Ann. Sci. For. 55 (1998) 771-784

Original article

Nutrient cycling in deciduous forest ecosystems of the Sierra de Gata mountains: nutrient supplies to the soil through both litter and throughfall

Juan F. Gallardo[a*], Alejandro Martín[b], Gerardo Moreno[a], Ignacio Santa Regina[a]

[a]C.S.I.C., Aptdo. 257, Salamanca 37071, Spain
[b]Area de Edafología, Facultad de Farmacia, Salamanca 37080, Spain

(Received 2 September 1997; accepted 17 October 1997)

Abstract – The present work fits into a general study on nutrient cycling in four *Quercus pyrenaica* oak forests and one *Castanea sativa* chestnut coppice located in the Sierra de Gata mountains (Central System, western Spain). The work consists of an estimation of bioelement supplies to the soil by the litter of these species and by throughfall from the canopy with a view to defining their role in the soil and, more generally, in ecosystem bioelement dynamics. It is concluded that the greatest differences between the oak stands and the chestnut coppice lie in the fact that in the latter ecosystem potentially more N, P, K, Mg, Na and Mn return through the litter owing to greater production in the chestnut coppice (and/or root uptake). Additionally, the relative importance of some bioelements (N, P, K and Mn) in the chestnut coppice is different from that of the oak forests. It is also possible to differentiate three groups of bioelements: 1) those that potentially return almost exclusively through the litter (C and N); 2) those for which both litter and throughfall must be taken into account to determine the potential return of bioelements (Ca, Mg, P, K, Fe and Mn); and 3) those that return almost exclusively through canopy leaching (Na, Cu and Zn). Despite this, on attempting to calculate the actual minimum annual returns, the three groups must be reduced to two: bioelements that almost exclusively return by throughfall (Na, Cu and Zn), and bioelements that return through litter decay and canopy leaching. Exceptionally, Fe behaves in a special way in the sense that it tends to be immobilized by decaying leaf litter. (© Inra/Elsevier, Paris)

nutrient cycling / throughfall / bioelement return / forest litter / broadleaf forest ecosystems

Résumé – Cycle des bioéléments dans des écosystèmes forestiers de la Sierra de Gata : apport d'éléments nutritifs au sol par le pluviolessivage et la décomposition de la litière. Le recyclage de bioéléments dans quatre chênaies à *Quercus pyrenaica* et dans une châtaigneraie à *Castanea sativa*, localisées dans la Sierra de Gata (Système Central, ouest de l'Espagne) a fait l'objet de cette étude. Il s'agit d'une estimation des éléments biogènes qui retournent au sol par décomposition de la

* Correspondence and reprints
E-mail: jgallard@gugu.usal.es

litière et par le pluviolessivage des arbres. L'objet de l'étude est de définir le rôle et la dynamique des bioéléments dans le sol et l'écosystème.
On peut conclure que la plus grande différence existante entre les peuplements de *Q. pyrenaica* et de *C. sativa* est que ce dernier écosystème peut potentiellement restituer davantage de N, P, K, Mg, Na et Mn par la litière, à cause d'une plus forte production de biomasse aérienne chez le châtaignier (et/ou plus forte absorption par les racines). On observe, en outre, que la relative importance de quelques bioéléments (N, P, K et Mn) est différente dans la châtaigneraie et les autres chênaies.
Il est ainsi possible de différencier trois groupes d'élément biogènes : tout d'abord, ceux qui peuvent potentiellement retourner majoritairement par la litière (C et N); en deuxième lieu, ceux qui retournent soit par la décomposition de la litière soit par le pluviolessivage (Ca, Mg, P, K, Fe et Mn); et finalement, ceux qui retournent presque exclusivement par pluviolessivage (Na, Cu et Zn).
En revanche, en ce qui concerne l'apport réel annuel de bioéléments, deux groupes peuvent se différencier : d'une part, celui des bioéléments qui retournent par pluviolessivage (Na, Cu et Zn); et d'autre part, les bioéléments qui retournent soit par décomposition de la litière, soit par pluviolessivage.
Le Fe, au contraire, a un comportement spécial car il est immobilisé dans la litière en décomposition.

cycle des bioéléments / pluviolessivage / retour d'éléments nutritifs / litière / forêt caducifoliée / écosystème

1. INTRODUCTION

Plant litter returns the nutrients and energy stocked in the vegetation to soils, with the important participation of microorganisms; nutrients circulate in the ecosystem and play a special and important role, essential for the life of all components [17, 19, 25, 45]. Litter quality, litter decomposition and quantitative inputs to the soil affect pedogenesis and the productivity of ecosystems. Knowledge of these different aspects is a determining factor for understanding the functions of nutrient flows in ecosystems.

Bioelement inputs from throughfall to the forest floor, and then to the soil, are the result of a complex interaction of atmospheric, hydrological and biogeochemical processes [34]. The final composition of the water flowing from the canopy is determined by the initial composition of the rainfall water, the wash-off of dry atmospheric dust, and water interception, leaching and/or uptake of ions by the forest canopy [39].

The quantities of bioelements brought to the soil through these processes and also the quality of solubilized substances are of major interest for ecosystem function and productivity [5, 25]. Knowledge of these nutrient contributions (mostly in available form for plants) is of great importance for plant nutrition [17, 37].

Studies on the inputs of biogenous elements in broadleaf forest populations have been carried out by Lossaint [24], Rapp [40], Aussenac et al. [1], Lemee [21], Santa Regina et al. [43, 44], Hernández et al. [18], Moreno et al. [34] and Martín et al. [27, 28], among others.

The present work fits into a general study on nutrient cycling in four *Quercus pyrenaica* oak forests and one *Castanea sativa* coppice located in the Sierra de Gata mountains (Central System, western Spain). The work aims at estimating total bioelement supplies to the soil by the litter of these species and by throughfall with a view to defining their role in the soil and, more generally, in ecosystem bioelement dynamics. A further aim is to attempt to estimate the true minimum annual nutrient input to the soil.

2. MATERIALS AND METHODS

2.1. Characteristics of the study site

The study area is located in the El Rebollar district (Sierra de Gata mountains, western Spain); its coordinates are 40° 19' N and 6° 43' W [14, 16]. The wooded area is mainly formed of *Quercus pyrenaica* Willd. (deciduous oak), *Pinus pinaster* Ait. (maritime pine) and, at the southern border of the El Rebollar district, *Castanea sativa* Miller (chestnut).

The four selected *Q. pyrenaica* oak plots situated at Navasfrías (NF), El Payo (EP), Villasrubias (VR) and Fuenteguinaldo (FG) according to a decreasing rainfall transect, display the following characteristics: a tree density ranging from 1 040 trees ha^{-1} at VR to 406 trees ha^{-1} at EP (*table I*). The plot with the lowest density (EP) has the highest mean trunk diameter (25.4 cm) and greatest tree height (17 m); the lowest values of these parameters are in VR plot (11 cm and 8.5 m, respectively; *table I*). The leaf area index (L.A.I.) ranges from 1.8 to 2.6 $m^2\,m^{-2}$ on the NF and FG plots, respectively. Basal area ranges from 0.135 and 0.212 $m^2\,m^{-2}$ on the VR and FG plots, respectively (*table I*).

The selected coppice of *Castanea sativa* chestnut is situated in San Martín de Trevejo (SM) and has a density of 3 970 trees ha^{-1}, with a mean diameter of 10 cm and a height of 13 m. The mean basal area of 0.306 $m^2\,m^{-2}$ and the L.A.I. is 3.7 $m^2\,m^{-2}$ (*table I*).

The climate of the area is characterized by rainy winters and hot dry summers, falling under the classification of humid Mediterranean, with an average rainfall and temperature of approximately 1 580 mm $year^{-1}$ and 10.4 °C for NF and 720 mm $year^{-1}$ and 12.9 °C for FG (*table I*).

The soils of these areas are generally *humic Cambisols* [11] developed on slates and graywackes at NF and VR and on Ca-alcaline granite at EP and FG [13]. At SM, owing to the strong slope (approximately 45 %), granitic sands predominate, sometimes with man-made terraces.

2.2. Chemical compositions of litterfall and throughfall

The litter fallen over the year was sampled at varying intervals depending on its rate of fall (between 2 weeks and 1 month [18]. After collection, the litter was separated into different fractions (leaves, branches, flowers, fruits, barks, etc.) and then dried, air cleaned and weighed [29].

Table I. General characteristics of the forest plots (production in kg ha^{-1} $year^{-1}$).

Plots parameters	Fuenteguinaldo (FG, oak)	Villasrubias (VR, oak)	El Payo (EP, oak)	Navasfrías (NF, oak)	San Martín Trevejo (SM, chestnut)
Altitude (m a.s.l.)	870	900	940	960	940
Long-term mean P (mm^{-1})	720	872	1 245	1 580	1 152
Mean annual t (°C)	12.9	N.d.	8.1	10.4	14.2
Geology	granite	slate	granite	slate	granite
Soils [11]	*humic Cambisol*	*humic Cambisol*	*humic Cambisol*	*humic Cambisol*	*humic Cambisol*
Soil pH (Ah)	5.4	4.6	4.7	4.9	5.1
Ah org. C (mg g^{-1})	42	67	77	105	45
Density (tree ha^{-1})	738	1 043	406	820	3 970
Mean D.B.H. (cm)	16.5	11.0	25.4	15.2	10
Area basal ($m^2\,m^{-2}$)	0.21	0.14	0.20	0.16	0.31
Mean height (m)	12	8.5	17	13	13
L.A.I. ($m^2\,m^{-2}$)	2.6	2.0	1.9	1.8	3.7
Aboveg. production	4.09	2.83	3.49	2.60	5.25
Leaf production	2.83	2.21	2.35	2.09	3.43

D.B.H.: mean diameter at breast height (1.3 m); L.A.I.: leaf area index; P: annual rainfall; t: temperature; Ah: superficial soil horizon. N.d.: no data available.

Study of the decomposition of oak and chestnut leaves was followed using the classic litterbag method [27, 30]. Field material (leaves, branches, twigs, water) was suitably treated prior to determining the following bioelement concentrations: litter organic C by a Carmhograph 12 Wösthoff; litter N by a Heraeus Macro-N-analyzer; P by spectrophotometry (Varian DMS 90) using either the vanadomolybdophosphoric yellow method for determining litter P or the ascorbic acid method for determining water P; water pH was determined with a Beckman 3500 pH meter; water-dissolved total and organic C by a Beckman 315A T.O.C.A. Water-dissolved anions were determined by ionic chromatography (Dionex 350). The determination of dissolved cations and these bioelements in litter was carried out by atomic absorption spectroscopy (Varian 1475) and water-dissolved micronutrients by plasma spectrometry (Perkin-Elmer ICP-2).

We use the term 'potential return of one bioelement' to refer to the total content of this element in the litterfall [17]; that is, the total quantity of one bioelement which is released from the decomposing litter when it has completely decomposed (including the more recalcitrant fractions of the litter); then, the potential return of each bioelement is estimated by multiplying the litterfall by its composition (weighting the different fractions [17]).

As is known, significant fractions of bioelements are usually retained in the organic remains. The potential return of nutrients generally has a higher value than the actual return. We use the term 'actual minimum input of one nutrient to the soil' to refer to the calculated minimum real contribution of the decomposing litter, according to the pattern of release of each element as determined by the litterbag method [30, 45].

It should be mentioned that the contribution by the roots to potential bioelement return was not taken into account in the present work. Khanna and Ulrich [19] estimated that the root bioelement content represents about 20 % of the total potential return.

The contributions of bioelements reaching the forest floor through canopy leaching may come from three different sources: rainfall, dry deposition and throughfall, each of them having a different degree of quantitative importance for all the elements considered. In this article throughfall and canopy leaching are used as synonymous, even though they are not exactly the same [35]. Furthermore, according to Moreno et al. [36] rainfall water represents the main source of bioelements reaching the forest floor through canopy leaching.

3. RESULTS

3.1. Total nutrient input to the soil by litter

Aspects related to aboveground production of these forests will be discussed elsewhere [16], although some figures are shown in *table I*.

The data concerning the annual potential return of bioelements through litterfall to the forest soil of the five forest systems are shown in *table II*.

The oak forest at FG has the highest potential bioelement return and litterfall production (4.1 Mg ha^{-1} $year^{-1}$, equivalent to 1.9 Mg ha^{-1} $year^{-1}$ of C). VR and NF are the plots with the lowest potential bioelement return and also the lowest litterfall (2.8 and 2.6 Mg ha^{-1} $year^{-1}$, respectively, equivalent to 1.3 and 1.2 Mg ha^{-1} $year^{-1}$ of C, respectively). Additionally, significant differences were found (*table II*) in the potential return of bioelements between forests developed on slates and those on granites.

Because the chestnut coppice is the most productive forest (*table I*), the highest levels of potential return (*table II*) of macronutrients (sum of N, P, Ca, K and Mg) and micronutrients (Na, Fe, Mn, Cu and Zn) were obtained there (127 and 6.6 kg ha^{-1} $year^{-1}$, respectively); 2.6 Mg ha^{-1} $year^{-1}$ of organic C were also returned at the chestnut coppice (*table II*). By contrast, 108, 87, 65 and 57 kg ha^{-1} $year^{-1}$ of macronutrients and 2.9, 3.0, 2.1 and 3.3 kg ha^{-1} $year^{-1}$ of micronutrients were returned annually through the litterfall at FG, EP, NF and VR oak forests, respectively (*table II*).

3.2. Inputs of bioelements to soils by throughfall (canopy leaching)

The results are shown in *table II*.

Table II. Potential inputs of bioelements (kg ha^{-1} $year^{-1}$) to the soil of the experimental forest plots.

Plots	Bioelements	C	N	P	Ca	Mg	K	Na	Mn	Fe	Cu	Zn	Macro-nutrients	Micro-nutrients
	litter	1 213	34.1	1.6	18.1	5.0	6.0	0.45	1.3	0.24	0.03	0.06	65	2.1
Navasfrías	throughfall	96	3.0	0.70	12.8	4.7	8.4	4.9	0.44	0.27	0.25	1.7	30	7.6
(NF, oak)	total inputs	1 309	37.1	2.3	30.8	9.7	14.4	5.4	1.8	0.51	0.28	1.8	94	9.7
	litter	1 656	48.9	3.0	19.8	5.8	9.4	0.73	1.6	0.49	0.05	0.09	87	3.0
El Payo	throughfall	116	3.5	1.5	12.3	5.9	15.3	5.5	0.73	0.25	0.25	1.3	38	8.0
(EP, oak)	total inputs	1 773	52.4	4.5	32.0	11.6	24.7	6.2	2.4	0.73	0.29	1.4	125	11.0
	litter	1 353	28.9	1.9	14.5	6.1	6.4	0.62	2.3	0.37	0.04	0.06	58	3.3
Villasrubias	throughfall	118	3.1	1.2	11.8	6.3	13.6	5.0	0.97	0.27	0.16	1.5	36	7.9
(VR, oak)	total inputs	1 471	32.1	3.0	26.2	12.4	19.9	5.6	3.2	0.64	0.21	1.5	94	11.3
	litter	1 912	51.3	4.6	32.9	8.0	11.9	0.97	1.4	0.41	0.04	0.09	109	2.9
Fuenteguinaldo	throughfall	132	3.4	2.5	11.0	6.3	17.7	3.5	0.55	0.27	0.15	1.6	41	6.1
(FG, oak)	total inputs	2 044	54.7	7.0	43.9	14.3	29.5	4.5	2.0	0.68	0.19	1.7	149	9.1
	litter	2 547	58.0	7.9	26.1	13.3	21.7	2.1	3.84	0.47	0.07	0.15	127	6.6
San Martín T.	throughfall	91	1.1	1.0	8.5	5.1	10.7	4.5	0.77	0.15	0.02	1.5	26	7.0
(SM, chestnut)	total inputs	2 638	59.1	8.9	34.6	18.4	32.4	6.6	4.6	0.62	0.09	1.7	153	13.5

In canopy leaching, C was the element with the greatest contribution to soil, far higher than those observed for the other elements.

The major cations were Ca and K, while N had lower values (above 3 kg ha^{-1} $year^{-1}$, lower at SM). Ca values were close to 12 kg ha^{-1} $year^{-1}$, lower at SM. K and Mg had values close to 15 and 5 kg ha^{-1} $year^{-1}$, respectively, lower at NF and higher at SM.

Phosphorus had a very low concentration, at values close to those of micronutrients.

In general, in terms of mass, the order of importance of the different elements present in the thoughfall would be:

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

No large differences can be seen between the different forest ecosystems, except for K and P in FG (higher soil pH), and Ni and Cu in SM (chestnut coppice).

4. DISCUSSION

4.1. Litterfall versus litterfall inputs

Annual litterfall production (*table I*) is the main factor governing the annual potential return of macronutrients (except K; *table II*). A noteworthy observation was that VR, being the oak forest with the poorest soil (see soil pH, *table I*; also Martin et al. [28]) had a high potential return of Mn; the chestnut coppice also has a relatively high potential return of Mn.

Leaves are the litter fraction accounting for about 75 % of total bioelement return by litter [16]. This value ranged from 70 to 85 % of the total return; for Mg and Mn, the percentage of total return through the leaves may increase to 88 % in soils on slates, indicating nutrition imbalance [27, 28]. The opposite trend is seen for K in the chestnut coppice and this is consistent with the findings of Pires et al. [38], who reported that this percentage depends on forest management.

Data relating to the water and bioelement fluxes in the four oak forests have previously been discussed by Moreno et al. [34, 35], and those concerning the chestnut coppice by Gallardo et al. [15]. These authors took into account the monthly variation in water composition and bioelement uptake or leaching. In the contribution of bioelements through canopy leaching it is possible to distinguish different sources [34]: bulk precipitation, dry deposition, stemflow and throughfall.

The measured contributions of C by throughfall are similar to those reported by Santa Regina and Gallardo [42], Edmonds et al. [10] and Krivosonova et al. [20], but much greater than those described by Stevens et al. [46] and Van Breemen et al. [48].

The high C input indicates a possible local source of nutrient elements found in the bulk precipitation, due to deposition of suspended particles coming from the forest itself [23, 39]. However, as estimated by Moreno [32], atmospheric dust only represents 2–3 % of the N and Ca measured and less than 1 % of the remaining nutrients.

In general, the values of these macronutrients are very similar to those obtained by other authors on the Iberian Peninsula [2, 4, 8, 41] or slightly lower [42]. In all cases, the contributions may be considered moderate to low [37]. The lowest inputs of bioelements by canopy leaching occurred on the plot on slates, pointing to lower soil fertility at this plot [28].

Nitrogen values are very similar to those reported by Likens et al. [22] and Belillas and Roda [3], and clearly lower than those found in industrialized areas [7, 48].

Phosphorus is an element that tends to be present at very low concentrations in bulk precipitation [36], at values close to those of micronutrients; it is a bioelement with a very closed plant–soil cycle and the contribution from the atmosphere is low. Accordingly, the contribution from bulk precipitation is very low, as reported by other authors (e.g. [22, 37, 42, 46]).

The oligoelements Fe, Mn, Zn and Cu, like N, have very low values, lower than those obtained in more industrialized areas because the precipitation in the area studied (as pointed out) comes almost entirely from the West (Atlantic Ocean), with little or no influence from air masses coming from the East (continent).

The total contribution of all the elements analysed in the throughfall water are greater than those of the rain water [36], indicating that the content of these elements in the rain water increases as the water passes through the forest canopy. The elements showing the greatest increase in concentration in the throughfall water with respect to rain water are P, K, Mn, Mg and C [34]. This increase in concentration is a fairly common phenomenon observed in forests [32, 37] and is due to different factors: thus, the evaporation of intercepted water contributes to a small increase in concentration (about 19 %, [33]) and to a large extent the enrichment in nutrients is due to the washing of dry depositions (mainly Ca, P, Fe, Cu and Zn, and Mg on some plots) and leaching processes (mainly C, Mg, K and Mn). The latter four elements are considered to be readily leachable by Tukey [47]. However, these data are not consistent with the findings reported by Ferres et al. [12], for whom only K is clearly enriched during its passage through the canopy.

The results for Ca contrast with those found for Mg (*table II*); in this sense, in the first case low throughfall values are obtained with respect to those found in the literature cited; by contrast, the values found for Mg are higher. This suggests that Mg replaces the role of Ca owing to the scarceness of the latter element in the acid soils studied [27].

The entry of C to the soil depends almost exclusively on the litter (*table II*), while throughfall input of C is not very relevant.

Nitrogen reaches the soil mainly through the litter (92 % at the oak forest and 98 % at the chestnut coppice; *figure 1*), the canopy not contributing to the release of this element.

Ca and P also reach the soil mainly through the litter (*table II*), as found by Parker [37]; there is also an important contribution of Ca by throughfall and of P by dry deposition [36].

The contributions of Mg by both routes (litter and throughfall) are very similar (except in the chestnut coppice, where the litter contribution prevails; *figure 1*), throughfall being very important. By contrast, in the case of K the major contributions are due to throughfall (except at the chestnut coppice), although the litter is important (38 %; *figure 1*) and canopy leaching is also relevant (*table II*).

Na, Cu (except at the chestnut coppice) and Zn are mainly contributed by throughfall (*table II*); according to Moreno et al. [36] incident rainfall is very important as regards Na and Zn, and leaf leaching for Cu.

To a large extent, Mn comes from the litter [37], throughfall being relatively unimportant (approximately 3 % on the oak stands and 1 % at the chestnut coppice). Finally, the return of Fe is very similar through both routes (*figure 1*), the contribution due to throughfall being unimportant.

Accordingly, the most important return of C and N is through the litter, whereas the return of Na, Cu and Zn is greater through throughfall. Regarding the other elements, the contributions through both routes are balanced, with the exception of P and Mn, which are slightly higher in the litter and K in oak stand throughfall (*figure 1*). In the light of these general characteristics, it should be stressed that the return of Ca through the litter, both at FG and at the chestnut coppice, represents 75 % of the total (*figure 1*) owing to the larger amounts returned by this litter. Moreover, the higher

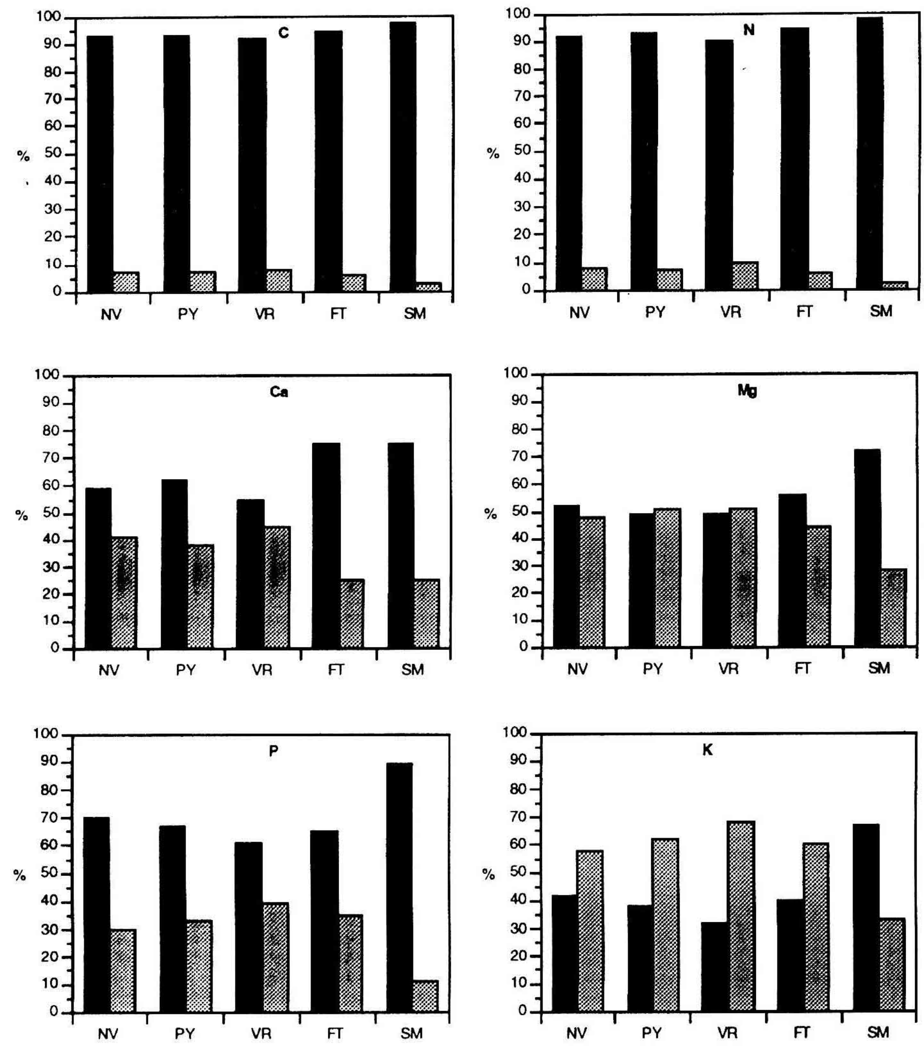

Figure 1. Comparison between percentages of the contribution of both litterfall and throughfall to the potential inputs of bioelements to the soil at five experimental plots (Navasfrías: NF; El Payo: EP; Villasrubias: VR; Fuenteguinaldo: FG; and San Martín de Trevejo: SM).
■ Litter. ▒ Throughfall.

concentrations of Mg, P and K in chestnut leaves mean that the contributions are higher in the litter (*table II*), with percentages of 72, 89 and 67 %, respectively.

In the light of the data offered in *table II*, it could be concluded that throughfall (a factor indicating nutrient exchange at canopy level) represents mean percentages, with respect to the total contribution, of 3 % for C; 4 % for Ca; 23–15 % for Mg; 12–1 % for P; 35–7 % for K; 15–8 % for Mn; 8 % for Fe; 45 % for Cu and 8 % for Zn (where

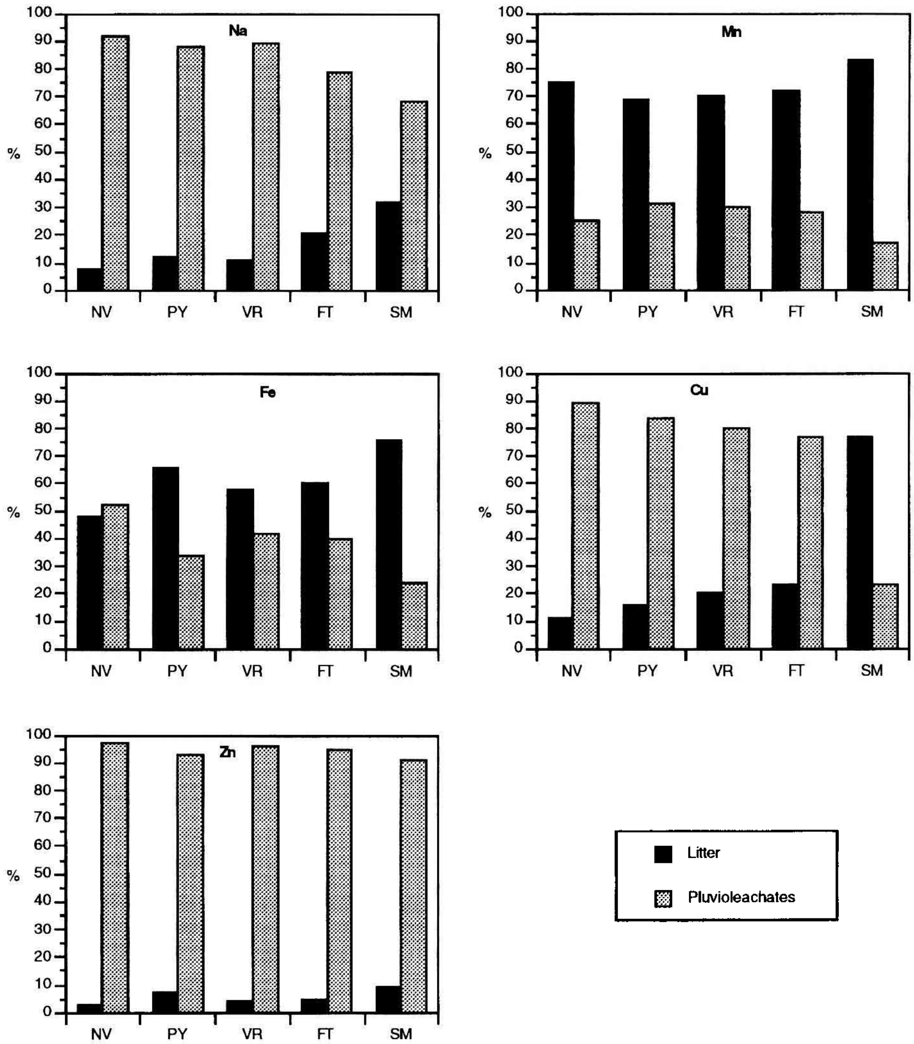

Figure 1. continued.

two values appear, the second one corresponds to the chestnut coppice and the first, or single value, to the mean figure found for the four oak forests). These figures are comparable with those reported by Parker [37] for oak forests, and moderately low for the chestnut coppice.

4.2. Minimum real inputs of nutrients to the soil

The release of each nutrient (Ert) can be estimated [17] by multiplying the remaining litter (Bt) by the content of each element (Et) at the sampling time (t), and subtracting the result from the initial content of that nutrient in the litterfall biomass (Bo):

$$\textbf{Ert}\ (\mathrm{g\ m^{-2}\ year^{-1}}) = \textbf{Bo}\ (\mathrm{kg\ m^{2}\ year^{-1}}) \times \mathrm{Eo}\ (\mathrm{g\ kg^{-1}}) - \textbf{Bt}\ (\mathrm{kg\ m^{-2}\ year^{-1}}) \times \textbf{Et}\ (\mathrm{g\ kg^{-1}})$$

The minimum real contributions reaching the soil annually through the leaves can be estimated since the leaves, as is known, represent the main source of return in the litter [30]. The data offered in *table III* are based on knowledge of the mean potential return through the leaf litter (*table II*) and the capacity to release bioelements over 3 years from the leaves contained in litter bags [30, 45]. It should be noted that this is an underestimation of the actual return of bioelements because in bags the degradation processes are slowed down, and also because, of the total litter, only the leaves are considered; one is thus referring to the minimum real inputs of available nutrients to the soil.

The chestnut litter is the one that releases the largest amounts of bioelements over the 3 years (*table III*) due both to a greater potential return (*table II*) and to a faster decomposition rate [30]. Despite this, there are two elements (Na and Fe) that are not released in net form (negative sign in *table III*) owing to the strong degree of accumulation undergone during the first year of decomposition [30]. The greatest return occurs in the chestnut coppice at SM (the most demanding species). Among the oak forests, return depends on the elements (*table III*), although the lowest return values are seen at the oak forest in VR since this is the most dystrophic ecosystem (see soil pH, *table I*); such dystrophy is also reflected in the possible Ca/Mg nutritional imbalance [28] since it is on this latter plot (VR) where the least return of Ca and the greatest return of Mg occurred (*table III*) in the oak forests.

The amount of P released by the leaves is higher on granite soils than on soils developed over slates; undoubtedly, the scarceness of this (except at the FG and SM plots) must be the factor governing its retention by microbial activity (biological immobilization [9]).

The losses of K from decomposing leaves are slightly higher in the oak forests developed over granites than those located on slates (*table III*), although much lower than those seen at the chestnut coppice. Despite the greater richness in K of the chestnut coppice floor [25], the greater requirement of K on this plot leads its external cycle to become more fluid and its internal cycle to become more intense, canopy leaching being lower (*table II*), with a more marked release during decomposition (*table III*; [45]).

The behaviour of elements considered to be minor ones in this study (Na, Mn, Fe, Cu and Zn) to a large extent depends on the contributions through canopy leaching (*table II*) and soil conditions [28]. Thus, it may be seen (*table III*) that in many instances these elements are accumulated in the decomposing litter after 3 years because the needs of the plants for them are low and are largely or even wholly supplemented by the atmosphere [31].

It is possible to estimate the minimum annual amount of bioelements reaching the soil by adding the amount of nutrients released by decomposing leaves during the first 3 years of leaf decomposition (*table III*) to those afforded by throughfall (*table II*). These amounts will be underestimated if only the leaf fraction of the litter is considered and if one estimates what is released in 3 years [30, 45]. Accordingly, the actual amount of nutrients reaching the soil will range between the values offered in *table II* (maximum) and those shown in *table III* (minimum).

It should be stressed that the values obtained for the actual return of Na, Fe, Cu and Zn (negative values) by the leaves are due to enrichment of the litters undergoing decomposition due to external contributions after their emplacement [36, 45]. Thus, in these cases no real return is produced by the

Table III. Actual minimum inputs (kg ha^{-1} year^{-1}) and percentage of bioelements to the soil of the experimental forest plots.

Plots	Bioelements	N	P	Ca	Mg	K	Na	Mn	Fe	Cu	Zn
	Decomposing leaves*	5.5	0.7	7.3	2.1	2.6	0	0.68	0.01	0	0
	throughfall	3.0	0.7	12.8	4.7	8.4	4.9	0.44	0.27	0.25	1.7
Navasfrías	total inputs	8.5	1.4	20.1	6.8	11.0	4.9	1.1	0.28	0.26	1.7
(NF, oak)	% d. leaves*	65	49	36	31	24	0	60	4	2	0
	% throughfall	35	51	64	69	76	100	40	96	98	100
	Decomposing leaves*	7.8	1.2	6.8	1.5	3.5	–0.85	0.59	–0.22	0.02	0
	throughfall	3.5	1.5	12.3	5.9	15.3	5.5	0.73	0.25	0.25	1.3
El Payo	total inputs	11.3	2.7	19.0	7.4	18.7	4.6	1.3	0.03	0.26	1.3
(EP, oak)	% d. leaves*	69	44	36	20	18	0	44	0	6	0
	% throughfall	31	56	64	80	82	100	56	100	94	100
	Decomposing leaves*	1.0	0.6	5.9	2.4	2.6	–0.19	0.31	–0.27	0	–0.01
	throughfall	3.1	1.2	11.8	6.3	13.6	5.0	0.97	0.27	0.16	1.5
Villasrubias	total inputs	4.1	1.8	17.7	8.7	16.1	4.8	1.3	–0.01	0.16	1.5
(VR, oak)	% d. leaves*	24	34	34	28	16	0	24	–	0	0
	% throughfall	76	66	66	72	84	100	76	–	100	100
	Decomposing leaves*	4.3	1.6	10.9	1.6	4.5	–0.38	0	–0.59	–0.01	0
	throughfall	3.4	2.5	11.0	6.3	17.7	3.5	0.55	0.27	0.15	1.6
Fuenteguinaldo	total inputs	7.7	4.1	21.8	7.9	22.1	3.2	0.55	–0.32	0.14	1.6
(FG, oak)	% d. leaves*	56	39	50	21	20	0	0	–	0	0
	% throughfall	44	61	50	79	80	100	100	–	100	100
	Decomposing leaves*	19.7	4.3	12.3	6.8	12.2	–0.03	1.6	–0.30	0.03	0.05
	throughfall	1.1	1.0	8.5	5.1	10.7	4.5	0.77	0.15	0.02	1.5
San Martín T.	total inputs	20.7	5.3	20.8	11.9	22.9	4.5	2.4	–0.15	0.05	1.6
(SM, chestnut)	% d. leaves*	95	81	59	57	53	0	67	–	61	3
	% throughfall	5	19	41	43	47	100	33	–	39	97

* Minimum actual return of bioelements through the leaves.

leaf litter after 3 years; additionally, owing to the high contents of these elements (Na, Cu and Zn) in throughfall, it could be assumed, as has been commented above, that such enrichments would be a result of canopy leaching and would therefore represent an amount of nutrients coming from the atmosphere or from the canopy that does not reach the soil but rather is retained in the humus layer [26]. In view of this, on calculating the total contribution of nutrients to the soil, it would be necessary to subtract that accumulation from the contribution by throughfall. Fe, by contrast, shows a different trend since its contribution through throughfall is not sufficient to account for the enrichment (negative values of the total contribution) at VR, FG and SM and hence an origin in the soil should be sought [28]. In acid medium, the Fe content increases in the soil solution [6], favouring greater immobilization by organisms, and hence the negative value of the total contribution represents the annual enrichment of the humus due to the soil, apart from the fact that the activity of the soil mesofauna also has a contaminating effect on the decomposing litter by Fe.

Overall, it may be seen that the contributions of nutrients by throughfall are very similar to (and sometimes even higher than) the minimum contributions received by the soil through litter decomposition, highlighting the importance of this flow in forest nutrition.

5. CONCLUSIONS

The following main conclusions can be drawn from the present work.

1) The greatest differences between the oak forests and the chestnut coppice lie in the fact that in the latter ecosystem more N, P, K, Mg, Na and Mn potentially return through the litter, undoubtedly due to a greater degree of tree uptake and/or production in the chestnut coppice. Among the oak forests, VR shows a nutritional imbalance.

2) It is possible to differentiate three groups of bioelements, namely: a) those that potentially return through the litter almost exclusively (C and N); b) those for which both the litter and throughfall must be taken into account to explain their potential return (Ca, Mg, P, K, Fe and Mn); and c) those that return almost exclusively through throughfall (Na, Cu and Zn).

3) Despite the foregoing, after calculation of the minimum annual returns, the above three groups become reduced to two: bioelements that almost all return effectively through canopy leaching (Na, Cu and Zn); and bioelements that return through both litter decomposition and throughfall. However, Fe behaves in a special fashion in the sense that it tends to be immobilized by the decomposing litter.

ACKNOWLEDGEMENTS

The authors thank the collaboration of the Junta de Castilla y León. This work was also sponsored by the European Union (CAST/ENVIRONMENT and MEDCOP/AIR Projects) and the Spanish National Funds (*CICYT/INIA*). Technical support was received from M. Tapia, M.L. Cosme, J. Hernández and C. Pérez. The English version has been revised by N. Skinner and D. Garvey.

REFERENCES

[1] Aussenac G., Bonneau M., Le Tacon F., Restitution des éléments minéraux au sol par l'intermédiaire de la litière et des précipitations dans quatre peuplements forestiers de l'Est de la France, Oecol. Plant. 7 (1972) 1–21.

[2] Avila A., Balanç d'aigua i nutrients en una conca d'alzinar del Montseny. Estudis i Monografies, Diputación de Barcelona, 1988, 219 pp.

[3] Belillas M.C., Rodá F., Nutrient budgets in a dry heatland watershed in northeastern Spain, Biogeochemistry 13 (1991) 137–157.

[4] Bellot J., Análisis de los flujos de deposición global, translocación, escorrentía cortical y deposición seca en el encinar mediterráneo de L'Avic (Sierra de

Prades, Tarragona), thesis, University of Alicante, 1989.

[5] Berg B., Lundmark J.E., Decomposition of needle in *Pinus contorta* and *P. sylvestris* monocultures: a comparison, Scand. J. For. Res. 2 (1987) 3–12.

[6] Black C.A., Relaciones suelo-planta, Hemisferio Sur, Buenos Aires, 1975, 866 pp.

[7] Brechtel H.M.., Balazs F., Lehnardt F., Precipitation input of inorganic chemicals in the open field and in forest stands. Results of investigations in the State of Hesse, in: Georgii H.W. (Ed.), Atmospheric Pollutants in Forest Areas, D. Reidel, Dordrecht, 1986, pp. 47–67.

[8] Calvo D.E. Anta R.M., Paz A., Díaz-Fierros F., Nuevos datos de la influencia en la vegetación en la formación de suelo en Galicia. II. Aportes de elementos por lavado de la cubierta y tronco, An. Edaf. Agrobiol. 39 (1979) 1675–1691.

[9] Duchaufour P., Edafología: Edafogénesis y clasificación, Masson, Barcelona, 1984, 494 pp.

[10] Edmonds R.L., Thomas T.B., Rhodes J.J., Canopy and soil modifications of precipitation chemistry in a temperate rain forest, Soil Sci. Soc. Am. J. 55 (1991) 1685–1693.

[11] F.A.O., Soil Map of the World: The Legend, F.A.O., Rome, 1991.

[12] Ferres L.L., Rodá F., Verdú A.M.C., Terradas J., Circulación de nutrientes en algunos ecosistemas forestales del Monseny (Barcelona), Mediterranea, Ser. Biol. 7 (1984) 139–166.

[13] Gallardo J.F., Egido J.A., Prat L., Suelos forestales de El Rebollar (Salamanca). I. Consideraciones generales, Anu. Cent. Edafol. Biol. Apl. 6 (1980) 193–213.

[14] Gallardo J.F., Cuadrado S., Egido J.A., González M.I., Rico M., Santa Regina I., Gallego H.A., Martín A., Menéndez I., Moreno G., Quilchano C, Schneider K, Turrión B., Forteza J., Saavedra J., Moyano A., Memoria final del Proyecto STEP/CEE: Nutrient cycling in degenerate natural forests in Europe in relation to their rehabilitation, CSIC/University of Salamanca, Salamanca, 1992, 201 pp.

[15] Gallardo J.F., Egido J.A., González M.I., Rico M., Santa Regina I., Gallego H., Martín A., Menéndez I., Moreno G., Schneider K., Turrión B., Saavedra J., Nutrient cycles in chestnut ecosystems of Sierra de Gata (western-central Spain), in: Romane F. (Ed.), Biological Criteria for Sustainable Developments in Natural Degenerate Forests of Mediterranean Europe: A Case Study of Chestnut Ecosystems, CNRS, Montpellier, 1994, pp. 23–44.

[16] Gallardo J.F., Martín A., Santa Regina I., Nutrient cycling in deciduous forest ecosystems of the Sierra de Gata mountains: aboveground litter production and potential nutrient return, Ann. Sci. For. 55 (1998) 749–769.

[17] Gallardo J.F., Santa Regina I., Harrison A.F., Howard D.M., Organic matter and nutrient dynamics in three ecosystems of the Sierra de Béjar mountains, Acta Oecol. 16 (1995) 447–459.

[18] Hernández I.M., Gallardo J.F., Santa Regina I., Dynamic of organic matter in forests subject to a Mediterranean semi-arid climate in the Duero Basin, Acta Oecol. 13 (1992) 55–65.

[19] Khanna P.K., Ulrich B., Ecochemistry of temperate deciduous forests, in: Röhrig E., Ulrich B. (Eds.), Ecosystems of the World. 7. Temperate Deciduous Forests, Elsevier, Amsterdam, 1991, pp. 121–163.

[20] Krivonosova G.M., Yanova G.N., Verveyko Y.I., Composition of precipitation and inputs of chemical elements into the soils of the Western forest steppe of the Ukraine, Agrokhimiya 5 (1990) 130–134.

[21] Lemee G., Recherches sur les écosystèmes des réserves biologiques de la forêt de Fontainebleau. IV. Entrées d'éléments minéraux par les précipitations et transfert au sol par le pluviolessivage, Oecol. Plant. 9 (1974) 187–200.

[22] Likens G.E., Bormann F.H., Pierce R.S., Eaton J.S., Johnson N.M., Biogeochemistry of a Forested Ecosystem, Springer Verlag, New York, 1977, 148 pp.

[23] Lindberg S.E., Lovett G.M., Richter D.D., Johnson D.W., Atmospheric deposition and canopy interaction of major ions in a forest, Science 231 (1986) 141–145.

[24] Lossaint P., Influence de la composition chimique des litières forestières sur la vitesse de décomposition, thèse, Univesity of Strabourg, 1953, 107 pp.

[25] Mangenot F., Toutain F., Les litières, in: Pesson P. (Ed.), Actualités d'écologie forestière, Gauthier-Villars, París, 1980, pp. 3–69.

[26] Martín A., Reciclado de bioelementos a través de la hojarasca en ecosistemas forestales de la Sierra de Gata (Sistema Central español), thesis, University of Salamanca, 1995, 356 pp.

[27] Martín A., Rapp M., Santa Regina I., Gallardo J.F., Leaf litter decomposition dynamics in some mediterranean deciduous oaks, Eur. J. Soil Biol. 30 (1994) 119–124.

[28] Martín A., Santa Regina I., Gallardo J.F., Interaction between litter and soil epipedons in forest ecosystems of the Sierra de Gata mountains, Province de Salamanca, Spain, Arid Soil Res. Rehabil. 10 (1995) 299–305.

[29] Martín A., Gallardo J.F., Santa Regina I., Aboveground litter production and bioelement potential return in an evergreen oak (*Q. rotundifolia*) woodland near Salamanca, Ann. Sci. For. 53 (1996) 811–818.

[30] Martín A., Gallardo J.F., Santa Regina I., Long-term decomposition process of leaf litter from *Quercus pyrenaica* forest across a rainfall gradient (Spanish Central System), Ann. Sci. For. 54 (1997) 191–202.

[31] Miller H.G., Cooper J.M., Miller J.D., Effect of nitrogen supply on nutrients in litter fall and crown leaching in a stand of Corsican pine, J. Appl. Ecol. 13 (1976) 233–248.

[32] Miller H.G., Miller J.D., Cooper J.M., Transformation in rainwater chemistry on passing through forested ecosystems, in: Coughtrey M., Martin M., Unsworth M. (Eds.), Pollutant Transport and Fate in Ecosystems, Blackwell, Oxford, 1987, pp. 171–180.

[33] Moreno G., Balances de agua y nutrientes en rebollares (*Quercus pyrenaica* Willd.) de la vertiente salmantina de la Sierra de Gata, thesis, University of Salamanca, 1994, 470 pp.

[34] Moreno G., Gallardo J.F., Cuadrado S., Deposición atmosférica de bioelementos y su modificación por la cubierta vegetal en bosques de *Quercus pyrenaica* de la Sierra de Gata (Salamanca), in: Gallardo J.F. (Ed.), Biogeoquímica de ecosistemas, Junta de Castilla y León, Valladolid, 1994, pp. 201–215.

[35] Moreno G., Gallardo J.F., Ingelmo F., Hernández J., Soil water budget in four *Quercus pyrenaica* forests across a rainfall gradient, Arid Soil Res. Rehabil. 10 (1996) 65–84.

[36] Moreno G., Gallardo J.F., Schneider K., Ingelmo F., Water and bioelement fluxes in four *Quercus pyrenaica* forests along a pluviometric gradient, Ann. Sci. For. 53 (1996) 625–639.

[37] Parker G.G., Throughfall and stemflow in the forest nutrient cycle, Adv. Ecol. Res. 13 (1983) 57–134.

[38] Pires A.L., Portela E., Martins A., Nutrient cycling in chestnut groves in the Tras-Os-Montes region, in: Romane F. (Ed.), Biological Criteria for Sustainable Developments in Natural Degenerate Forests of Mediterranean Europe: A Case Study of Chestnut Ecosystems, CNRS, Montpellier, 1994, pp. 9–22.

[39] Potter C.S., Ragsdale H.L., Swank W.T., Atmospheric deposition and foliar leaching in a regenerating Southern Appalachian forest canopy, J. Ecol. 79 (1991) 97–115.

[40] Rapp M., Cicle de la matière organique et des éléments minéraux dans quelques écosystèmes méditerranéens, CNRS, Paris, 1971, 184 pp.

[41] Rodá F., Biogeoquímica de las aguas de lluvia y drenaje en algunos ecosistemas forestales del Montseny, thesis, Universidad Autónoma of Barcelona, 1983, 428 pp.

[42] Santa Regina I., Gallardo J.F., Biogeochemical cycles in forests of the Sierra de Béjar: return of bioelements in rainfall, Acta Oecol., Oecol. Plant. 10 (1989 433–438.

[43] Santa Regina I., Gallardo J.F., San Miguel C., Ciclos biogeoquímicos en bosques de la Sierra de Béjar (Salamanca, España): 2. Retorno potencial de bioelementos por medio de la hojarasca, Rev. Écol. Biol. Sol. 26 (1989) 155–170.

[44] Santa Regina I., Gallardo J.F., San Miguel C., Ciclos biogeoquímicos en bosques de la Sierra de Béjar (Salamanca, España). 3. Descomposición de la hojarasca, Rev. Écol. Biol. Sol. 26 (1989) 407–416.

[45] Santa Regina I., Rapp M., Martín A., Gallardo J.F., Nutrient release dynamics in decomposing leaf litter in two Mediterranean decidous oak species, Ann. Sci. For. 54 (1997) 747–760.

[46] Stevens P.A., Hornung M., Hughes S., Solute concentration fluxes and major nutrient cycles in a Mataure Stitka-Spruce plantation in Beddgelert forest, North Wales, For. Ecol. Manag. 27 (1989) 1–20.

[47] Tukey H.B., The leaching of substances from plants, Annu. Rev. Plant Physiol. 21 (1970) 305–324.

[48] Van Breemen N., Visser W.F.J., Pape T.H., Biogeochemistry of an oak-woodland ecosystem in the Netherlands affected by acid atmospheric deposition, Agric. Res. Repp., PUDOC, Wageningen, 1989, 197 pp.