

Organic matter and nitrogen dynamics in a mature forest of common beech in the Sierra de la Demanda, Spain

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Abstract – Aboveground biomass, litterfall, leaf weight loss due to decomposition, N return and seasonal leaf N dynamics were studied in the Sierra de la Demanda, Spain, a Mediterranean climatic zone. The forest ecosystem considered was a climax beech (*Fagus sylvatica* L.) forest. Aboveground biomass was estimated by cutting and weighing seven trees from a beech stand according to diameter classes, recording the categories of trunk, branches and leaves. The results indicate a total biomass of 132.7 Mg ha⁻¹. The litterfall was 4682 kg ha⁻¹ yr⁻¹, although variations from year to year were observed, mostly due to water stress in summer. Greater *K* (Jenny's constant) and *K_o* (Olson's constant) values were obtained for total litter than for leaves alone. It is possible that the mean soil humidity might not be a limiting factor in the decomposition process and that this effect would be due to the distribution of rainfall rather than to the total amount of precipitation together with elevated temperature and airing of the holorganic soil horizon. The leaf N contents of beeches growing in the Sierra de la Demanda were studied, relating the contents to other structural stand characteristics. For this, N was analysed in shed leaves, in leaf biomass and in leaves decomposing on a test plot in the "Tres Aguas" beech forest. Leaf nitrogen contents were measured over a vegetative cycle in the above beech forest. Finally, leaf nitrogen contents were studied in thirty beech stands in the Sierra de la Demanda located at different altitudes. Annual nitrogen accumulation in leaf biomass was 79.4 kg ha⁻¹ yr⁻¹, of which 22.9 kg ha⁻¹ yr⁻¹ were returned to the soil substrate through shedding and 2.1 kg ha⁻¹ yr⁻¹ were actually incorporated into the soil. Nitrogen cannot be a limiting factor for the development of the beech stands studied because all of them surpassed the leaf deficiency threshold. Only other factors such as soil texture and structure or silvicultural treatment have a decisive effect on the production of the stand studied. The correlations for leaf nitrogen contents and the structural stand characteristics explored revealed that leaf nitrogen was only slightly correlated with the mean height of the trees at the plot.

aboveground biomass / litterfall / weight loss / nitrogen / forest ecosystem

Résumé – Dynamique de la matière organique et de l'azote dans une hêtraie de la Sierra de la Demanda (Espagne). La biomasse aérienne, la retombée de litière, la perte de poids de feuilles en décomposition, le retour et la dynamique saisonnière de l'azote des feuilles, ont été estimés dans une hêtraie (*Fagus sylvatica* L.) de la Sierra de la Demanda, (Espagne). La biomasse a été estimée par coupe et pesée de sept arbres selon la distribution des diamètres. Les poids des troncs, branches et feuilles ont été mesurés. Les résultats indiquent une biomasse totale de 132,27 Mg ha⁻¹. La chute de litière est de 4682 kg ha⁻¹ an⁻¹, cependant on a observé des variations inter-annuelles, principalement dues au stress hydrique estival. Les index de décomposition de Jenny (*K*) et Olson (*K_o*) sont plus élevés pour la litière totale que pour les feuilles seulement. L'humidité moyenne du sol n'est pas un facteur limitant du processus de décomposition. Les teneurs en azote dans les feuilles ont été mesurées pour la biomasse totale, et au cours de la décomposition, pendant un cycle végétatif, et dans les feuilles de trente parcelles de hêtre. L'accumulation annuelle d'azote dans les feuilles de la biomasse fut de 79,4 kg ha⁻¹ an⁻¹ dont 29,9 kg ha⁻¹ an⁻¹ retournent au sol par la chute de litière et 2,1 kg ha⁻¹ an⁻¹ sont incorporés

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annuellement au sol. L'azote ne semble pas être le facteur limitant dans les parcelles de hêtraie étudiées, d'autres facteurs comme la texture, la structure du sol ou le traitement sylvicole, interviennent dans l'explication des variations observées. Les corrélations entre les contenus en azote et les caractéristiques structurelles des parcelles indiquent que seulement l'azote est corrélé avec la hauteur moyenne des arbres.

biomasse aérienne / retombée de litière / perte de poids / azote / écosystème forestier

1. INTRODUCTION

Aboveground litter plays a fundamental role in the nutrient turnover and in the transfer of energy between plants and soil, the source of the nutrient being accumulated in the uppermost layers of the soil. This is particularly important in the nutrient budgets of forest ecosystems on nutrient-poor soils, where to a large extent the vegetation depends on the recycling of the nutrients contained in the plant detritus [86].

The primary net productivity of forest vegetation is subject to external environmental factors such as soil and climate, and to inherent factors such as age and the kind of tree-cover [77]. Plants retain a substantial part of their production in perennial structures, (trunks, branches, roots, etc.) whose nutritive elements form the mineral mass of the phytocenosis [20].

The production of litter is intimately related with the soil-climatic factors of the zones in such a way that the total mass due to shedding is directly proportional to the fertility of the soil [23]. Root biomass and turnover are difficult to estimate, owing to the difficulty of performing measurements [94].

Nutrient release from decomposing litter is an important internal pathway for the nutrient flux in forested ecosystems. Nutrients may be released from litter by leaching or mineralisation [90]. The rate at which nutrients are released depends on several factors, as indicated in [85]: the chemical composition of the litter, the structural nature of the nutrients in the litter matrix, the microbial demand for the nutrient, and the availability of exogenous sources of nutrients. Litter release factors include litter quality [2, 10, 11, 26, 53], macro- and micro-climatic variables [51] and microbial and faunal biotic activity [71]. Litter quality affects not only the rates of mass loss, but also the patterns and rates of nutrient immobilization or release. Climatic factors influencing litter decomposition rates include soil temperature [22, 36, 48, 57, 96]; and soil moisture [35]. Soil fertility is directly related to the activity of decomposers [15, 97].

Together with water and phosphorus, nitrogen may be one of the limiting elements in the productivity of Mediterranean forests. Its importance lies in both its structure and in its composition in different types of

communities since the element affects the development of ecosystems and the processes occurring therein [59].

The nitrogen content of the leaf organs of forest systems decreases throughout the vegetative cycle, significant differences being observed between winter and the other three seasons. Leaf nitrogen contents decrease before abscission and are transferred to the ligneous organs. This general tendency of nitrogen to decrease at the end of the vegetative cycle in leaves (retranslocation) before they have been shed has been reported by several authors [11, 31, 55, 56, 60, 67, 75, 76, 82, 83, 89].

Seasonal variations are very important for the period of leaf litter collection for later analysis, although such analyses only reflect a given point of the nutrient cycle, corresponding to a given period of the year and also to a given state of development of the trees, linked to their age. It is therefore of interest to know the variations occurring in mineral composition with the age of the trees or, preferably, with the age of their organs [75, 81].

The aim of the present work was to quantify and determine the temporal and spatial distribution of the organic matter and to establish the return of nitrogen in the southern climax beech forests of the Sierra de la Demanda (Spain), characterized by their low production.

2. MATERIALS AND METHODS

2.1. Site description

The experimental zone is located in part of the Sierra de la Demanda in the province of Burgos (Spain). The topography is mountainous; its Palaeozoic massif is located on the Northwest flank of the Iberian Range. Its coordinates are: 42°20' N, 4°10' E and, chorologically, the area lies in the Mediterranean Region, Carpetano-Ibérico-Leonesa province, Ibérico-Soriano sector [72].

The "Tres Aguas" beech (*Fagus sylvatica* L.) forest is a naturally regenerating forest with a density of 523 trees ha⁻¹, consisting of 300 young trees (4–20 cm DBH) and the rest adults, reaching >1 m in diameter (*figure 1*). The soil has a wide range of depths, the clay content increasing with depth, and can be classified as Humic Acrisol [24]. This and other soil characteristics are indicated in *table 1*.

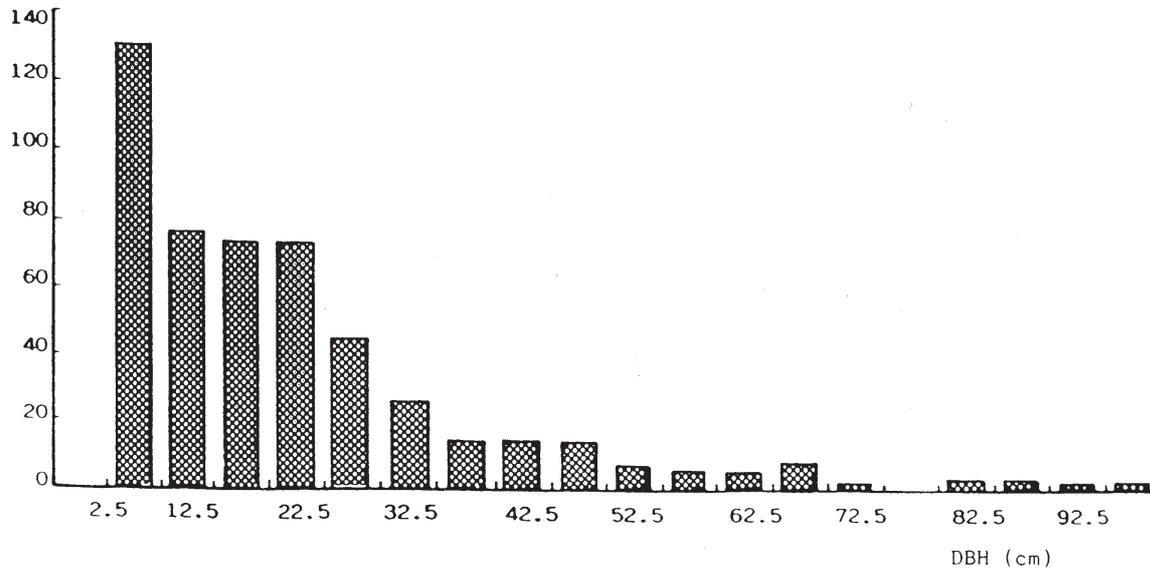


Figure 1. DBH class distribution in the beech stand.

Table I. Characteristics of the forest stand.

Plot characteristics	Tres aguas
Elevation (m)	1100
Geology	State
Soil units	Humic Acrisol
Humus type	Mull
Soil pH (Ah)	5.6
O.M. (%)	16.1
C/N	15.5
C.E.C. (C mol kg ⁻¹)	21.3
Available P ₂ O ₅ (mg kg ⁻¹)	43.5
Density (N ^o of trees ha ⁻¹)	523
Basal area (m ² ha ⁻¹)	25.7
Mean height (m)	20–22
Long-term mean precipitation (mm yr ⁻¹)	890
Mean annual temperature (°C)	12.4

O.M.: Soil organic matter; C.E.C.: Total cation exchange capacity.

The climate in the study area is attenuated meso-Mediterranean and becomes sub-Mediterranean with increasing altitude (1100 m). Figure 2 shows the ombrothermic temperature and precipitation diagrams of the site; a period of summer drought typical of Mediterranean climates is patent [19].

The general data from the Pradoluengo weather station, located near to the beech plot at 960 m altitude, referring to 18 years from 1961 to 1980, give an annual mean temperature of 12.4 °C, the means of the absolute monthly maxima and minima being 35.1 and 6.5 °C, respectively. The annual mean rainfall recorded for the above period was 895 mm and annual mean evapotranspiration was 705 mm (345 mm for summer). The mean duration of the dry period is two summer months per year, and the duration of the cold period six months (7 °C).

On comparing the distribution of the trees according to their diameter classes, the beech forest is distributed in such a way that the smallest trees are the most common. This behaviour reflects their structural characteristics such as stand age, degree of maturity and management [81].

2.2. Methods

Seven *Fagus sylvatica* trees representative of different DBH classes (figure 1) were felled to establish their aboveground biomass. Each tree harvested was divided into trunk, branches and leaves. The trunks were separated into sections, according to their height (from 0–1.30 m;

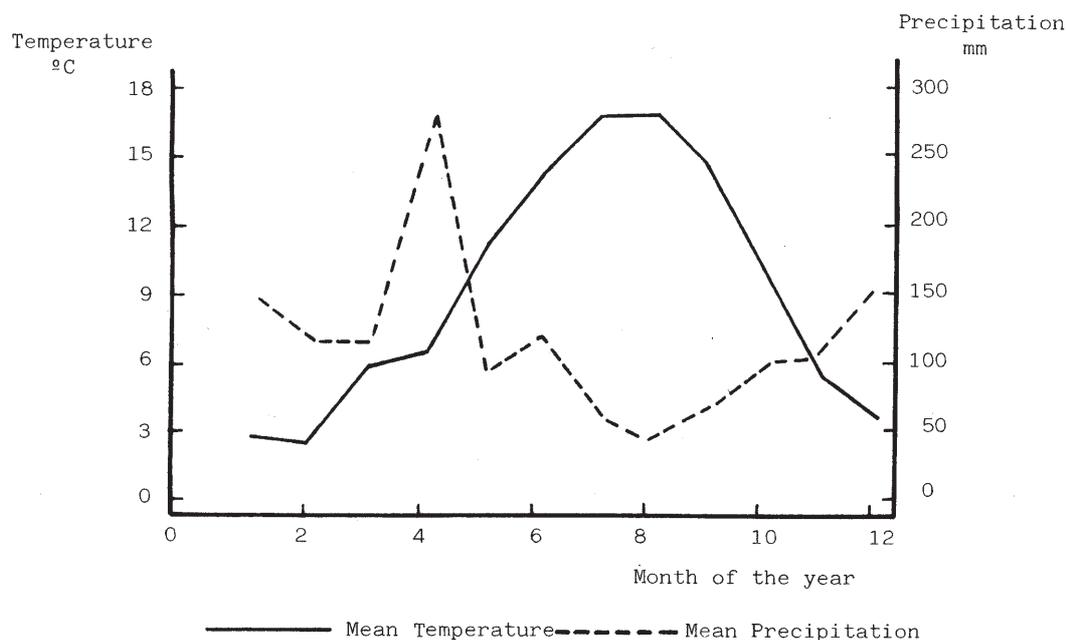


Figure 2. Diagram of the monthly average temperature and pluviometry (three years).

3 m; 3–5 m; 5–7 m; and so on) and weighed in the field. The wood was separated from the leaves.

Fifteen litter traps with a diameter of 50 cm and a height of 100 cm were randomly distributed on the experimental site during a three-year period. The litter was removed monthly and the material collected subdivided into different respective plant organs (branches, leaves, fruits and flowers). In the laboratory, the samples were air-dried, ground, homogenised and mass was expressed on a surface area basis (ha).

Leaf decomposition dynamics were assessed in litterbags made of nylon with a pore diameter of 1 mm and a 400 cm² surface area. Each litterbag contained 5.0 g of recently fallen beech leaves. Forty-five litterbags were placed over the holorganic horizon distributed in three different locations of the plot. The experiment started in December 1990, every 2 months, during 30 months, 3 bags, 1 from each of the 3 locations, were collected. Additionally, litter samples were collected from a 50 × 50 cm area of the (holorganic horizon) to determine the indices of natural decomposition [80].

For the evaluation of litter dynamics, we used the coefficient K from [39], which relates the humus and the above-ground litter. K is a constant for any given ecosystem and is defined by

$$K = A / (A + F)$$

where A is the leaves or litter returned to the soil annually and F is the leaves or litter accumulated on the surface soil before the period of massive litter shedding.

The losses in the annual production (P) of leaf or litter can be established from

$$P = AK.$$

Calculation of the decomposition coefficient K_o [61] is obtained with

$$K_o = A / F$$

The parameter K_d , a coefficient of accumulation of leaf or litter, was also determined

$$K_d = (A - P) / A.$$

The data were subjected to a one-way statistical analysis of variance algorithm (ANOVA). The regression curves were also established according to the best r^2 . Linear regressions were performed with the natural logarithm of the mean dry matter remaining at each time to calculate K , a constant representing the overall fractional loss rate for the period studied, following the formula:

$$\ln(X_t / X_0) = Kt$$

where X_t and X_0 are the masses remaining at time t and time zero, respectively [61]. The organic matter

remaining on the soil was calculated immediately before the annual litter fall peak.

Seasonal N variations

Monthly leaf samples were collected during a vegetative cycle at three height levels (lower, medium and higher parts of the trees) within nine representative trees of different DBH classes of the stand. The samples were taken to the laboratory for later analysis of N.

Thirty beech trees in the Sierra de la Demanda were selected following the phenological map of the zone [92]. Three groups of 10 forests were selected according to different elevations where the growth of *Fagus sylvatica* in the Sierra de la Demanda was best. The first elevation encompassed the trees situated between 1600 and 1700 m; the second one those situated above 1400 m, while the third elevation corresponded to the trees below 1000 m altitude. This method permitted us to equate the period of activity of the forest for each group and hence the trees' real period of growth and production. During July, 100 leaves from the lowest branches of 10 trees with DBH values between 10–20 cm were collected from the thirty beech stands studied. The leaves were taken from the branches directly and stored at -20°C until analysis of total nitrogen.

At the same time, homogeneous plots of 10×25 m were set up on 17 of the beech stands studied and the following structural population characteristics were studied:

- The number of trees;
- The DBH of all the trees;
- The DBH of the dominant tree;
- Mean tree height;
- Distance to closest neighbour.

Laboratory procedures

Subsample biomass and litter fractions and decomposing leaves were ground and then used for chemical analysis according to the procedure proposed in [18]. The organic matter was cleaned and dried at 80°C to constant weight to determine the moisture content [81]. After mineralisation of the plant material, total N was determined by the Kjeldhal method or with a Macro-N Heraeus analyser.

3. RESULTS

For all seven trees, leaf weights were correlated with DBH using regression analysis (*table II*). Several regression equations were calculated for all the trees studied, with the finding that the power regression equation was the one that had the best coefficient of determination.

Table II shows the diameter at breast height (DBH, 130 cm)-biomass relationship in the different compartments of the trees.

Table III summarises the overall set of dendrometric and weight characteristics of the 7 felled trees, the total

Table II. Diameter at breast height (DBH, 130 cm)-Biomass ratio in the different trees of the forest stand.

Beech trees	Regression equations $n = 7$	r^2
DBH-total biomass	$y = 1.4160 x^{0.426}$	0.98
DBH-trunk biomass	$y = 0.0894 x^{2.4679}$	0.99
DBH-branch biomass	$y = 0.0317 x^{2.3931}$	0.89
DBH-leaf biomass	$y = 0.0145 x^{1.9531}$	0.98

Table III. Dendrometric and weight characteristics of the felled trees.

DBH (cm)	Height (m)	Leaves Biomass (kg)	Branches Biomass (kg)	Trunk Biomass (kg)	Total Biomass (kg)	Trees (ha^{-1})	Total Biomass (Mg ha^{-1})
4.0	6.1	0.2	1.1	2.7	4.0	87	0.3
8.5	9.0	1.1	5.1	15.3	21.5	70	1.5
16.2	12.4	2.7	17.4	90.1	110.2	60	6.6
17.6	19.8	3.1	19.7	138.3	161.1	77	12.4
26.0	17.0	6.5	79.4	271.7	363.5	77	28.0
26.8	18.9	12.2	103.1	277.6	387.0	74	28.6
34.5	18.4	17.0	179.4	512.1	708.5	78	55.3
Biomass Mg ha^{-1}		3.4	30.7	98.6	132.7		132.7
% total biomass		2.5	23.1	74.4	100.0		

aboveground biomass in Mg ha^{-1} , and the percentage of different fractions of the trees with respect to total biomass according to diameter classes.

The trunk is the part of the tree that most contributes to the total biomass. This has a value of 74.4%, with 98.6 Mg ha^{-1} . The branches follow a similar pattern to the trunks (table III), with mean percentage of 23.1% and 30.7 Mg ha^{-1} . In the beech stand, the contribution of the leaves to the total biomass is 2.5%, with $3.4 / \text{Mg ha}^{-1}$ and an r^2 correlation coefficient of 0.97.

Table IV shows the average nitrogen contents in several tree fractions of the seven trees felled. The values are means of the seven trees and the maximum and minimum values established.

3.1. Litter fall

The amounts of yearly litter fall for leaf litter and total litter (leaves + wood + reproductive organs + indeterminate organs) are indicated in table V.

Table V shows the average annual production values obtained for the different fractions together with the percentages that these represent in the whole set of litter. The importance of knowing the amounts of each of these fractions is evident since the return of N to the soil will follow different recycling patterns, which may overlap in space and time.

As in the case of most forest ecosystems, the leaves comprise the most important fraction, $2897 \text{ kg ha}^{-1} \text{ yr}^{-1}$, representing 61.9% of the total contribution. The branches fraction occupies the second most important place in the amount contributed to the soil: $823 \text{ kg ha}^{-1} \text{ yr}^{-1}$ and 17.6%. Only the fruit and "others" fractions represent important amounts: $576 \text{ kg ha}^{-1} \text{ yr}^{-1}$ and 12.3% and $351 \text{ kg ha}^{-1} \text{ yr}^{-1}$ and 7.5% respectively.

3.2. Litter decomposition

The decomposition indices were determined for leaves only and for total litter (table VI). Considering both total litter and leaves separately, higher K and K_0 decomposition indices were observed for total litter than for leaves alone. The annual loss constant is defined by the equation: $K = A / (A + F)$ where A is annual litterfall mass and F is the mass of litter on the soil. All these values are given in table VI: 0.29 for leaves and 0.37 for total litter.

At the end of the decomposition period (two years), the loss of dry matter for leaf litter was 40% (table VII).

Table IV. Average of nitrogen contents in the different tree fractions of the seven felled trees.

	Leaves	Branches	Trunk
N %	1.90 ± 0.12	0.32 ± 0.04	0.21 ± 0.04
Min. Max.	1.76–2.13	0.25–0.38	0.18–0.30

Table V. Litter production of beech stand and partial percentage of different litter fractions.

Litter fraction	$\text{kg ha}^{-1} \text{ yr}^{-1}$	%
Leaves	2897 ± 482	61.9
Branches	823 ± 136	17.6
Fruits	576 ± 98	12.3
Flowers	35 ± 8	0.7
Others	351 ± 68	7.5
Total	4682 ± 699	100.0

Table VI. Leaf decomposition index estimated in the litterfall and its accumulation.

Organs	A	F	$A \pm F$	K'	K	P
Leaves	2897.0	7229.0	10126.0	0.29	0.34	842.6
Litterfall	5385.9	9068.8	14454.7	0.37	0.46	1992.8

A: Annual production; F: Accumulated leaves on the soil; K' : Jenny's decomposition constant; K : Olson's decomposition constant; P: Losses.

3.3. Nitrogen dynamics

3.3.1. Nitrogen content at the "Tres Aguas" beech forest

a) The total nitrogen/DBH ratio was considered. In this ratio, an r^2 of 0.98 was obtained and the equation defining this ratio was:

$$N = 0.00042 \text{ DBH}^{2.2946},$$

where N is given in $\text{kg ha}^{-1} \text{ yr}^{-1}$ and DBH in cm.

It is possible to calculate a relationship between the nutrients returning to the soil in litter fall and the nutrients immobilised in biomass:

$$\frac{\text{Leaf fall nitrogen (kg ha}^{-1} \text{ yr}^{-1})}{\text{Biomass nitrogen (kg ha}^{-1} \text{ yr}^{-1})}$$

This relationship can be defined as turnover, and has a value of 0.29.

Table VII. Dry matter loss and nitrogen content in litterbags at beech stand.

Days	Leaves remaining %	N (g kg ⁻¹)	N (g)	Initial N*(%)
0	100	10.2 ± ²	1.02 ± ^{0.2}	100.0
116	91	11.2 ± ²	1.02 ± ^{0.2}	99.9
179	90	11.5 ± ³	1.04 ± ^{0.3}	101.5
241	90	11.5 ± ³	1.04 ± ^{0.3}	101.5
272	91	12.8 ± ⁴	1.16 ± ^{0.5}	114.2
334	82	10.1 ± ²	0.83 ± ^{0.2}	81.2
365	77	9.9 ± ²	0.76 ± ^{0.1}	74.9
393	73	14.0 ± ³	1.02 ± ^{0.2}	100.2
453	74	12.5 ± ⁴	0.93 ± ^{0.2}	90.7
515	71	9.4 ± ²	0.66 ± ^{0.2}	65.4
582	71	13.1 ± ⁵	0.93 ± ^{0.3}	91.2
610	69	12.6 ± ⁴	0.86 ± ^{0.2}	85.2
672	67	12.6 ± ⁴	0.84 ± ^{0.1}	82.8
707	60	15.2 ± ⁶	0.91 ± ^{0.3}	89.4

* Percentage of the weight in relation to initial nitrogen.

b) Relative and absolute N enrichments in the beech leaf litterbags were observed throughout the leaf decomposition process (*table VII*). The value reached 15.2 g kg⁻¹ at the end of the second experimental cycle while at the end of the first year it was almost identical to the initial values. However, in absolute values, the greatest amount of nitrogen -1.16 g with respect to the initial 1.02 g - was found after the first nine months.

With knowledge of the potential return and the bioelement transfer rate of the litter, the minimum amounts of nitrogen that the beech forest ecosystem can return annually to the surface of the soil (A_n horizon) were calculated. The leaf turnover results are given in *table VIII*.

3.3.2. Seasonal patterns of nitrogen contents at the "Tres Aguas" beech forest

Table IX shows the results of the nitrogen content analysis in green leaves at the plot during the vegetative cycle studied (1991). The highest concentration of nitrogen in the leaves was determined in the spring and sum-

mer months, during initial leaf growth. Thereafter, they decreased due to retranslocation during the autumn period of leaf fall.

3.3.3. Leaf nitrogen in the thirty beech stands

Table X shows the characteristic mean structural population values obtained for the beech stands in the Sierra de la Demanda. The table also offers the values of nitrogen in the thirty sampling zones; these range between 2.66 % and 2.05 % in the leaf organs.

Study of the correlations for all the variables (*table XI*) shows that leaf nitrogen contents are only slightly correlated with the mean height of the beech stands studied (0.3805).

4. DISCUSSION

4.1. Total biomass

The procedure most commonly used to estimate the biomass in forest ecosystems involves destructive techniques in combination with the application of regression equations to manage the data. The best fitted model is $Y = X^b$, where Y is biomass and X tree diameter at a height of 1.30 m. It should be stressed that this model is quite complicated; indeed some authors [5, 6, 87] have proposed corrections with a view to avoiding underestimations of the true values. This method has been used by several authors [69, 81].

The tree distribution in the beech stand is constituted by many trees in the lower classes and only a few in the upper ones, and the aboveground biomass obtained was 132 Mg ha⁻¹ (*table III*).

The references found in the literature report conflicting data, depending on the forest species studied, the age of the stand, the kind of soil, and the environmental conditions. In populations of *Fagus sylvatica* [17] established an above-ground biomass of 319 Mg ha⁻¹; [62], for an age 50 years, reported 164 Mg ha⁻¹; in gymnosperms of 50-year-old communities [74] described a

Table VIII. Nitrogen ponderary characteristics in the "Tres Aguas" beech forest.

	Biomass (kg ha ⁻¹)	Litterfall (kg ha ⁻¹ yr ⁻¹)	Decomposition (kg ha ⁻¹ yr ⁻¹ Annual Weight)	% Loss	Leaf fall nitrogen (kg ha ⁻¹) Biomass nitrogen (kg ha ⁻¹)
Leaves	4160.0	2897.0	666.0	22.5	
Nitrogen	79.4	22.9	2.1	9.3	0.29

Table IX. Variation in nitrogen contents in the beech forest studied during a vegetative cycle. Translocation index IR: nitrogen content in green leaves/nitrogen content in litterfall leaves.

	Trees	Height	Isophene	DDBH	DheightD	NITROC	MDBH	M Height
Tree	1.0000							
Height	0.4818	1.0000						
Iso	-0.3729	-0.9549	1.0000					
DDBH	-0.5930	-0.3378	0.2237	1.0000				
Dheight	0.5604	-0.7731	0.6732	0.6297				
NITRO	-0.0533	0.0018	-0.1529	0.0053	-0.0304	1.0000		
C	-0.7792	-0.6068	0.4830	0.7451	0.7754	0.1408	1.0000	
MDBH	0.5125	-0.6923	0.5774	0.3981	0.6886	0.3805	0.6725	1.0000
M Height								

Table X. Characteristic mean structural stand values and nitrogen content in the thirty sampling zones.

Plots	Altitude (m)	Isophene	Tree (h)	Medium DBH (cm)	Dominant DBH (cm)	Nitrogen content (%)	Medium height (m)	Dominant height (m)
1. Alarcia	1130	5	400	27.0	35.8	2.3	14.8	6.50
2. Monte Bajero	1120	5	432	27.3	36.8	2.5	22.8	25.40
3. Monte Bajero	1200	5	352	39.9	54.5	2.7	24.8	34.80
4. Las Zarras	1290	5				2.1		
5. Montelacelda	1650	5	2416	14.1	24.0	2.2	12.0	17.80
6. Los Castillejos	1440	2				2.2		
7. Tejera	1425	3	432	33.5	45.0	2.4	18.3	22.60
8. Tejera	1380	3	1200	24.0	28.0	2.2	14.1	16.70
9. Genciana	1380	3				2.4		
10. Gilas	1140	3				2.5		
11. Valle Urbión	1480	5	448	25.1	41.2	2.4	15.0	22.50
12. Vallegoria	1600	3	1616	22.2	39.2	2.6	14.5	16.70
13. Valhondo	1600	2	1792	14.2	22.0	2.5	12.2	13.40
14. Valhondo	1420	2				2.3		
15. Ardubira	1610	3	928	23.0	42.5	2.3	14.5	18.50
16. Ardubira	1640	2				2.4		
17. Ticumbea	1500	2	1260	24.0	46.0	2.4	11.3	16.20
18. Ticumbea	1490	3	832	21.5	39.0	2.3	15.3	16.60
19. Las Siemprevivas	1600	3	784	19.6	42.5	2.3	13.6	18.00
20. Zarzabala	1610	2	1360	20.7	30.9	2.6	14.7	16.90
21. Zarzabala	1620	2				2.3		
22. Zarzabala	1690	2	944	23.1	53.0	2.5	12.4	18.20
23. Las Zarras	1690	2				2.1		
24. Las Zarras	1460	2				2.1		
25. Paulejas	1460	3				2.3		
26. Paulejas	1260	3				2.1		
27. Las Rasadas	1300	5	752	25.4	36.8	2.1	16.4	22.90
28. Las Rasadas	1160	5	562			2.1	21.0	
29. Tres Aguas	1130	5				2.2		
30. Tirón	1200	5				2.3		

range of 92–169 Mg ha⁻¹, while [91] reported 102–136 Mg ha⁻¹ in stands of 50–90 years of age.

The trunk is the part of the tree that most contributes to the total biomass. This has a value of 75%. A value of

100.7 Mg ha⁻¹ was obtained (*table III*). In *Fagus sylvatica* [17] obtained 89.1% with respect to total aboveground biomass. On estimating trunk biomass according to DBH (*table II*) we obtained a correlation coefficient of $r^2 = 0.99$.

Table XI. Correlations between the different variables and the nitrogen content ($P < 0.005$ not significant).

Date		3/05/91	3/06/91	11/07/91	8/09/91	13/10/91	11/11/91	11/12/91
Maximum Temperature (°C)		20.0	23.50	30.00	9.50	29.50	22.0	15.00
Minimum Temperature (°C)		3.50	0.50	4.50	2.00	2.00	4.00	-12.00
Green leaves N (g kg ⁻¹)	Beech Budding beginning		26.9	25.1	24.9	19.3	10.7	litterfal
Litterfal Litterfall N (g kg ⁻¹)	Beech		25.8	20.4	18.9	7.9	6.8	
IR	Beech		1.04	1.23	1.31	2.44	1.57	

On exploring the biomass of branches with respect to DBH (*table II*), the correlation coefficient obtained was $r^2 = 0.89$.

The contribution of the leaves to total biomass was 3.1%, with 4.5 Mg ha⁻¹ and an r^2 correlation coefficient of 0.97.

The literature reports different values: in *Fagus sylvatica* [17] calculated 2.7 Mg ha⁻¹ or 0.8% of leaves; [45] reported 3.5 Mg ha⁻¹ or 0.8% of leaves; [45] reported 3.5 Mg ha⁻¹ and [46] 3.1 Mg ha⁻¹; in *Juniperus occidentalis*, [29] reported 20% of needles; in *Pinus sylvestris*, [73] established values of 9.6% and 5.5% of needle biomass with respect to total forest biomass.

4.2. Litterfall

As in the case of most forest systems, the leaves comprise the most important fraction, representing 61.9% of the total contribution. This shows that the forest systems in question are immature, since according to [42], especially in the beech stand, maturity is reached when leaf shedding tends to account for 50% of the total.

Leaf abscission follows a seasonal trend, coinciding with that observed for the overall production. The formation of tissues triggers a mobilisation of nutrients towards the leaves from older organs, which in turn leads to the abscission of older leaves and twigs [43].

The early senescence observed in the forest studied in the present work is probably a direct consequence of the summer drought in Mediterranean regions, which according to [66] triggers the early senescence of plant organs.

The differences appearing between the estimated leaf biomass and the leaf litter are mostly related to the date of biomass sampling. Canopy leaf mass varies during the season. If biomass estimation is carried out in summer, at the peak of leaf growth, the results could explain the differences in leaf litter amounts. In addition, leaf litter was only sampled from September to December, underestimating some possible earlier leaf-litterfall.

Branches occupy the second most important place in the amount of aboveground biomass within the whole set of litter components (823 kg ha⁻¹ yr⁻¹ in the beech plot, representing 17.6% (*table V*)).

The fraction corresponding to the fruits displays a period of maximum return. This fraction represents 12.3%. The flowers and other fractions are small with respect to total litterfall.

4.3. Litter decomposition

In the beech forest ecosystem, greater K and K_0 indices were obtained for total litter than for leaves alone. Similar values have been reported by [14, 22] and [58]. The values reported by [49] were higher and those of [27] lower.

The litterbags may have hindered free access by the mesofauna [40] and may have created microclimatic conditions that delayed the decomposition rate. Also, the F values may be underestimated, since it is often difficult to distinguish decomposing leaves from other plant remains, especially when the latter (plant remains) are very small. F had fairly low values that cannot be entirely explained by the presence of twigs and barks rich in lignin substances [51] and low in N [8, 50].

During the first 3 months of the decomposition period, a noteworthy loss of weight was observed. The precipitation recorded created conditions conducive to the leaching of water-soluble substances from the decomposing material. During the ensuing summer period the process ceased, and a second and slower stage of degradation occurred that affected molecules with stronger bonds. During this phase, soil microorganisms play a more active role. Finally, a new acceleration of decomposition was observed in weight loss during the autumn-winter period.

Lemée and Bichaut [46] reported an annual weight loss between 15% and 40% in *Fagus sylvatica* and *Pinus sylvestris* while [9] reported a value of 31% and [75] a value of 27%.

It may be seen that the leaf litter decomposition constant is lower than that of the total litter decomposition. Despite this, however, the total litter includes more wood lignin (twigs, branches) than the leaves or needles alone [51, 53].

4.4. Nitrogen dynamics

Nitrogen, an essential element for plants, seemed to be present in sufficient but never limiting amounts on the beech plots in the Sierra de la Demanda [93]. The increased availability of nitrogen accelerated the turnover of this element throughout the system but not its accumulation in perennial organs. Unlike oak species [3, 37, 41, 47, 84], beech and other hardwood species do not exhibit differential storage and concentrations of nutrients in the different parts of the tree.

The relationship between biomass production and nutrient recycling in leaf litter has been studied by [16, 33] and [64]. These studies indicate that nutrient-poor habitats may be dominated by slow growing species with a high recycling rate [7].

A mean nitrogen concentration of 1.9% was estimated in the leaf biomass, obtaining 79.4 kg ha^{-1} . During the observation period, the annual mean content returning to the soil substrate was $22.9 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (*table I*). This value is similar to that reported by other authors in fagaceous forests [21, 68]. It is necessary to consider possible losses of nitrogen due to volatilisation and denitrification, such as the volatilisation of ammonia in senescent leaves [25] or relative increases in litter when it becomes humified, or due to microbial nitrogen fixation from the atmosphere [12]. Accordingly, extreme caution should be exercised when attempting to establish definitive balances for this element.

Absolute and relative enrichments in the content of nitrogen in the beech leaves were observed throughout the leaf decomposition process (*table VII*).

Increases in the concentration of nitrogen, both absolute and relative, have been reported by several authors [1, 13, 14, 28, 30, 63, 75]. Microbial fixation of atmospheric nitrogen contributes to this absolute increase since there is an abundant source of carbon-energy in the leaf litter and suitable humidity and temperature for nitrogen fixers [79].

Berg and Staaf [11] reported a certain relationship between the decomposition process and the accumulation of nitrogen. Low N concentrations in soil give rise to larger increases in N during the initial stages of decomposition. It is possible, however, that the abundance of polyphenolic substances, could exert an

inhibitory action on fungal growth, leading to slow hyphal growth in decomposing leaves and hence low immobilization by the fungal biomass [54].

Our results indicate that the process of decomposition in a Mediterranean climatic zone follows rates similar to those seen in more temperate situations.

Nitrogen is incorporated into the leaf litter to form humus mainly through two routes: the fixation of atmospheric nitrogen and precipitation throughfall from the tree canopies [32, 44]. Attiwil [4] concluded that forests with low N contents seem to be more resistant to losses of N. This observation is supported by the present findings. Nitrogen in microbial biomass in litter estimated by the fumigation-extraction method in a warm-temperate forest gave values between 0.1 and 0.5 mg N g^{-1} litter (Gallardo and Schlesinger, unpublished data). This amount would explain a significant percentage of immobilized nitrogen in some species.

The decomposition indices of leaves when confined to litterbags were lower than those obtained under natural conditions (22.5% in the litterbags; $K' = 0.29$ and $K = 0.34$ under natural conditions (*table VI*).

Accordingly, it is possible to establish an annual accumulation of nitrogen in the leaf biomass of $79.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$, of which $22.9 \text{ kg ha}^{-1} \text{ yr}^{-1}$ return to the soil substrate through litterfall and $2.1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ are actually incorporated into the soil (*table VIII*).

During spring and summer the growth phase is accompanied by intense mitotic activity due to cellular activity and a strong demand for nutrients, in particular N [74, 78]. Thereafter, the contents of this element decrease throughout the vegetative cycle and above all during the period of senescence (autumn). It is therefore evident that a retranslocation to perennial tissues occurs before total abscission.

The retranslocation index was also established during the same period (*table IX*) (that is, the relationship established between the N contents in green leaves and the contents of this element in shed leaves). As is logical, the highest IR index was found at the beginning of autumn and the lowest in spring.

Accordingly, the periods showing the highest percentages of N may be intimately correlated with those in which leaf shedding is premature, in many cases considerably distanced from senescence phenomena and more related to climatic effects (winds, freezing, etc.). In this case, the concentrations of the element will be closer to those of the leaves retained on the trees [31].

Efficient retranslocation of essential elements is a typical characteristic of the climax phase of any forest ecosystem [65, 88, 95]. Accompanied by a reduction in nutrient restitution (through leaf litter) and requirements, this retranslocation affords the ecosystem a certain independence from the soil medium and the possibility of good management of the available elements [52].

The study reported by [38] points to a negative correlation between the monthly amount of leaves undergoing abscission and the nitrogen concentration during that month (October).

The seasonal patterns of nitrogen in the green leaves at "Tres Aguas" (table X) again clearly reveal a decrease in the contents of the element from June, with 2.70%, to November, when the leaves of the trees still adhering to the branches only had 1.07% of the element. This value should be contrasted with that obtained for the same date from leaves that fell during shedding: 0.68%, the contents in the leaves decreasing in favour of an increase in nitrogen in branches and bark for the same date when abscission occurs. This has been reported by other authors [75].

ANOVA was performed with the results obtained and the characteristic structural population values (table XI); this showed that there were only significant differences between the three groups of beech studied (high, medium and low) as regards the dominant tree height variable, the beeches located at greatest altitude being the shortest ones. Altitude above sea level is strongly and negatively correlated (99%) with dominant tree height. Regarding leaf N, no differences among the three groups studied are apparent [93].

Study of the leaf N contents of thirty beech stands in the Sierra de la Demanda reveals that the limits of leaf N are above 0.80% d.m. in all cases analysed [83]. However, a certain negative correlation is seen between the nitrogen contents of the lowest beech stands already in contact with the *Festuco heterophyllae-Quercus pyrenaicae* oak series.

In a similar study of 66 populations of beech in France during August, Lemée [45] reported between 2.44 and 1.77% of leaf nitrogen. This author sets the leaf N limit at 0.8%, 1.30% being the optimum value for avoiding repercussions on tree growth.

5. CONCLUSIONS

The early senescence observed in the forest studied is probably a direct consequence of the summer drought in Mediterranean regions.

During the first three months of decomposition period, a noteworthy loss of weight was observed. During the ensuing summer period the process ceased, and a second and slower stage of degradation occurred. Finally a new acceleration of decomposition was established in weight loss during the autumn-winter period.

The decomposition indices of leaves when confined to litterbags were lower than those obtained under natural conditions. The litterbags may have hindered free access to the mesofauna and may have created microclimatic conditions that delayed the decomposition rate.

The seasonal patterns of nitrogen in the green leaves at "Tres Aguas" reveal a decrease in the contents of the element from June, with 2.70%, to November, when the leaves of the trees still adhering to the branches only had 1.07% of this element. The content in the leaves decreasing in favour of an increase in nitrogen in branches for the same date when abscission occurs.

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