

Nutrient cycling in a natural beech forest and adjacent planted pine in northern Spain

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Summary

Above-ground leaf biomass, leaf litterfall, leaf weight loss due to decomposition, redistribution of leaf litter and C and N return to the soil, and seasonal leaf nutrient dynamics have been studied in the Sierra de la Demanda, Spain, a Mediterranean climatic zone. The tree species considered were a climax beechwood (*Fagus sylvatica* L.) at 'Tres aguas' and planted Scots pine (*Pinus sylvestris* L.) at 'La Rasada'. The above-ground biomass was estimated by cutting and weighing seven trees from each site according to their diameter classes, recording the categories of trunk, branches and leaves. The carbon and nitrogen contents in the different fractions were also analysed. The calculated total biomass ranged from 132.7 Mg ha⁻¹ in the beech stand to 152.1 Mg ha⁻¹ in the pine stand, and leaf biomass from 3.4 Mg ha⁻¹ to 7.0 Mg ha⁻¹ in the beech and pine, respectively. The C : N (carbon : nitrogen) ratio was greater in the pine forest leaves. The total litterfall was 5791 kg ha⁻¹ per year in the pine forest and 4682 kg ha⁻¹ per year and the leaf litterfall was 2917 kg ha⁻¹ per year and 2897 kg ha⁻¹ per year in the pine and beech sites, respectively. The annual mean amount of N returning to the soil substrate was 29.9 kg ha⁻¹ per year on the beech and 23.3 kg ha⁻¹ per year on the pine. Weight loss of leaf litter due to decomposition was monitored for 2 years in the two forest ecosystems studied. The results indicated that weight loss was similar at the end of the experimental period in the two forest stands: 40 per cent in beech and 43 per cent in pine. Jenny's decomposition index (*K*) and Olson's decomposition index (*K_O*) were higher for the pine stand than for the beech stand. The dynamics of total C and N throughout the study period was similar on both experimental plots. The evolution of N in green leaves follows the same pattern in beech and pine stands. The highest leaf N concentration was observed in the spring and summer months, during initial leaf growth. Thereafter, it decreased due to retranslocation during the period of leaf-fall in autumn.

Introduction

The adaptations of perennial plants to different levels of nutrients in soils are often studied in terms of the efficiency of nutrient use, where efficiency is the relationship between biomass production and the loss of nutrients in leaf litter

(Gray, 1983; Boerner, 1984; Pastor *et al.*, 1984). Thus, nutrient-poor habitats may be dominated by slow-growing species with a high recycling rate (Berendsen and Aerts, 1987).

The resorption of nutrients or their removal from senescent leaves and their accumulation or storage in the perennial parts of trees is a common

phenomenon (Ryan and Bormann, 1982). This retranslocation of nutrients may supply a significant demand of the nutritional requirements for the production of new biomass (Sollins *et al.*, 1980; Chapin and Kedrowski, 1983; Meier *et al.*, 1985; Lim and Cousens, 1986). Similarly, retranslocation is a beneficial process because the tree is less subject to fluctuations in nutrient availability in the soil and losses due to biomass decomposition decrease.

In short-lived plants, biomass production per unit of absorbed nutrient is simply the inverse of the concentration of the nutrient in question in the tissues of the plant; however, in long-lived plants some bioelements undergo reabsorption (called retranslocation or resorption) from senescent tissues, which allows the plants to use the same units of absorbed nutrient to produce several vegetative organs (Vitousek, 1982). In this sense, Blair (1988) has stated that the definition of NUE depends on the ecosystem in question. As a result, nutrient concentrations only afford a very approximate idea of the efficiency of nutrient use in forest plots. In these cases, it seems more appropriate to estimate efficiency by measuring net primary production (aerial and underground) per unit of nutrient absorbed over the year. Under controlled conditions, such measurements are possible; however, they are not very feasible under field conditions (Birk and Vitousek, 1986). As an alternative, Vitousek (1982) defined NUE as the amount of organic matter shed by the plant (as litterfall and root return) plus that stored permanently in the plant (in the wood), divided by the amount of nutrients lost (as litterfall, leaching from the canopy or through root return) plus the nutrients remaining stored owing to the growth of the vegetation (uptake, according to Cole and Rapp, 1981). Accordingly, Vitousek (1982, 1984) defined the NUE in a forest as the amount of dry matter in litterfall per unit of that nutrient contained in it (i.e. the inverse of the concentration of the nutrient). Later, the litterfall production:litterfall nutrient ratio was used as an index of nutrient efficiency (NUE; production per unit of resource uptake), distinguishing this from resource response efficiency, defined as the production per unit of resource availability. Nevertheless, soil nutrient parameters sometimes bear no relationship to plant nutrient uptake (usually in both fertile and very unfertile soils).

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 (Santa Regina, 1987; Santa Regina *et al.*, 1997a).

In any type of forest a massive fall of leaf litter occurs every year in a given season, leading to a large accumulation of organic material on the surface. This, in turn, gives rise to the formation of humus whose structure and composition typifies each forest ecosystem. All this organic matter immediately undergoes successive catabolic transformations of greater or lesser intensity, leading to the release of biogenic elements necessary for producer survival and to the formation of humic substances, which are important in the development of soil structure and the cation exchange capacity of the soil (Santa Regina, 1987; Santa Regina and Tarazona, 1995).

Nutrient release from decomposing litter is an important internal pathway for nutrient flux in forested ecosystems. Nutrients may be released from litter by leaching or mineralization (Swift *et al.*, 1979). Nutrient release from decomposing litter affects ecosystem primary productivity (Blair, 1988), since these nutrients thus become available for plant uptake and are not lost from the system.

The rate at which nutrients are released depends on several factors, as indicated by Seastedt (1984): the chemical composition of the litter, the structural nature of the nutrient in the litter matrix, the microbial demand for the nutrient, and the availability of exogenous sources of nutrients. Litter release factors include litter quality (Fogel and Cromack, 1977; Aber and Melillo, 1980; Berg and Staaf, 1980, 1981; Melillo *et al.*, 1982), macro- and micro-climatic variables (Meentemeyer, 1978) and microbial and faunal biotic activity (Reichle, 1977). Several authors have defined litter quality in terms of initial N concentrations, the C : N ratio, initial lignin concentrations, and the lignin : N ratio. 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 (Lousier and Parkison, 1976; Heal, 1979; Edmonds, 1980; Moore, 1986; Witkamp, 1966); and soil moisture (Hayes, 1965). Soil fertility is directly related to the activity of decomposers (Bocock and Gilbert, 1957; Witkamp and Van der Drift, 1961).

According to Thiebaut (1984), southern beech trees which thrive in adverse conditions are a different breed from those found in Euro-Siberian Europe. Their resistance to summer droughts points to a possible adaptation of this genotype to the characteristics of many Spanish mountains for future reforestation.

The main aim of the present work was to estimate the nutrient-use efficiency and leaf nutrient dynamics in two forest formations in the Sierra de la Demanda (Burgos, Spain): a climax beech forest (*Fagus sylvatica* L.) and a replanted pine forest (*Pinus sylvestris* L.) in order to better understand the recycling of elements associated with the organic matter and to establish a general model for nutrient management processes under a Mediterranean climate.

Methods

Site description

The experimental site is located in the Sierra de la Demanda mountains in the provinces of Burgos and Logroño in northern Spain. The topography is mountainous and its Paleozoic massif is located on the northwest flank of the Central Iberian Range. Its coordinates are 42°20' N, 4°10' E.

The climate in the study area is attenuated meso-Mediterranean and becomes sub-Mediterranean with increasing altitude (1000 m). Figure 1 shows the ombrothermic diagrams of the site and the plots studied; the summer drought typical of Mediterranean climates is readily seen.

The weather station at Pradoluengo, at an altitude of 960 m, has an annual mean temperature of 12.4°C, the average of the minima and of the absolute monthly maxima being 6.5°C and 35.1°C, respectively. The annual mean rainfall recorded during the study period was 895 mm (data from 1961 to 1980). Mean annual evapotranspiration was 705 mm (345 mm in June, July and August). The mean duration of the dry period

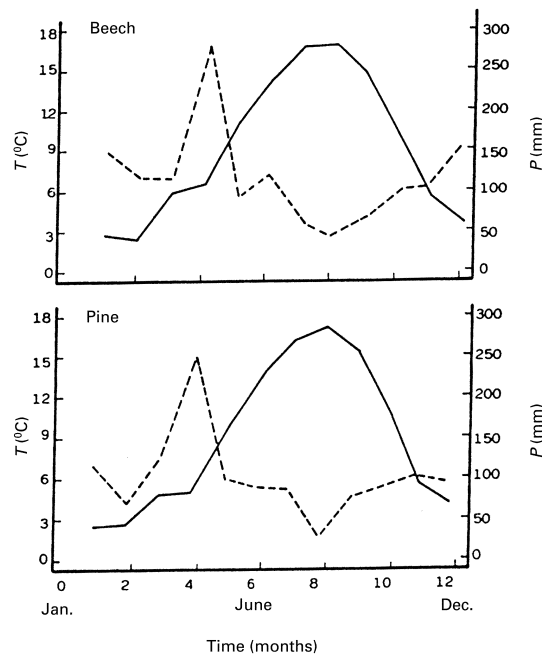


Figure 1. Diagram of monthly mean temperature (T ; continuous lines) and precipitation (P ; dashed lines) (1986–1988).

in the area is 2 months per year (summer) and the duration of the cold period is 6 months per year ($+7^{\circ}\text{C}$) (Santa Regina and Tarazona, 1995).

The Mediterranean index of the area is 3.1 (Rivas-Martínez, 1987). The thermicity index is 195, corresponding to the lower supra-Mediterranean bioclimatic horizon.

In the Sierra de la Demanda, beech forests are distributed in small islets, each occupying some 5000 ha at the bottom of valleys and on N aspects at altitudes between 900 and 1600–1700.

During the cold season, the beech forest displays a lower thermal fluctuation ($+3^{\circ}\text{C}$) than the Scots pine forest and has a higher maximum temperature ($+1^{\circ}\text{C}$). Table 1 shows the values obtained at the sites studied and those obtained from the National Weather Station at Pradoluengo, near the experimental plots.

Relative humidity in the beech forest is always from 1–1.5 per cent lower than in the pine forest. Accordingly evapotranspiration is higher in the pine forest (Table 2).

The beech stand at 'Tres Aguas' is a mature

Table 1: Monthly average maximum ($\bar{X} T_{\max}$) and minimum ($\bar{X} T_{\min}$) temperature ($^{\circ}\text{C}$) and precipitation (P) at three sites in Spain

Area	$\bar{X} T_{\max}$ ($^{\circ}\text{C}$)	$\bar{X} T_{\min}$ ($^{\circ}\text{C}$)	P (mm a^{-1})
Pradoluengo*	16.3	7.4	886
Tres Aguas (beechwood)	13.9	4.3	1630
La Rasada (pinewood)	13.2	4.6	1257

* Data from the official meteorological station of Pradoluengo for a period of 18 years.

Table 2: Average of the maximum ($\bar{X} T_{\max}$) and minimum ($\bar{X} T_{\min}$) temperature and percentage of the maximum ($\bar{X} H_{\max}$) and minimum ($\bar{X} H_{\min}$) relative humidity of the air during the study period

Forest type	$\bar{X} T_{\max}$ ($^{\circ}\text{C}$)	$\bar{X} T_{\min}$ ($^{\circ}\text{C}$)	Temperature variation ($^{\circ}\text{C}$)	$\bar{X} H_{\max}$ (%)	$\bar{X} H_{\min}$ (%)
Pinewood (summer)	17.5	7.8	(-2,+34)	88.9	51.1
Beechwood with leaves	17.9	7.3	(-4,+33)	87.6	48.3
Pinewood (winter)	7.7	0.7	(-11,+16)	90.5	56.7
Beechwood without leaves	8.8	0.6	(-10,+14)	89.0	52.8

forest, with a density of 526 trees ha^{-1} , comprising 300 young trees (4–20 cm diameter at breast height (d.b.h.)) and the rest adult, the latter of which have diameters greater than 1 m in some cases (Figure 2). Mean height ranges from 20 to

22 m. The estimated mean age of the plot is 50 years. The soil varies considerably in depth, clay contents increasing with depth and is classified as humic acrisol (FAO, 1973).

The Scots pine at La Rasada were planted in a

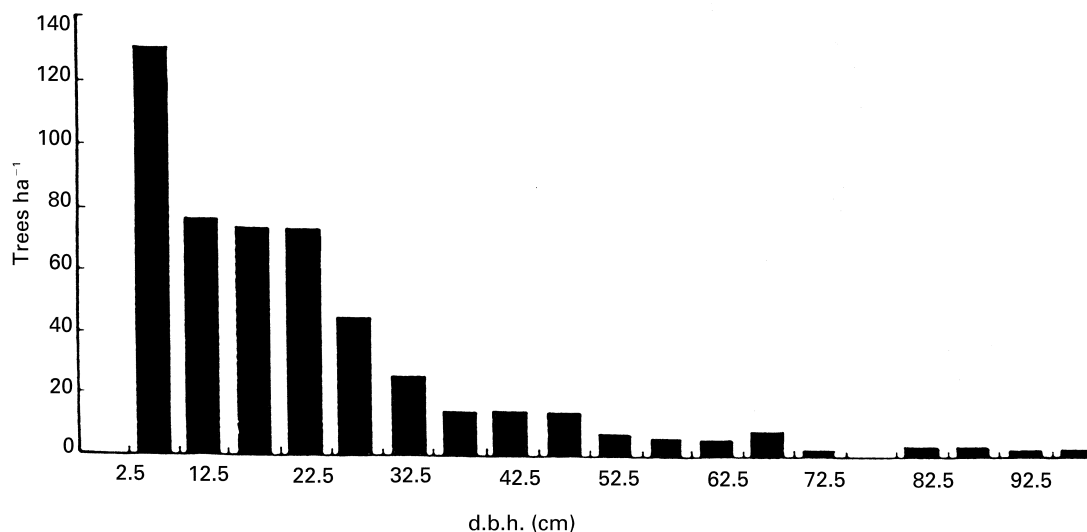


Figure 2. Diameter at breast height (d.b.h.) class distribution in the beech forest.

reforestation project initiated 50 years ago on land suitable for beech. Mean tree density at this plot is 581 trees ha⁻¹ with a predominance of trees with diameters between 30 and 40 cm (292 trees) (Figure 3). Their mean height is approximately 15 m. The soil of this plot varies in depth and has a low clay content, an acid (pH 5.2) and desaturated character and is classified as a humic cambisol (FAO, 1973).

On comparing the distribution of the trees according to their diameter classes, the Scots pine forest is seen to display a typical Gaussian bell-shaped curve in which most trees are concentrated around the intermediate diameter class (32.5–37.5 cm). The beech forest is distributed in such a way that the smallest trees are the most representative, and their distribution is closer to a negative exponential. This different behaviour reflects structural differences such as age, degree of maturity and management (Santa Regina *et al.*, 1997a).

Experimental design and installation

The d.b.h. of all trees on each experimental plot was measured and their distributions in diameter classes were calculated for the two sites (Figure

4). Fourteen representative trees of different diameter classes were felled to establish their above-ground biomass: seven *F. sylvatica* and seven *P. sylvestris*. Each tree thus harvested was divided into trunk, branch and leaves. The trunks were separated into sections, according to their height (0–1.30, 1.30–3, 3–5 and 5–7 m . . .) and weight. The wood was separated from the leaves (Santa Regina *et al.*, 1997a). The leaf subsamples were brought to the laboratory for further analyses: moisture content after drying to constant weight at 80°C. For each tree, leaf weights were correlated with d.b.h. using regression analysis (Table 3). Several regression equations were calculated for all the trees studied, indicating that the power regression equation was the one that had the best determination coefficient.

Fifteen litter traps were randomly distributed on the two experimental sites. Leaf samples were collected monthly or every 2 weeks during the period of most rapid litterfall. In the laboratory, the samples were air-dried, ground, homogenized and expressed on a surface area basis (ha).

Leaf decomposition dynamics were assessed in nylon litter-bags with a pore diameter of 1 mm and a surface area of 400 cm². Each litter-bag contained 5 g of beech leaves or pine needles

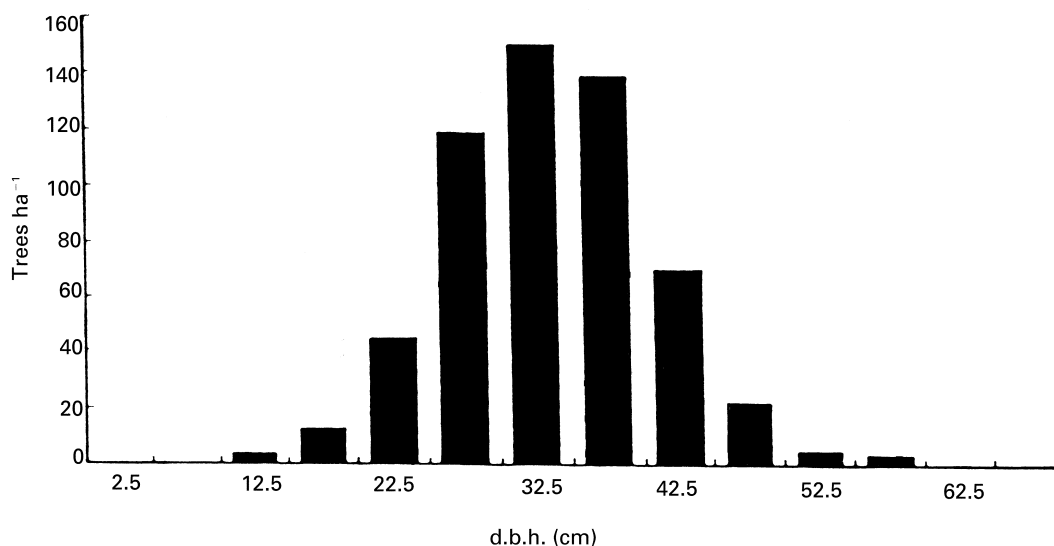


Figure 3. Diameter at breast height (d.b.h.) class distribution in the pine forest.

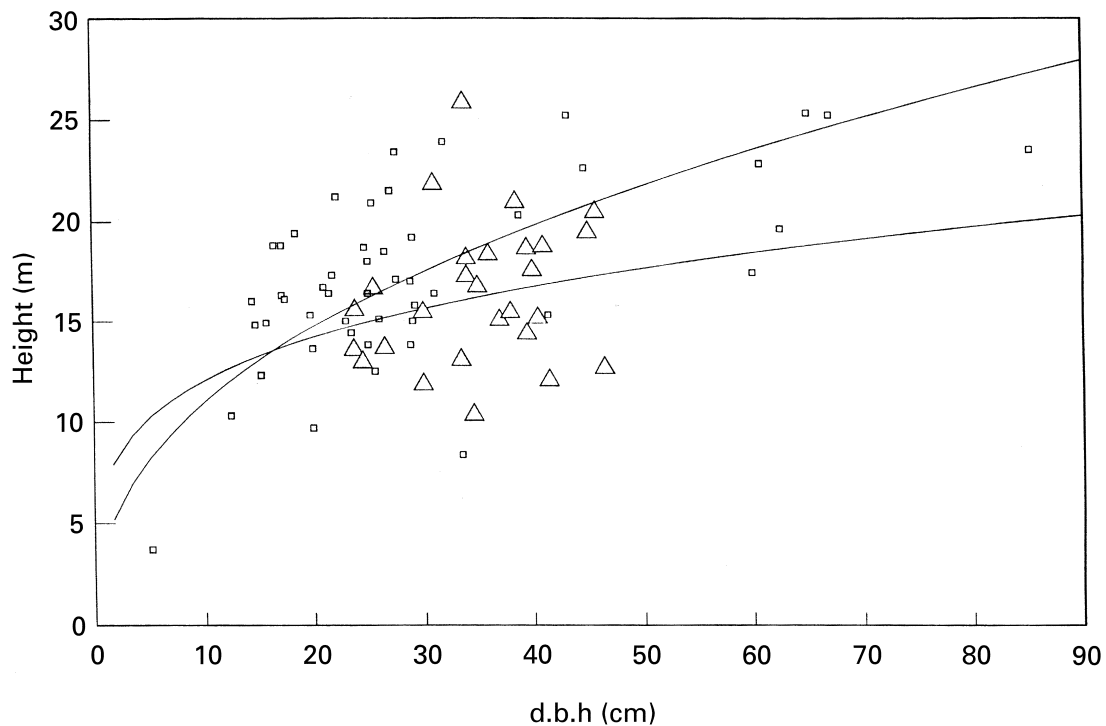


Figure 4. Relationships between d.b.h. and height in both forests studied (squares = beech; triangles = pine).

Table 3: The d.b.h.–biomass relationship in the different trees of the two forest ecosystems

Stand	Regression equations	r^2
Beech forest		
d.b.h.–total biomass	$y = 1.4160x^{0.426}$	0.98
d.b.h.–leaf biomass	$y = 0.0145x^{1.9531}$	0.98
d.b.h.–C	$y = 0.0435x^{2.4472}$	0.99
d.b.h.–N	$y = 0.0004x^{2.2946}$	0.98
Pine forest		
d.b.h.–total biomass	$y = 1.9410x^{0.238}$	0.99
d.b.h.–leaf biomass	$y = 81.4780e^{1.384x}$	0.97
d.b.h.–C	$y = 72.6630e^{2.1267x}$	0.99
d.b.h.–N	$y = 0.4418e^{1.9633x}$	0.98

collected from each canopy site, (dried at room temperature and their humidity determined at 80°C) and the bags were placed over the litter in three different locations at each plot. Forty-five litter-bags were placed in each ecosystem, distributed in three groups depending on the topography of each site.

Every 2 months, over a complete vegetative cycle, three bags per plot – one from each of the three locations – were collected. Also, for each site, litter samples were taken from a 50 × 50 cm area of the ground in order to determine the indices of natural decomposition in each forest.

The coefficient K (Jenny *et al.*, 1949) considers the humus present in the soil system and the remains produced during shedding. It is constant for any given ecosystem and is defined by:

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

where A is the leaf litter returning annually to the soil and F is the leaf litter accumulated on the forest soil before the period of massive shedding of plant organs.

The losses in the annual production of leaf litter can be established from:

$$P = A K$$

where P is the annual loss of leaf litter and A and K are as described above.

Calculation of the decomposition coefficient (K_O) (Olson, 1963) is done with:

$$K_O = A/F$$

with A and F as above

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

Seasonal N variations

Monthly leaf samples were collected during a vegetative cycle at three tree heights from several representative trees of different d.b.h. classes of the two stands. The samples were taken to the laboratory for later analysis of N.

Laboratory procedures

Representative leaf biomass, leaf litter and decomposing leaves were ground and then used for chemical analysis according to the procedure proposed by Chapman and Pratt (1979). After mineralization of the plant material, total N was determined by the Kjeldahl method or with a Macro-N Heraeus analyser, and total C was determined using a Wosthoff carmograph.

The chemical results, expressed as percentages of plant tissue, were correlated with leaf biomass or leaf litterfall values to determine the amount of nutrients in the leaf biomass or leaf litterfall on a given surface area. Data were subjected to a one-factor 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 of the overall fractional loss rate for the study period, following the formula:

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

where X_t and X_0 are the mass remaining at time t and time zero, respectively (Olson, 1963). Both masses remaining on the soil were calculated immediately before the annual litterfall peak.

Results

Above-ground leaf biomass

For each individual felled, measured and weighed tree, leaf biomass was determined using a single

regression equation between the d.b.h. and the above-ground leaf biomass, including all the trees from the two studied sites (Table 3).

Table 4 summarizes the weight and percentage biomass characteristics of the each plot studied representative of each population.

Figure 4 shows the d.b.h. : height ratio. The predictions give a maximum of 18 m approximately for the beech and 15 m for the pine.

Table 5 shows the average carbon (C) and nitrogen (N) contents and the C : N ratio in leaf fraction of the seven trees felled in the two plots studied. These values are the means of the seven trees and the maximum and minimum values established.

Leaf litterfall

The amounts of yearly litterfall for leaf litter and total litter, and C and N amounts are indicated in Table 6. Leaf litter production was very similar in both forests while total litter production was greater in the pine forest.

A mean N concentration of 1.9 per cent was estimated in the leaf biomass, giving an amount of 79.4 kg ha⁻¹ in the beech forest (Tables 7 and 8) and a mean N concentration of 1.25 per cent for the pine forest giving an amount of 140.7 kg ha⁻¹ (Tables 5 and 13). For C the amounts were 1901 kg ha⁻¹ and 5177 kg ha⁻¹ in the beech and pine forest, respectively.

The differences between the estimated leaf biomass and leaf litter are mostly related to the date of biomass sampling. Canopy leaf mass varies through the season. If biomass estimation is performed in summer, at the peak of leaf growth, this could explain the differences with the amounts of leaf litter. In addition, leaf litter

Table 4: Weight and percentage biomass characteristics of the two plots studied

	Leaves	Total biomass
Beechwood		
Biomass (Mg ha ⁻¹)	3.4	132.7
Total biomass (%)	2.5	100.0
Pinewood		
Biomass (Mg ha ⁻¹)	7.0	152.1
Total biomass (%)	4.6	100.0

Table 5: Mean of carbon (C) and nitrogen (N) contents and C : N ratio in the leaves of the seven felled trees in each forest studied

Site	C (%)	N (%)	C : N ratio
Beech forest			
Mean	45.7 ± 1.1	1.90 ± 0.12	24.2 ± 1.9
Min–Max	43.7–47.2	1.76–2.13	20.5–26.9
Pine forest			
Mean	46.0 ± 1.5	1.25 ± 0.12	37.0 ± 3.1
Min–Max	43.6–48.2	1.13–1.51	31.3–40.4

Table 6: Litterfall and amounts of carbon (C) and nitrogen (N) returning annually to the soil (kg ha⁻¹)

Litter fraction	Site	Organic matter	C	N
Leaves	Tres Aguas	2897	1419	12.9
	La Rasada	2917	1463	23.3
Total litter	Tres Aguas	4682	2294	39.8
	La Rasada	5791	2867	46.3

was only sampled from September to December, underestimating possible earlier leaf litterfall.

Leaf litter decomposition

Decomposition indices were determined for total litter in each forest ecosystem and for the leaves only of both plant species (Table 9). Considering both total litter and leaves separately, higher K and K_0 decomposition indices were observed in the pine forest than in the beech forest. However, the K index in the beech forest was higher for total litter than for leaves alone. The greatest losses were from the pine litter and the beech leaves.

The decomposition indices of leaves when confined to litter-bags were lower than those obtained under natural conditions (0.29 and 0.31 versus 0.37 and 0.46; Table 9). During the decomposition cycle, the loss of dry matter was 40 per cent in the beech forest and 43 per cent in the pine forest (Tables 10 and 11).

A loss of C was observed in both types of leaves throughout the decomposition process, at least as far as absolute values are concerned (Tables 7 and 8), although in relative terms certain transient increases were noted; these occurred in parallel

with the processes of humification and were more pronounced on the pine plot.

During the first 3 or 4 months of experimentation, a strong loss of C was observed in both forest ecosystems, accompanied by a weight loss. The latter was due to the higher rate of the overall decomposition process. In the beech forest 15 per cent was lost and in the pine forest 17 per cent.

Following this, slight losses were observed in the beech forest and a strong increase in the pine stand up until the beginning of the winter season (Tables 10 and 11). Such increases run parallel to the processes of humification (loss of hydroxyl and methoxyl groups and gains in aromaticity; Kononova, 1961; Flaig, 1971; Stevenson, 1982).

Seasonal patterns of nitrogen contents

Table 12 shows the results of the analysis of N contents in green and litterfall leaves at the two plots during the vegetative cycle studied. In the two stands, the highest leaf N concentration was observed in the spring and summer months, during initial leaf growth. Thereafter, they decreased due to retranslocation during the period of leaf fall in autumn.

NUTRIENT CYCLING IN BEECH AND PINE FORESTS

Table 7: Dry matter carbon (C) and nitrogen (N) contents in litter-bags placed in the beech stand

	Biomass (kg ha ⁻¹)	Litterfall (kg ha ⁻¹ a ⁻¹)	Biomass - litterfall (kg ha ⁻¹ a ⁻¹)	Decomposition		Leaf fall nitrogen (kg ha ⁻¹) Biomass nitrogen (kg ha ⁻¹)
				Annual weight		
				kg ha ⁻¹ a ⁻¹	loss (%)	
Leaves	4160	2897	651.8	22.5		
Nitrogen	79.4	22.9	56.5	9.3		
Carbon	1901	1419	482	28.8		0.29

Table 8: Dry matter, carbon (C) and nitrogen (N) contents in litter-bags placed in the pine stand

	Biomass (kg ha ⁻¹)	Litterfall (kg ha ⁻¹ a ⁻¹)	Biomass - litterfall (kg ha ⁻¹)	Decomposition		
				Annual weight		Leaf fall nitrogen (kg ha ⁻¹) Biomass nitrogen (kg ha ⁻¹)
				kg ha ⁻¹ a ⁻¹	loss (%)	
Leaves	11255	2917		525.1	18.0	
Nitrogen	140.7	23.3	117.4	9.5	40.6	0.17
Carbon	5177	1463	3714	338.0	23.1	

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Table 9: Litter and leaf decomposition indices in the two forest ecosystems

Ecosystem	A	F	A + F	K	K _O	P	K _d
Litter							
Beechwood	5386	9069	14 455	0.37	0.59	1.992	0.63
Pinewood	5791	6796	12 587	0.46	0.82	2.664	0.54
Leaves							
Beechwood	2906	7229	10 134	0.29	0.40	843	0.71
Pinewood	2418	5395	7 813	0.31	0.45	750	0.69

A, annual production; F, litter or leaves accumulated on the soil; K, Jenny's index; K_O, Olson's index; P, annual loss from fallen litter or leaves; K_d, coefficient of accumulation of fallen litter or leaves. The constants and parameters are according to the equations: $K = A/(A + F)$, $P = AK$, $K_O = A/F$, $K_d = (A - P)/A$.

Table 10: Changes in concentration and weights of nitrogen (N) and carbon (C) in the litter-bags placed in the 'Tres Aguas' beech forest

Day	Leaves (g)	C (%)	N (%)	C (g)	N (g)	Initial C*(%)	Initial N*(%)
0	100	53.2	1.02	53.2	1.02	100.0	100.0
116	91	50.5	1.12	46.0	1.02	86.4	99.9
179	90	49.7	1.15	44.7	1.04	84.0	101.5
241	90	49.4	1.15	44.5	1.04	83.6	101.5
272	91	49.2	1.28	44.8	1.16	84.2	114.2
334	82	48.5	1.01	39.7	0.83	74.7	81.2
393	73	49.5	1.40	36.1	1.02	67.9	100.2
453	74	46.1	1.25	34.1	0.93	67.2	90.7
515	71	50.6	0.94	35.9	0.66	67.5	65.4
582	71	46.6	1.31	33.1	0.93	62.2	91.2
610	69	47.1	1.26	32.5	0.86	61.1	85.2
672	67	47.3	1.26	31.7	0.84	59.6	82.8
707	60	49.8	1.52	29.9	0.91	56.1	89.4

* Percentage of the weight in relation to initial carbon or nitrogen.

Discussion

A clear divergence can be seen in the determination of the biomass of leaf organs. In the beech forest, the contribution of the leaves to total biomass is 2.5 per cent with 3.4 Mg ha⁻¹ (Table 4); in the pine forest these values are 4.6 per cent and 7.0 Mg ha⁻¹, with r^2 correlation coefficients of 0.97 for the beech and 0.88 for the pine forest (Table 4).

However, on establishing leaf biomass with respect to the d.b.h. parameter (Figure 5), the greatest productivity is also obtained for the beech forest.

The literature reports different values: in *F.*

sylvatica, Calamini *et al.* (1983) calculated 2.7 Mg ha⁻¹ or 0.8 per cent of leaves; Lemée (1974) reported 3.5 Mg ha⁻¹ and Lemée and Bichaut (1971) 3.1 Mg ha⁻¹; in *Juniperus occidentalis*, Gholz (1980) reported 20 per cent of needles; in *P. sylvestris*, Rodin and Bazilevich (1967) established values of 9.6 per cent and 5.5 per cent of needle biomass with respect to total forest biomass.

The average C content in the leaf biomass fraction of the seven felled trees was similar on both experimental plots (Table 5) and the correlation coefficients were the same: $r^2 = 0.99$. The small differences in the distribution of carbon in leaf biomass are similar to those reported for the quality of the substratum (Keyes and Grier, 1981).

Table 11: Changes in concentration and weights in litter-bags placed in the 'La Rasada' pine forest

Day	Leaves (g)	C (%)	N (%)	C (g)	N (g)	Initial C*(%)	Initial N*(%)
0	100	53.5	1.36	53.5	1.16	100.0	100.0
116	89	50.0	1.16	44.5	1.03	83.3	75.9
179	86	51.4	1.00	44.2	0.86	82.7	63.2
241	88	51.3	1.27	45.2	1.12	84.5	82.2
272	87	51.1	1.04	44.5	0.90	83.1	63.5
334	83	51.1	1.00	42.4	0.83	79.3	61.0
393	81	49.2	0.97	39.8	0.79	74.5	57.8
453	74	51.5	1.13	38.1	0.84	71.3	61.5
515	73	53.1	1.03	38.7	0.75	72.5	55.3
582	75	53.5	1.19	40.1	0.89	75.0	65.6
610	70	50.2	1.21	35.1	0.85	65.7	62.3
672	65	52.1	1.54	34.4	0.10	64.3	73.6
707	58	51.5	1.28	30.1	0.74	56.2	54.6
747	57	51.1	1.51	29.1	0.86	54.5	63.3

* Percentage of the weight in relation to initial carbon or nitrogen.

Table 12: Variation in nitrogen (N) content in the two forests during a vegetative cycle (temperature values are absolute for this period)

	3/05/88	3/06/88	11/07/88	8/09/88	13/10/88	11/11/88	11/12/88
Maximum temperature (°C)	20.0	23.5	30.0	29.5	29.5	22.0	15.0
Minimum temperature (°C)	3.5	0.5	4.5	2.0	2.0	4.0	-12.0
Green leaves (% N)							
Beech	Budding	2.69	2.51	2.49	1.93	1.07	Total
Pine	beginning	1.45	1.36	1.11	0.80	0.86	litterfall
Litterfall (% N)							
Beech		2.58	2.04	1.89	0.79	0.68	
Pine		1.38	1.22	0.99	0.59	0.64	

Larger differences are seen on comparing the total-N content in the leaf biomass of both forests if the total-N : d.b.h. ratio is considered (Table 5). In this ratio, correlation coefficients of 0.98 were obtained for the two plots. In a comparison of both species, the relative N contents were higher in the beech forest.

Leaf litterfall and return of C and N to the soil

Leaf litter production was very similar in the both forests while total litter production was somewhat higher in the pine forest.

The totals of the two elements analysed (C and N) were higher in the pine forest, particularly in the case of N (Table 6).

Nitrogen, the most essential element for plants, seemed to be present in sufficient and never limiting amounts in the beech plots in the Sierra de la Demanda. The increased availability of N accelerated the turnover of this element throughout the system and not its accumulation in perennial organs. Beech and other hardwood species do not exhibit differential storage and concentrations of nutrients in the different parts of the tree, unlike oak species (Albert and Prescoller-Tiefenthaler, 1992; Helmisaari, 1992; Jokela *et al.*, 1981; Lemoine *et al.*, 1988; Saur *et al.*, 1992).

The relationship between biomass production and nutrient recycling in leaf litter has been studied by Gray (1983), Boerner (1984) and Pastor *et al.* (1984). These studies indicate that

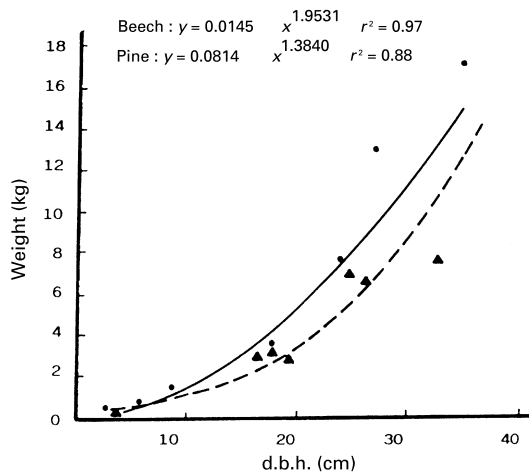


Figure 5. Leaf biomass in relation to the d.b.h. for individual trees of beech (filled circles and continuous line) and pine (filled triangles and dashed line).

nutrient-poor habitats may be dominated by slow growing species with a high recycling rate (Berendsen and Aerts, 1987).

It is possible to calculate a relationship between the nutrients returning to the soil in the litterfall and nutrients immobilized in the biomass:

$$\frac{\text{litterfall nutrients (kg ha}^{-1}\text{)}}{\text{biomass nutrients (K ha}^{-1}\text{)}}$$

This relationship can be defined as turnover or the rotation coefficient and has the following values for the two forests considered: Beech, C = 5.3, N = 13.5; Pine, C = 4.6, N = 18.4.

From the point of view of weight, N is the most important bioelement in forest litter. During the observation period, the annual mean content returning to the soil substrate was 12.9 kg ha⁻¹ on the beech stand and 23.3 kg ha⁻¹ on the pine stand (Table 6). These values are similar to those reported by other authors in fagaceous forests (Duvigneaud *et al.*, 1969; Rapp and Cabanettes, 1980). It is necessary to consider possible losses of N due to volatilization and denitrification, such as the volatilization of ammonia in senescent leaves (Farquhar *et al.*, 1979) or relative increases in litter when it becomes humified, or due to microbial N fixation from the atmosphere (Black, 1975). Accordingly, extreme caution should be exercised when attempting to establish definitive balances for this element.

Carbon was recycled in the same proportion at both sites, although the total amounts were different.

Leaf litter decomposition

Different decomposition indices were established considering the total leaf litter in each forest ecosystem or leaves alone of both plant species (Table 9). Considering both total leaf litter and leaves separately, higher *K* and *K_O* decomposition indices were observed in the pine forest than in the beech forest. However, the *K* index in the beech forest was found to be higher for total leaf litter than for the leaves alone, such that the greatest losses were estimated to occur from the pine leaf litter and the beech leaves. Similar values were reported by Bockock (1963), Gosz *et al.* (1973), Edmonds (1980) and O'Connell (1987); the values reported by Maheswaran and Attiwill (1987) are higher and those of Schlesinger (1985), Mitchell *et al.* (1986) and Gallardo and Merino (1993) are lower.

In both forest systems, greater *K* and *K_O* indices were obtained for total leaf litter than for leaves alone. This is possibly due to the fact that soil humidity is not a limiting factor in the decomposition process and the effect would be due to the distribution of rainfall rather than to its actual amount, together with temperature and the airing of the holorganic horizon of the soil, or more likely due to fact that non-foliage litter has higher C : N ratio.

It was also observed that the decomposition indices of leaves when confined to litter bags were lower than those obtained under natural conditions. The litter-bags may have hindered free access for the mesofauna (Bockock, 1964; Joergensen, 1991) and may have created microclimatic conditions that delayed the decomposition rate. It should also be noted that *F* may be underestimated since it is often difficult to distinguish decomposing leaves from other plant remains, above all when small sizes are involved; consequently, *F* was not fully counted. This can be checked since the values of the decomposition index (*K*) for total litter (Table 9) were fairly low and cannot be fully explained by the presence of twigs and bark rich in lignin substances (Meentemeyer, 1978) and low in N (Berg, 1988; Martín, 1992).

Towards the end of the first two years of observation, processes of humification and mineralization alternated on both plots, a loss of 44 per cent of the initial values being reached in both beech leaves and pine needles. These latter phases would be governed by the decomposition of lignin.

Enrichments in the N content in the pine needles and relative and absolute enrichments in beech were observed throughout the leaf decomposition process (Tables 10 and 11). No differences in N contents were seen along the cycle, perhaps because the climatic conditions were very similar since both forest ecosystems are close to each other. However, different partial behaviours are seen; these are affected by the physical medium and by the action of specific and broadly differing microflora and mesofauna. Increases in the N concentration, both absolute and relative, have been reported by several authors (Bocock, 1963; Aber and Melillo, 1980; Gloaguen and Touffet, 1980; Parmentier and Remacle, 1981; Garay *et al.*, 1986; Santa Regina, 1987; Blair, 1988; Hernández, 1989). Microbial fixation of atmospheric N contributes to this absolute increase since there is an abundant source of C-energy in the leaf litter and suitable humidity and temperature for N-fixers (Santa Regina *et al.*, 1986).

In any case, N is incorporated into the leaf litter to form humus mainly through two routes: one of them acts through the N-fixers themselves, using the C source of the leaf litter, and the other through leaf fall from the tree canopy (Gosz *et al.*, 1973; Lemée, 1974), which contaminates the underlying leaf litter. Attiwill (1968) concluded that forests with low N contents seem to be more resistant to losses of N. This observation is supported by the present findings, since in the pine forest, whose substrate is N-poor, mineralization was slower than in the beech ecosystem.

Berg and Staaf (1981) reported a particular relationship between the decomposition process and the accumulation of N. 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, typical of conifer residues (Millar, 1974), could exert an inhibitory action on fungal growth, leading to slow hyphal growth in decomposing leaves, and hence low immobilization by the fungal biomass.

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

Seasonal variations in N

Table 12 shows the results of the analysis of N contents in green leaves at the two plots during the vegetative cycle studied. The highest concentration of N in the leaves was determined in the spring and summer months, during initial leaf growth. Thereafter they decreased, due to retranslocation during the period of leaf-fall in autumn.

During spring and summer growth flow is accompanied by intense mitotic activity due to cellular growth and a strong demand for nutrients, in particular N (Ryan and Bormann, 1982). Thereafter the contents of this element decrease throughout the vegetative cycle and above all during the period of senescence (autumn). It is evident that a retranslocation to perennial tissues occurs before total abscission.

The vegetative cycle of deciduous forest leaves undergoes three stages of development: the first is of rapid growth; the second refers to maturation, and the third involves senescence. During the first stage, the dry matter and the absolute amounts of nutrients increase rapidly. In forests of *Quercus elipsodalis* Hill., Bockheim and Leide (1991) established that nutrients such as N reach 60–90 per cent of their maximum contents 5 weeks after leaf budding. The maturation of the leaves in the ecosystem studied by those authors occurred in July–August and was characterized by a substantial reduction in the increase in leaf mass and an increase, followed by a decrease, in absolute amounts.

Finally, during the senescence period an important decrease in the absolute amounts of the above elements was observed. These changes have been attributed to reabsorption from the leaves towards perennial tissues (Luxmoore *et al.*, 1981; Tyrrell and Boerner, 1987).

Accordingly, the periods of the highest percentages of N may be intimately correlated with those in which leaf shedding is premature, in many cases departing strongly from phenomena of senescence and more related to climatic affects (winds, freezing, etc). In this case, the

concentrations of the element are closer to those of the leaves retained on the trees (Gosz *et al.*, 1973).

Efficient retranslocation of essential elements is a typical characteristic of any forest ecosystem (Whittaker *et al.*, 1979; Staaf and Berg, 1981; Prescott *et al.*, 1979). Translocated P and N could supply most of the demand for these nutrients for the production of new leaves during the following cycle. This retranslocation, accompanied by a reduction in nutrient restitution (through leaf litter) and requirements, affords the ecosystem a certain independence from the soil medium and the possibility of good management of the available elements (Melillo, 1981).

During abscission, the soluble fraction of N increases and this nutrient is retranslocated toward other structures: trunks, branches or roots. Thus, only small amounts would be lost by leaching (Foster, 1974; Tukey, 1970). This displacement of N implies low levels of the element in shedding and its withdrawal from the internal cycle of the element in the ecosystem.

Temporal immobilization of N in the litter is important as a mechanism for conserving a usually scarce element, thus avoiding meaningless losses through leaching. Boerner (1982) has proposed that this phenomenon would be one of the strategies used for nutrient conservation in oligotrophic ecosystems. Attiwill (1968) concludes that forests with low N capital seem to be more resistant to losses of this element.

The study of Hernández (1989) points to a negative correlation between the monthly amount of leaves undergoing abscission and the N concentration during that month. This is suggestive of an internal redistribution phenomenon of N towards perennial structures associated with leaf senescence. In this way, the plants would be guaranteed minimal losses of an element that is often scarce in forest soils, and it would be ensured that a certain amount of N would be available for the development of new organs during the growth period.

The evolution of N in the green leaves at 'Tres Aguas' (Table 10) again clearly reveals a decrease in the contents of the element from June, with 2.70 per cent, to November, when the leaves still adhering to the branches have only 1.07 per cent of the element. These values should be contrasted with those obtained for the same date from leaves

that fell during shedding; 0.68 per cent, the contents in the leaves decreasing in favour of an increase in N in branches and bark for the same date as when abscission occurs. This has been reported by other authors (Santa Regina, 1987; Santa Regina *et al.*, 1997b.).

The evolution of N in the green leaves at 'La Rasada' (Table 10) follows the same pattern as the beech forest, but with lower concentrations.

Various approaches have been employed to depict the nutrient-use efficiency of forest species (Bockheim and Leide, 1991). A commonly used indicator is the proportion of leaf resorption, which is estimated as the difference between the maximum and minimum leaf nutrient contents divided by the maximum leaf nutrient content (Chapin and Kedrowski, 1983). This technique does not take into account any canopy leaching or dry-fall impaction that would occur during leaf maturation.

Fagus sylvatica and *P. sylvestris* conserve nutrients by having a lower nutrient requirements, investing lower amounts of nutrients in foliage and woody tissues per unit of leaf of perennial production, retaining greater proportions of nutrients in perennial production and returning lower amounts of nutrients through the litterfall and fine-root turnover. Similar conclusions have been reported by Bockheim and Leide (1991).

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