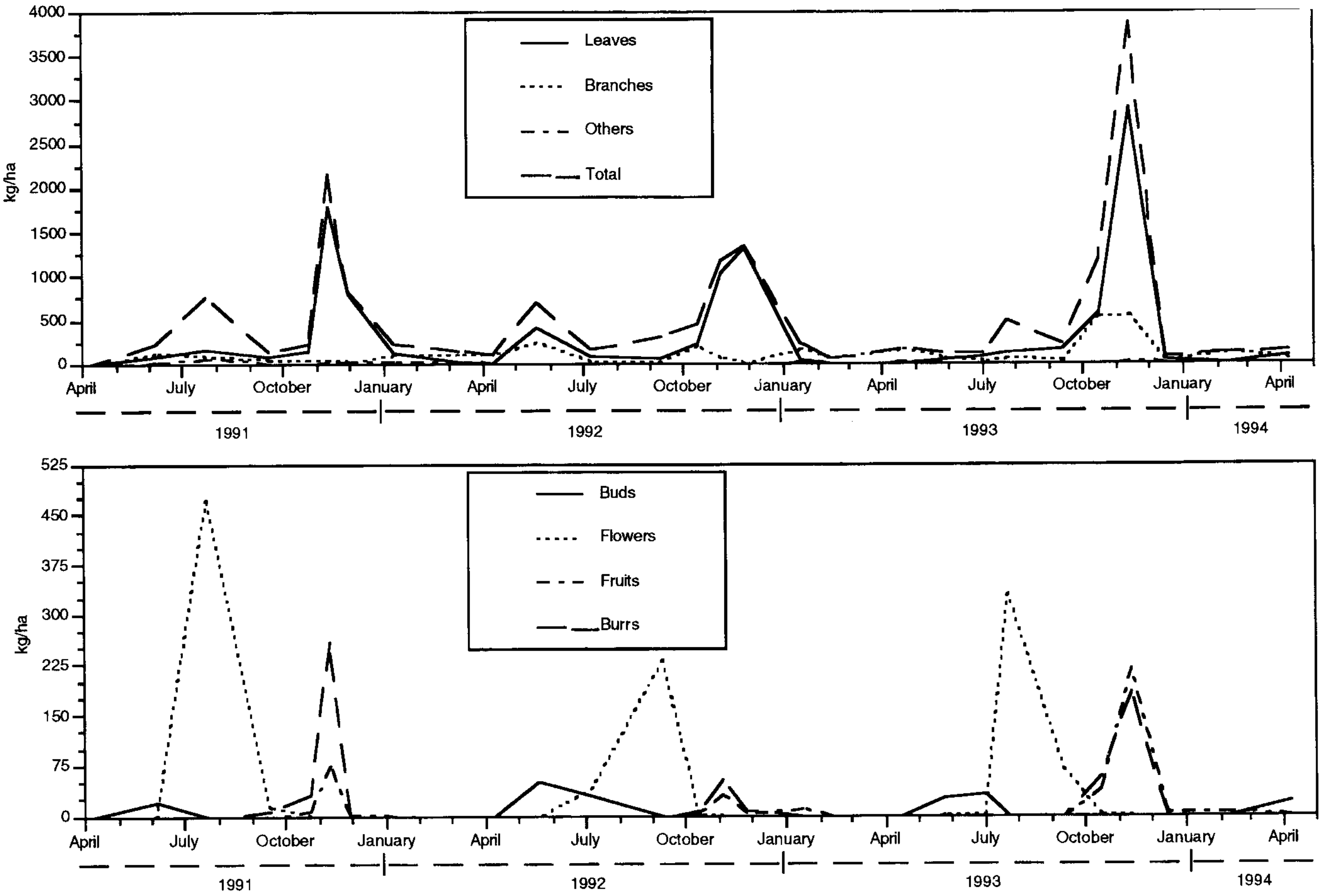

Figure 4. Variation with time of different litterfall fractions in the chestnut coppice.

period of the oak trees. These values are similar to those reported by Carceller et al. [5] and Gallardo et al. [14] for *Q. pyrenaica* and *C. sativa* stands (around 5.0 and 6.3 Mg ha^{-1} $year^{-1}$, respectively); O'Neill and DeAngelis ([32]; 5.2 Mg ha^{-1} $year^{-1}$), Anderson ([1]; 3.6 Mg ha^{-1} $year^{-1}$) and Bray and Gorham ([3]; 3.2 Mg ha^{-1} $year^{-1}$) for deciduous species; futhermore, Leonardi et al. [25] obtained a litter production of about 5.5 Mg ha^{-1} $year^{-1}$ in chestnut coppices (10–30 years old; Sicily).

A significant decrease ($P < 0.05$) was also obtained in litterfall production during the third vegetative cycle both at NF and at FG (this was also seen at EP, but was not significant). The same was the case when only the leaf fraction was considered. It was probably a consequence of the low rainfall recorded during the study period (mainly the second year; *table II*); thus, the recorded rainfall values only represent around 60 % of the values recorded as long-term mean annual rainfall. This situation is further worsened by the fact that these forests received a similar amount of rainfall during the previous year, with the added drawback of a very dry spring in 1991 (*table II*), so that the trees could have undergone considerable water stress [30]. This would have limited the uptake of nutrients and hence would have obliged the trees to use nutrients stored in the perennial parts (retranslocation; [10]). Litterfall production of forests on poor soils can be explained in terms of the internal transfer of nutrients [42] from the old organs to the younger growing ones (resorption; Gallardo et al., in preparation), representing an efficient independence strategy on the part of trees as regards the mineral reserves of the soil. Along the same lines, Moreno et al. [30] stated that as rewatering of the soil on the study plots begins towards the end of September or the beginning of October, soil humidity levels remain near field capacity, with slight fluctuations: from the moment that field capacity is reached until the beginning of the tree active period (April at the earliest). The same authors reported that in 1990 and 1991 the soil dried up from April until the beginning of August, when water reserves were almost completely depleted. In chestnut, the litterfall production was significantly greater during the last year (1994: 6.39 Mg ha^{-1} $year^{-1}$ as compared with 4.79 and 4.55 Mg ha^{-1} $year^{-1}$ for the previous two cycles) because of a higher annual rainfall (*table II*).

Important annual variations were observed in the litterfall. Maximum litterfall production occurred in autumn (*figures 3* and *4*), although there were small peaks in spring and at the start of summer mainly due to the shedding of flowers, buds and leaves (*figures 1–3*) owing to adverse climatological conditions (late frosts). Even in the summer of 1990 a small maximum was observed at the EP plot; this was caused by a plague of leaf-eating insects. Accordingly, the annual fall cycle (deciduous species) is mainly determined by the cycle of leaf and branch abscissions.

The significant leaf contribution to the aboveground production (*table II*) represents about 80 % of the total litterfall at NF and VR, 70 % at FG and EP, and 66 % at SM. These values are similar to those reported by Meentemeyer et al. [28] in plant formations throughout the world. Their annual cycle of leaf fall is practically limited to October and November (*figures 1* and *4*), later contributions being due to the fact that the leaves still on the lower branches of the trees show a marked marscesence, and persist in their location over a large part of the winter; these contributions are also due to late frosts (of interest was the contribution of 400 kg ha^{-1} in the May 1992 chestnut-leaf recovery). The contribution of the chestnut leaves to litterfall was lower than that of the oaks, but similar to that estimated by Pires et al. [34] in Portuguese chestnut orchards (62 %), and above that recorded in Sicily by Leonardi et al. [25] in coppices of ages similar to our own (52 %), or that found by Gallardo et al. [14] in western Spain (also 52 %).

Hernández et al. [18] reported that the formation of large numbers of leaves on *Q. ilex* oaks may be accompanied by strong photosynthetic activity, giving rise to an accumulation of nutrient reserves for use over the following year in the production and maturation of reproductive organs. This also occurs in the case of the studied oak stands, since the greatest amount of inflorescences and fruits was recorded during the second year (*table II*) as a result of the accumulation of nutrients from the previous year (greater leaf production).

The annual contribution of oak branches to the soil varied between 278 kg ha^{-1} year^{-1} at NF and 649 kg ha^{-1} year^{-1} at EP (*table II*), representing a contribution lower than 10 %. The branches, as in the oak stand studied by Carceller et al. [5], did not display such a marked fall; and their fall was more spaced out over time (*figures 1* and *4*). In general, it may be assumed that in the study area the effect of wind did not markedly affect the seasonality of the contribution of plant debris to the soil (there are no significant correlations between wind speed and the fall of leaves, branches, or total aboveground production); thus, a possible explanation is that the low wind speed (maximum wind speeds less than 15 km h^{-1}) was recorded during a period when the trees had no leaves. The mean annual contribution of chestnut branches was higher (981 kg ha^{-1} year^{-1}, representing 18 %) and varied markedly from year to year (*table II*). There seem to be small peaks in the fall of branches, one in April and the other in October (1992–1993), indicating that their contribution to the soil may be governed by the frosts (because the peaks occurred in parallel with the first or last frosts of the year).

The estimated production of flowers ranged between 11 kg ha^{-1} year^{-1} at VR and 388 kg ha^{-1} year^{-1} at SM (54 kg ha^{-1} year^{-1} at FG). The value at SM was similar to that estimated by Leonardi et al. [25] in chestnut coppices (444 and 374 kg ha^{-1} year^{-1} for 10- and 30-year old trees, respectively). In most forest ecosystems the production of organs related to reproduction usually varies considerably from one cycle to another, and this variation also involves the other organs of the tree [10]. The shedding of inflorescences is subject to their annual cycle of fall, and practically restricted to May and June in oaks (*figure 2*), as pointed out by Gómez et al. [17] in *Q. rotundifolia*, and to July to September in SM (*figure 4*), as pointed out by Gallardo et al. [14] in *C. sativa*.

The fraction corresponding to the fruits displays a maximum period of fall corresponding to September–November in oaks and November–December in SM, with a marked seasonality (*figures 2* and *4*). Their mean estimated annual production ranged between 8 (at NF) and 266 kg ha^{-1} year^{-1} (at SM; 51 kg ha^{-1} year^{-1} at FG), implying a percentage of less than 5 %. These figures are much lower than those obtained for an oak stand in northern Spain [5] and two chestnut orchards in western Spain [14] and northern Portugal [34]. Additionally, it is well known that a large amount of oak acorn cups fell with undeveloped acorns (above all in September 1992) owing to the drought occurring during these years (*table II*). At the chestnut coppice, the amount of burs varied between 67 and 297 kg ha^{-1} year^{-1}.

The average percentage of buds was around 3 % (at FG it reached 5 %, with only 1 % at SM). The contribution of the buds to the soil, which is clearly seasonal (*figures 3* and *4*), is limited to May–July. These values are lower than those offered by Anderson [1], who estimated 150 kg ha^{-1} year^{-1} of buds.

The fall of lichens coincided with that of oak branches, since most lichens are present on the latter. Highly significant correlation coefficients ($P < 0.01$) of around 0.8 were estimated on comparing their contribution.

The fraction corresponding to other plant remains varied considerably among the different years of the study and among plots (*figures 2* and *4*), although it was always more abundant at FG owing to the greater density of its understorey, which is the main contribution to that fraction. Its maximum contribution was recorded in the dry season, allowing the understorey to release a high percentage of leaves, a resource for adapting to the lack of water to which the plant is subjected during the drought period [22].

In reference to the total aboveground productivity, the driest *Q. pyrenaica* oak forest (FG) had the highest productivity (*table II* and *figures 3* and *4*), despite the driest water regimen of the soil. This is because the dynamics and characteristics of the soil physico-chemistry are affected by rainfall [26]. At the driest plot (FG) the percentage of base saturation and pH of the soil epipedon (A_h horizon; *table I*) were the highest, while the C/N ratio was the lowest. The higher pH of this epipedon was due to a reduced leaching during winter (the deep water drainage is almost non-existent; [30]). This higher pH permits the development of herbaceous legumes, favouring a better C/N ratio and increasing the speed of the biogeochemical cycles [26].

The relative ease with which excess soil water occurred at the other plots (VR, EP, NF and SM; favoured by a moderate soil retention capacity) together with the strong correlation between the volume of rainwater and drained water [30] mean that an important degree of soil leaching occurs, provoking a loss of soil fertility which becomes greater as the positive direction of the rainfall gradient is followed (NF). As a result, the winter rainfall favours the loss of elements in these acidic media, resulting in a lower aboveground productivity.

Significant differences ($P < 0.05$) were seen among the oak stands as regards their aboveground production. FG emerged as the most productive oak plot (*figure 3*) for individual fractions (except for branches and lichens). EP contributed the greatest amounts of branches and lichens and occupied the second place in aboveground production; additionally, it had the lowest leaf/branch ratio (3.6 as compared with 4.7 at FG, 7.3 at VR and 7.5 at NF). This factor has been proposed as a sign of greater productivity by other authors [20]. Finally, there were no significant differences ($P < 0.05$) between VR and NF as regards aboveground production or the different fractions; these plots were then differentiated according to their geological substrates (slate). In any case, a low productivity can be inferred for the case of the oak forests studied.

Obviously, the chestnut coppice showed the highest litterfall production and its leaf/branch ratio was 3.5, the amount of chestnut leaves, branches, flowers and total litter falling annually to the soil being significantly greater (*table II*). In any case, the magnitude of litterfall in the chestnut coppice was similar to that reported by O'Neil and DeAngelis [32] for deciduous species, and that given by Bray and Gorham [3] for latitudes around 40° N.

The greater production in the chestnut coppice with respect to the oak stands seemed to be related to the species and the younger age of the former, while among the oak plots the differences were related to rainfall and soil fertility, as pointed out by Moreno et al. [31]. In any case, as stated earlier, the length of the active biological period is limited by low winter temperatures and the summer drought.

3.2. Potential nutrient input to the soil through litter

We call 'potential return of bioelements' the total amount of bioelements which can theoretically reach the soil after the total decomposition of the forest litter (in fact, significant fractions of bioelements are retained in the organic remains; [15]).

There were no large fluctuations between the annual mean composition of litterfall fractions (*table III*), although the higher concentrations of Na recorded in all the organs during the third year of sampling and the irregularity observed for K are striking (Na is of mainly maritime origin, and hence its contribution via rainfall may be important; [31]). In any case, greater fluctuations in chemical composition were also seen, considering the fractions whose contribution was smaller over time (flowers, fruits, etc.) and, accordingly, a weighted mean (taking into account the variation in composition of the organs) with all the data was obtained in order to more accurately describe the calculated results (*table II*). The content of mineral elements in the leaves proved to be similar to that found by other authors for the same species [25, 40], showing low Ca contents and high levels of Mg with respect to *Quercus* species from other sites [19, 36], taking into account the acidity of the soils of the Sierra de Gata mountains.

The monthly variations in the potential return of elements to the soil through litter (*table IV*) follow a similar evolution to shedding, since this variation is more important than that observed in the composition of the plant organs. Likewise, it should be noted that the interannual differences (*table II*) are mainly due to disparate productions during the three cycles studied and to the different proportions of each organ in that litter.

Carbon was the element which showed the highest concentrations in all organs (*table III*), with values of return ranging from 2.55 Mg ha^{-1} year^{-1} (at SM) to 1.21 ha^{-1} year^{-1} (at NF), similar to those estimated by Santa Regina et al. [39, 40]. Nitrogen was the major element as regards quantitative importance (after C), the branches being the organs which showed the lowest levels of this element (*table III*). The chestnut coppice contributed 58 kg ha^{-1} year^{-1}, followed by FG (51 kg ha^{-1} year^{-1}); the other oak stands contributed nearly half of these amounts. Leonardi et al. [25] found amounts of N and Ca similar to those in four Sicilian chestnut coppices; Lemée [23] also highlighted the importance of N in French oak forests.

From the point of view of the mean C/N ratio of the leaf litter (between 30 and 40; *table III*), its influence on the soil may be considered to be 'indifferent' (according to the terminlogy used by Duchaufour [8]), and soil characteristics (and climatic parameters) should mainly govern the biological activity.

Considering the P concentrations in the oak leaves, two groups of plots emerge; these can be differentiated according to their geological substrates (VR–NF and EP–FG; *table III*). SM had the highest P concentration in the leaves. The amounts of P circulating in the chestnut ecosystem through the leaves are in an intermediate position with respect to the data found in the literature referring to *C. sativa* [34]. Fractionwise, the leaves occupy the first place (as also reported by Santa Regina et al. [39, 40]), the chestnut flowers being poorer in P than those corresponding to oak forests (*table II*). Turrión et al. [45] pointed out that the amount of available

Table IV. Mean potential nutrient return of macronutrients (kg ha^{-1} $year^{-1}$) and micronutrients (g ha^{-1} $year^{-1}$) in the five experimental forest plots.

Plots	Components	C	N	P	Ca	Mg	K	Na	Mn	Fe	Cu	Zn
Fuenteguinaldo (FG)	Leaves	1 321	37.0	3.37	23.5	6.15	7.4	694	1 143	282	30	57
	Branches	284	5.38	0.52	6.04	0.96	1.7	152	145	40	5	18
	Other	307	8.96	0.66	3.34	0.90	2.7	122	116	88	7	12
	Total	1 912	51.3	4.55	32.9	8.00	11.9	968	1 405	409	42	88
Villasrubias (VR)	Leaves	1 058	22.4	1.47	11.5	5.30	4.9	486	1 996	255	36	40
	Branches	146	2.56	0.15	1.72	0.45	0.6	68	153	33	2	10
	Other	148	3.96	0.23	1.23	0.36	0.8	63	102	86	3	8
	Total	1 353	28.9	1.85	14.5	6.11	6.4	617	2 251	373	42	57
El Payo (EP)	Leaves	1 129	35.1	2.16	13.5	4.43	6.4	509	1 302	273	36	58
	Branches	307	6.67	0.36	4.06	0.76	1.5	128	221	70	5	21
	Other	220	7.13	0.47	2.28	0.56	1.5	95	114	143	5	15
	Total	1 656	48.9	2.99	19.8	5.75	9.4	732	1 636	487	47	94
Navasfrías (NF)	Leaves	971	29.2	1.30	14.4	4.35	4.7	331	1 160	167	26	43
	Branches	133	2.27	0.14	2.19	0.36	0.7	70	89	26	3	9
	Other	109	2.64	0.17	1.49	0.29	0.6	46	58	49	2	5
	Total	1 213	34.1	1.61	18.1	5.00	6.0	447	1 308	242	31	57
San Martín (SM)	Leaves	1 679	41.6	6.67	18.3	10.9	14.9	1 399	3 151	254	47	91
	Branches	475	7.4	0.35	5.6	0.98	1.1	387	405	133	7	39
	Other	394	9.0	0.86	2.1	1.50	5.7	292	286	78	14	15
	Total	2 547	58.0	7.88	26.1	13.3	21.7	2 079	3 842	466	68	145

soil P in the forests studied appeared to be sufficient to satisfy plant requirements as long as there were no adverse circumstances (prolonged summer drought). In fact, SM (7.9 kg ha^{-1} $year^{-1}$) and FG (4.6 kg ha^{-1} $year^{-1}$) plots contributed significantly higher amounts of P than the other oak stands.

The Ca contents were among the lowest found in the literature, both for leaves (*table III*) and for the other fractions [25, 34, 39, 40, 41], although it should be remembered that these coppices are located on very different types of soil. Moreover, the low concentrations of assimilable Ca and the low pH of the study soils (*table I*; [26]) seem to be strongly related to the low Ca and high Mn contents in these litters (*table III*). Additionally, on comparing different species, it is necessary to take into account the 'dilution effect' (an increase in biomass while maintaining the same amount of bioelements) that may occur due to the different amounts of litter; that is, if it is assumed that the same amount of Ca is absorbed on soils with the same amount of assimilable Ca, the concentration in the litter would be lower in forests with a greater production (the chestnut coppice is theoretically more efficient; [27]). Regarding distribution by organs, the higher concentration of Ca is seen to correspond to the long-lived structures (i.e. branches; *table III*) perhaps due to the fact that its concentration increases during the ageing and lignification processes of the tissues [7].

The Mg content of all the organs lies within the limits reported in the literature [19, 21], the highest values corresponding to the leaves (*table III*), and this element being more abundant than Ca in fruits. It would appear that the uptake of Mg into the leaves could be favoured by the scarcity of Ca (nutritional imbalance), above all on the plots developed over slates. This would account for the small difference observed for Mg leaf concentration among all the plots studied (*table III*). Similarly, a general trend for Ca to increase throughout the ageing and lignification processes can be seen. In this sense, the highest concentrations of this element are recorded in the branches, the lowest concentrations corresponding to shorter-lived structures (flowers and fruits) in spite of the antagonism between both elements. The chestnut coppice also had the highest return of Mg (13.3 kg ha^{-1} $year^{-1}$).

The highest K concentration is linked to a lower concentration in Ca due to the known antagonism between these two elements; accordingly, the highest concentrations are found in the shortest-lived organs. The K content in chestnut leaves was higher than that found in the case of oaks (*table III*), perhaps as a result of a higher content of assimilable K in the soil of SM. By contrast, Pires et al. [34] obtained higher values of K than Ca, unbdoubtedly due to the greater abundance of shorter-lived organs, where K acquires considerable importance.

There are few references in the literature regarding Na content. Despite this, the leaf Na concentration (*table III*) in the studied forests can be said to be similar to that reported by Santa Regina et al. [40] in the mountains of western Spain and to that found for other species not very close to the sea (the concentrations of this element are strongly affected by the amount of rainfall). The Na return in SM was more than double the amount in the other oak stands.

With respect to the other micronutrients studied (Mn, Fe, Cu and Zn), the high concentration of Mn is striking [36], especially for VR; likewise, the low concentration of Fe with respect to the chestnut litter studied by Leonardi et al. [25] or Pires et al. [34] is noteworthy; however, this is not the case when compared with the data reported by Santa Regina et al. [40]. Regarding Zn and Cu, the former is present in the branches at a high concentration, while that of Cu is low (*table III*). SM also returns more micronutrients than the other plots.

Accordingly, the distribution and transfer of the bioelements to the soil through litterfall varies as a function of several different parameters, some of them biological (such as the phenology of the vector organs) and others climatic, such as the effect of frosts, prolonged drought, etc. [18]. In this sense, since FG is the most productive oak stand (*table II*), it is also the plot with the highest potential return of bioelements to the soil (*table IV*), the difference in the case of Ca being important (33 kg ha^{-1} $year^{-1}$). VR and NF are those with the lowest potential return of bioelements to the soil, due above all to the fact that they are the least productive forests (2.83 and 2.60 Mg ha^{-1} $year^{-1}$, respectively; *table II*).

Values of 127, 108, 87, 65, and 57 kg ha^{-1} yr^{-1} of the major elements (sum of N, Ca, Mg, P and K) and 6.6, 2.9, 3.0, 2.1 and 3.3 kg ha^{-1} $year^{-1}$ of the micronutrients (sum of Na, Mn, Fe, Cu and Zn) are obtained for SM, FG, EP, NF and VR respectively. This gives a total return of 134, 112, 90, 67 and 61 kg ha^{-1} $year^{-1}$ respectively for each of the forests studied. These micronutrient values are lower than those reported by Santa Regina et al. [40] for the same species (130 kg ha^{-1} $year^{-1}$) and those of Rapp [36] for *Q. ilex* (268 or 120 kg ha^{-1} $year^{-1}$), but are similar to those given by Calvo de Anta et al. [4] for *Q. robur* (84 kg ha^{-1} $year^{-1}$).

Nevertherless, the chestnut coppice has higher macronutrient values than those reported by Leonardi et al. [25] for chestnut coppices cleared every 7 year (around 60 kg ha^{-1} $year^{-1}$), but they are similar (around 150 kg ha^{-1} $year^{-1}$) to those of chestnut coppices ranging from 10 to 30 years of age (the greatest differences observed were for Ca, probably due to the calcic nature of the Sicilian soils).

Important differences were observed in the potential nutrient return of elements between the two oak stands developed over slate (NF and VR) and those developed over granite, especially regarding N, P and K. In FG, the respective values were almost double those of plots developed over slate, and somewhat lower in EP; this fact coincides with the lower fertility of the soils developed on slate (*table I*). Significant differences are also seen between the oak stands FG and EP for Ca and P (*table IV*), perhaps owing to the presence of an understorey of Leguminosae in the former (because the pH is higher, and there are larger amounts of assimilable P; *table II*), which are more demanding as regards these mineral nutrients.

In all the forests studied, nutrient transfer fluctuates throughout the year and depends strongly on phenological factors. The leaves are the main vector through which the potential nutrient return of bioelements to the organic horizon occurs in the four oak forests studied (*table IV*), accounting for approximately 82 % of the nutrient return at NF and VR and 72 % at EP, FG, and SM (the contribution of roots was not determined, but it was estimated by some authors to be one-fifth of the total plant biomass; [21]). Thus, the percentage of the contribution of nutrients by the leaves is of the same order in relation to the total aboveground production. The branches are the second fraction in importance with respect to bioelement return; of these, Ca and Zn are the most important nutrients returned by the branches, since this fraction represents a mean percentage of between 12 to 19 % (lower values in stands on slate).

Management of *C. sativa* is of great importance as regards the proportion of the different fractions. In this sense, Pires et al. [34] observed that the chestnut fruits were the organs occupying the second place in importance in the return of bioelements in orchards used for fruit production.

Gallardo et al. [15] found that other factors (such as throughfall and dust deposition) also have a strong effect on the nutrient cycles in these forests.

3.3. Nutrients in order of abundance

From the evolution of the aboveground production summarized in *figures 1* to *4*, it is possible to determine a convergence in the abscission phenology between the chestnut coppice and the oak forests studied; this is because the relatively small difference in temperatures means that the active periods of tree cover are similar. Thus, highly significant ($P < 0.01$) correlation coefficients are obtained between the chestnut coppice and all the oak stands, r coefficients ranging between 0.82 and 0.96 for leaves and between 0.72 and 0.89 or the litter.

Accordingly, leaf abscission mainly follows its own phenophase in the vegetative cycle of the tree and is less susceptible to environmental influences (late frosts; [18]).

Regarding the abundance of bioelements by fractions, in general the leaves can be said to show the highest concentrations; N and Ca in the buds, Ca and Zn in the branches, K in the fruits, and above all Fe and Cu in the other plant remains are noteworthy. A general sequence in the concentration of nutrients (*table III*) in the different organs of oak litter can be established (>> separates major from minor nutrients).

The general scheme appears as follows:

Leaves: C > N > Ca > K > Mg > P >> Mn > Na > Fe > Zn > Cu
Branches: C > N > Ca > K > Mg > P >> Mn > Na > Fe > Zn > Cu
Buds: C > N > Ca > K > Mg > P >> Mn > Fe > Na > Zn > Cu
Flowers: C > N > Ca > K > Mg > P >> Mn > Na > Fe > Zn > Cu
Fruits: C > N > Ca > K > Mg > P >> Na > Mn > Fe > Zn > Cu
Other remains: C > N > Ca > K > Mg > P >> Fe > Mn > Na > Zn > Cu

This order is altered in nearly all the organs of the VR oak stand owing to the position occupied by Mn, since the soil acidity favours its uptake by the plant. Similarly, the order is often altered on the FG plot due to a phenomenon that is the opposite of the former; that is, the higher pH of this soil slows down the absorption of Mn, and Na becomes a more abundant element than Mn [27]. Apart from this effect of soil pH, the greater abundance of Ca than N in the branches at the FG site is striking, as is the greater accumulation of Mg than K in the leaves at VR, owing to the possible nutritional imbalance on the latter plot (lowest soil pH).

On establishing a sequence of nutrient concentrations according to the different organs, it may be seen that this is identical for both species of Fagaceae for the three major fractions (leaves, branches and flowers) and only slightly different for buds and other plant remains. The fraction corresponding to the fruits of these species is not comparable, since under the denomination of oak fruits both acorns and cups are included while in the case of chestnuts both fractions (chestnut fruits and burs) are separated, and do not have the same mineral composition.

Regarding this sequence, the chestnut coppice has a Mn and P composition that is identical to that of the oaks in branches, and Zn and Cu in flowers, which have a higher composition of P than of Mg, and the latter is higher than that of Ca in fruits. The Mn composition of the fruits is greater than that of Fe, and that of Cu is greater than that of Zn in the other plant remains.

The general sequence of the amount (kg ha^{-1} year^{-1}) of bioelements returning to the soil (*table IV*) in these forest ecosystems is as follows:

C > N > Ca > K > Mg > P >> Mn > Na > Fe > Zn > Cu

the only exception being VR (where due to the soil acidity Mn comes before P, owing to the high concentration of the former element in all the litter organs).

The sequence shown above is identical to that reported by Hernández et al. [19] for an oak (*Q. rotundifolia*) coppice in the semi-arid region of the Duero basin, but with some small exceptions in the case of micronutrients since these in many cases respond to a rapidly cycling model with a strong environmental dependence (throughfall and atmospheric dust deposition).

The soil and climatic characteristics affect the trophic requirements and, according to Martín et al. [27], plant organisms can be said to respond to the scarcity of a given bioelement, meaning that their metabolism will be maintained at minimum expense (increase in efficiency; Gallardo et al., in preparation).

4. CONCLUSIONS

As regards abscission phenology, convergence is seen among the ecosystems studied since they are subject to climatological conditions differing in intensity but not as regards their evolution over time. Furthermore, the intra-annual variations in production can be explained in terms of both the annual rainfall and its distribution over the year.

The differences regarding the return of bioelements to the soil in these ecosystems are governed by the different aboveground productions of the forests and, to a certain extent, are regulated by the chemical characteristics of the litter.

Leaves are the main vector of the potential return of bioelements to the A_h horizon in all the plots studied. The branches are the second fraction in importance as regards the return of bioelements, the case of Ca and Zn being especially striking.

The differences among the plots studied with respect to the potential return of bioelements through the litter are determined by the different productions of the forests and hence soil fertility. The oak stands developed on granite release larger amounts of bioelements to the soil, above all N, P and K; in this sense, the most productive oak stand, and in fact that with the lowest rainfall, is noteworthy because of its high returns of Ca and P.

Thus, the general sequence of the amount (in kg ha^{-1} $year^{-1}$) of bioelements returning to the soil in the forest ecosystems studied is practically identical for both species of Fagaceae, for the three major fractions (leaves, branches and flowers) and only slightly different for buds and other plant remains.

The low Ca content and the relatively high Mn content in the litterfall seem to be strongly linked to the low levels of assimilable Ca and the acid pH of these soils, the uptake of Mg by the leaves being favoured by the scarcity of Ca, above all on the plots developed over slate.

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