Ann. For. Sci. 56 (1999) 667–677

Original article

Organic matter dynamics in beech and pine stands of mountainous Mediterranean climate area

Ignacio Santa Regina[a*], Teresa Tarazona[b]

[a] IRNA-C.S.I.C., Cordel de Merinas 40, Apdo. 257, 37071 Salamanca, Spain
[b] J. C.L. Villar y Macías no. 1, Salamanca, Spain

(Received 4 March 1999; accepted 16 July 1999)

Abstract – Aboveground biomass, litter production and weight loss of litter due to decomposition were monitored in two forest ecosystems in the Sierra de la Demanda, Spain, a Mediterranean climatic zone, over a 3-years period. The two ecosystems were a mature beech forest (*Fagus sylvatica* L.) and a Scots pine plantation (*Pinus sylvestris* L.). The aboveground biomass was estimated by cutting and weighing seven trees from each site according to diameter classes, recording the categories of trunk, branches and leaves. The results indicate a total biomass of 152.1 $Mg \cdot ha^{-1}$ in the pine stand and 132.7 $Mg \cdot ha^{-1}$ in the beech stand. The percentage distribution of biomass weight of trunks, branches and leaves was similar in both forests. The higher biomass in relation to DBH was estimated in the beech forest, which seems to indicate that it would not be very suitable to reforest land that is appropriate for beech with pine. The litter fall was 5 791 $kg \cdot ha^{-1} \cdot year^{-1}$ in the pine forest and 4 682 $kg \cdot ha^{-1} \cdot year^{-1}$ in the beech forest, although variations from year to year were observed, mostly due to water stress in summer. Weight loss due to decomposition of litter was similar in the two forest ecosystems, apparently due to the similarity in rainfall distribution at the sites. Jenny's litter decomposition index (K) and Olson's litter decomposition index (K_0) were higher for the Scots pine stand than for the beech stand, K: 0.46 and 0.37, K_0: 0.82 and 0.59, respectively, and Jenny's leaves and Olson's decomposition indices were similar. © 1999 Inra/Éditions scientifiques et médicales Elsevier SAS.

aboveground biomass / litter fall / weight loss / forest ecosystems / *Fagus sylvatica* / *Pinus sylvestris*

Résumé – **Dynamique de la matière organique d'une hêtraie et d'une pinède en zone climatique méditerranéenne.** On a estimé pendant trois années la biomasse aérienne, la production de litière et la perte de poids à partir des litières de feuilles en décomposition dans une hêtraie (*Fagus sylvatica* L.) et une pinède (*Pinus sylvestris* L.) de la Sierra de la Demanda, (Espagne). La biomasse a été estimée par coupe et pesée de sept arbres dans chaque peuplement selon la distribution des diamètres. Le poids des troncs, branches et feuilles a été mesuré. Les résultats indiquent une biomasse totale de 152,1 Mg ha^{-1} dans la pinède et 132,7 Mg ha^{-1} dans la hêtraie, Les pourcentages de poids du tronc, branches et feuilles son similaires dans les deux forêts. En comparant les biomasses en relation avec les classes de diamètres qui sont les plus importantes dans la hêtraie, on peut penser qu'il n'est pas opportun de reboiser en pin sylvestre dans l'aire potentielle de la hêtraie,

La chute de litière est de 5 791 kg ha^{-1} y^{-1} dans la pinède et 4 682 kg ha^{-1} y^{-1} dans l'hêtraie, cependant on a observé variations chaque année, principalement dues au stress hydrique estival.

La perte de poids due a la décomposition de la litière est similaire dans les deux écosystèmes, en relation avec le fait que la distribution de la pluie est la même dans les deux stations. Les index de décomposition de Jenny (K) et Olson (K_0) son plus élevés dans la pinède: K = 0,46 et 0,37, K_0 = 0,82 et 0,59 respectivement, et ces index sont similaires pour les feuilles. © 1999 Inra/Éditions scientifiques et médicales Elsevier SAS.

biomasse aérienne / chute de litière / perte de pois / écosystème forestier / *Fagus sylvatica* / *Pinus sylvestris*

* Correspondence and reprints
ignac@gugu.usal.es

1. Introduction

Quality of organic matter is of prime importance for the majority of the functional processes occurring in the soil of forest ecosystems. The most important contribution to the soil humus occurs through plant aboveground and root litter [16]. Aboveground litter plays a fundamental role in the nutrient turnover and in the transfer of energy between plants and soil, being the source of the nutrients accumulated in the uppermost layers of the soil. It is particularly important in the nutrient budgets of forest ecosystems on nutrient-poor soils, where the vegetation depends to a large extent on the recycling of the nutrients contained in the plant detritus [46].

The primary net productivity of forest vegetation is subject to external environmental factors such as soil and climate, and by inherent factors such as age and the type of tree cover [43]. Plants retain a substantial part of their production in perennial structures (trunks, branches, roots, etc.) whose nutritive elements form the mineralomass of the phytocenosis [9].

Whittaker and Likens [51] established a general relationship between the aboveground biomass of the wood and its primary net productivity, enabling a comparison among the different productivities of different populations of plants [48]. It is also important to study carbon and nitrogen, both as regards the distribution of these elements within (i.e. structural) and among (i.e. compositional) community types since they affect the development processes and pathways of the ecosystem [32].

In any kind of forest, the highest litter fall occurs yearly during certain periods, depending on the phenology of the dominant species. The production of litter is intimately related to the edaphoclimatic factors of the zones in such a way that the total mass due to shedding is directly proportional to the fertility of the soil [11]. Root biomass and turnover are difficult to estimate owing to the difficulty in measuring them [50].

In a forest ecosystem, litter production is mainly expressed as a massive contribution of dead organic matter that accumulates on the ground [26]. This accumulated leaf litter on the soil surface, together with the contribution made by root decomposition [28], represents the basic source of energy, C, N, P, and other bioelements for the participating microflora and mesofauna of the soil, as well as a quantity of easily available nutrients [38].

The aim of the present work was to encompass within a general study on organic matter dynamics in a climax beech forest a comparison to that occurring in a pine stand planted on terrain suitable for beech over a 3-year period of experimentation.

2. Materials and methods

2.1. Site description

The experimental site is located in the Sierra de la Demanda mountains in the province of Burgos and Logroño in northern Spain. Its mountainous topography is located on the north-west flank of the Central Iberian Range. Its co-ordinates are: 42° 20' N, 4° 10' E.

The climate in the study area is attenuated meso-Mediterranean and becomes sub-Mediterranean with increasing altitude (1 000 m). *Figure 1* shows the ombrothermic diagrams of the site and the studied plots, the summer drought typical of the Mediterranean climates is readily seen.

The weather station at Pradoluengo, near the experimental plots, at an altitude of 960 m, has an annual mean temperature of 12.4 °C, the average of the minima and maxima of the monthly absolute being 6.5 and 35.1 °C, respectively. The mean annual 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

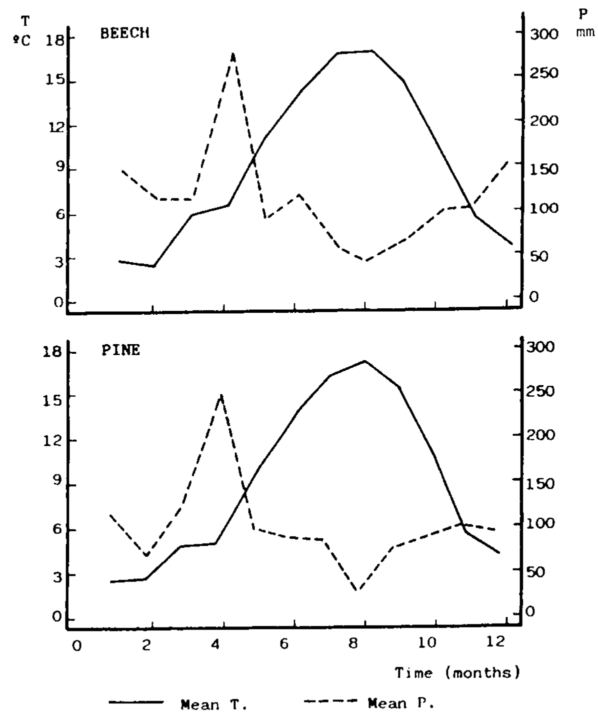

Figure 1. Diagram of the monthly average temperature and pluviometry.

Table I. Diagram of the monthly average temperature and pluviometry.

	$\bar{X}$tmax °C	$\bar{X}$tmin °C	P mm y^{-1}
Pradoluengo*	16.3	7.4	886
Beechwood Tres Aguas	13.9	4.3	1630
Pinewood La Rasada	13.2	4.6	1257

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

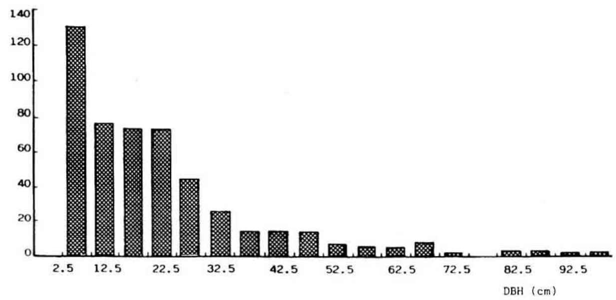

Figure 2. Diameter at breast height (DBH) class distribution in the beech forest.

period in the area is 2 months per year (summer), and the duration of the cold period is 6 months per year (+ 7 °C) [44].

The Mediterranean index of the area is 3.1 [40]. The thermicity index is 195, corresponding to the lower supra-Mediterranean bioclimatic horizon.

In the Sierra de la Demanda, the beech forest is distributed in small islets, each occupying some 5 000 ha at the bottom of valleys and on northern slopes from 900 to 1 600–1 700 m in altitude.

During the cold season, the beech forest displays a lower thermal fluctuation (+ 3 °C) than the Scots pine forest and a higher maximum temperature (+ 1 °C). *Table I* shows the values obtained at the studied sites and those obtained from the National Weather Station at Pradoluengo.

Relative humidity in the beech forest is always from 1 to 1.5 % lower than in the pine forest. Accordingly, evapotranspiration is higher in the pine forest (*table II*).

Tres Aguas is a mature beech (*Fagus sylvatica* L.) forest, with a density of 523 trees·ha^{-1}, comprised of 300 young trees (4–20 cm DBH, 30 years old), the rest being adults (70 years old approximately). The altitude is 1 100 m a.s.l. This stand is a coppice with standard (*figure 2*), with mean height ranging 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 [12]. These and other soil characteristics are indicated in *table III*.

The Scots pine trees (*Pinus sylvestris* L.) at La Rasada were planted in a 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 [12] (*table III*).

On comparing the distribution of the trees according to their diameter classes, the Scots pine forest displays a typical Gaussian bell-shaped curve in which most trees are concentrated around the intermediate diameter class (32.5–37.5 cm). The altitude is 1 250 m.a.s.l. (*table III*). The beech forest trees are 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 degree of maturity and management [45].

Table II. Average of the maxima and minima temperature and percentage of the maxima and minima relative humidity of the air during the study period.

	$\bar{X}$tmax °C	$\bar{X}$tmin °C	Thermic Amplitude °C	$\bar{X}$ Hmax %	$\bar{X}$ Hmin %
Pinewood	17.5	7.8	(–2, +34)	88.9	51.1
Beechwood with leaves	17.9	7.3	(–4, +33)	87.6	48.3
Pinewood	7.7	0.7	(–11, +16)	90.5	56.7
Beechwood without leaves	8.8	0.6	(–10, +14)	89.0	52.8

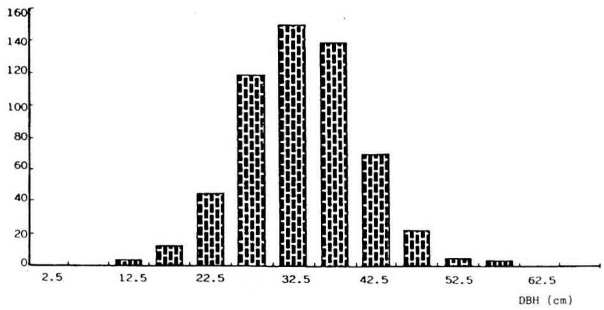

Figure 3. Diameter at breast height (DBH) class distribution in the pine forest.

2.2. Sampling

Seven *Fagus sylvatica* trees and seven *Pinus sylvestris* trees, representative of different classes, were felled to establish their aboveground biomass. Each tree thus harvested was divided into trunk, branch and leaves. The trunks were separated into sections, according to their height (0–1.30 m, 1.30–3 m, 3–5 m, 5–7 m.) and weighed. The wood was separated from the leaves.

Fifteen litter traps were randomly distributed on the two experimental sites during a 3-year period. The litter was removed monthly and the material collected subdivided into different plant organs (branches, leaves, fruits and flowers).

The leaf decomposition dynamics was assessed in litter bags, made of nylon with a pore diameter of 1 mm and a surface area of 400 cm^2. Each litter bag contained 5 g of beech leaves or pine leaves ('needles') recently fallen from their own tree canopy. The bags were placed over the holorganic horizon in three different locations at each plot. Forty-five litter bags were placed in each ecosystem, distributed in three groups. The experiment was begun in December 1990 and ended in January 1994. After December 1990, every 2 months, three bags per plot, one from each of the three locations, were collected during the study period. Additionally, from each site, litter samples were collected from a 50 × 50 cm area of the ground to determine the indices of natural decomposition in the two forests [44].

All subsamples were taken to the laboratory for further analysis. The leaves and the litter were cleaned and dried at 80 °C for 24 h to constant weight to determine the moisture content [45].

For the evaluation of litter dynamics, we used the coefficient K by Jenny et al. [19], which relates the humus and the aboveground litter. K is a constant for any given ecosystem and is defined by

Table III. General characteristics of the experimental forest stands.

Forest ecosystem Plots characteristics	*Fagus sylvatica* Tres aguas	*Pinus sylvestris* La Rasada
Elevation (m)	1100	1250
Geology	Slate	Granite
Soil units	Humic Acrisol	Humic Cambisol
Humus type	Forest mull	Forest mull
Soil pH (Ah)	5.6	5.2
O.M. (%)	16.1	19.7
C/N	15.5	16.7
CEC (C mol Kg^{-1})	21.3	30.6
Avail. P2O5 (mg Kg^{-1})	43.5	46.8
Density (tree ha^{-1})	523	581
Basal area (m^2)	25.7	29.6
Mean height	20-22	15
Long-term mean P (mm y^{-1})	890	905
Mean annual t (°C)	12.4	11.6

O-M-: Soil organic matter; C E C: Total cation exchange capacity; Avail: available; P: Rainfall; t: temperature.

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

where A is the annual leaf or litter fall to the soil and F is the leaf or litter accumulation on the surface soil before the period of massive litter shedding.

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

$$P = AK$$

where P is the annual loss of leaf litter produced.

Calculation of the decomposition coefficient K_o [33] is defined by

$$K_o = A/F$$

The parameter K_d (coefficient of accumulation of leaf or litter) was also determined

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

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.

3. Results

3.1. Aboveground biomass

Tables IV and *V* summarize the overall set of dendrometric and weight characteristics of the seven trees from

Table IV. Dendrometric and weight characteristics of the seven trees studied in the beech forest.

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	277.6	363.5	77	28.0
26.8	18.9	12.2	103.1	271.7	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		2.3	23.1	74.4	100.0		

Table V. Dendrometric and weight characteristics of the seven trees studied in the pine forest.

DBH cm	Height m	Leaves Biomass (kg)	Branches Biomass (kg)	Trunk Biomass (kg)	Total Biomass (kg)	Trees ha^{-1}	Total Biomass $Mg\ ha^{-1}$
2.5	2.7	0.4	0.6	0.6	1.6	4	0.1
17.5	12.4	3.5	6.5	46.5	56.6	18	1.0
19.1	15.4	2.7	10.4	89.5	102.6	46	4.7
23.5	12.1	7.4	30.7	133.3	171.4	60	10.3
25.0	13.9	6.9	24.7	129.4	161.0	60	9.7
33.2	15.7	7.4	30.1	228.3	265.8	242	64.3
36.5	12.6	27.1	121.0	251.8	399.9	155	62.0
Biomass $Mg\ ha^{-1}$		7.0	30.0	115.1	152.1		152.1
% total biomass		4.6	19.7	75.7	100		

each plot studied, representative of each population according to diameter classes.

Figure 4 shows the DBH/height ratio. Correlation coefficients of $r^2 = 0.84$ for the beech forest and $r^2 = 0.90$ for the Scots pine forest were obtained. These predictions give a maximum of approximately 18.2 m for the beeches and 15.3 m for the pines.

The following regression equations for the total aboveground biomass (kg), expressed in terms of DBH (cm), were calculated for each plot (*table VI*).

$$Y = 1.416\ x^{0.426} \text{ for the beech forest}$$

$$Y = 1.941\ x^{0.238} \text{ for the pine forest}$$

On comparing the values of total aboveground biomass obtained from the felled trees from both sites according to diameter classes (*figure 5*), a clear divergence may be seen especially in the mature phases. On relating DBH to biomass, the following regression equations are obtained (*table VI*)

$$\text{beech forest: } Y = 0.1326\ x^{2.4323}$$

$$\text{pine forest: } Y = 0.2206\ x^{2.0519}$$

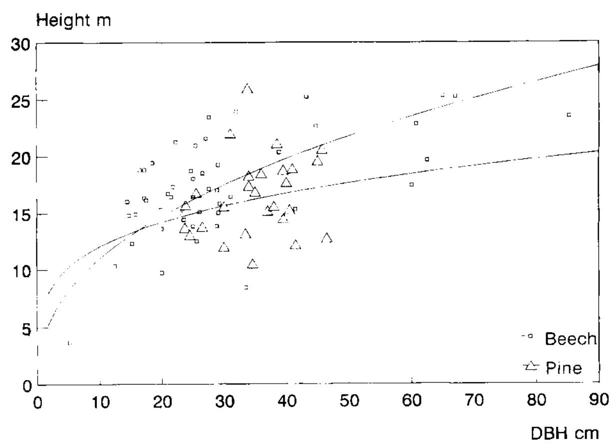

Figure 4. Relationship between DBH and height in both study forests.

The trunk is the part of the tree that most contributes to the total biomass. This has a value of 74.4 % in the beech forest (*table IV*) and 75.7 % in the pine forest (*table V*).

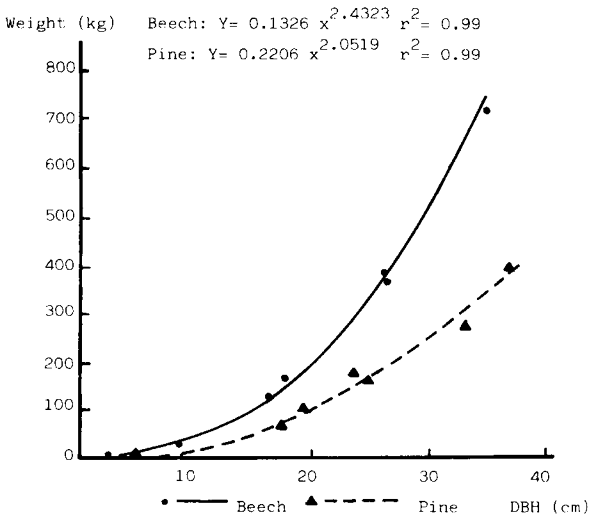

Figure 5. Total biomass in relation to the DBH for individual trees of beech and pine.

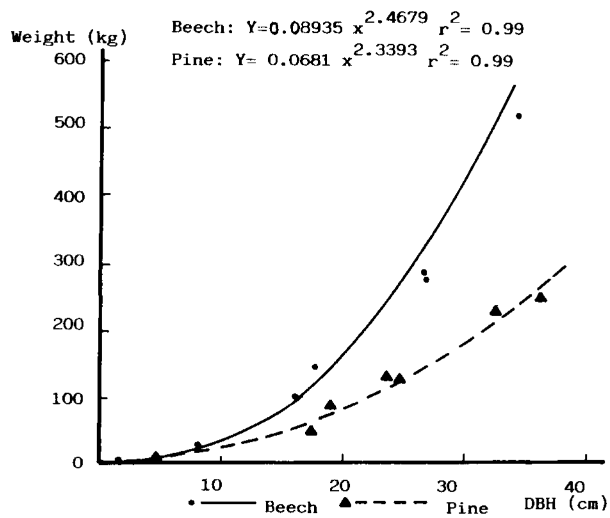

Figure 6. Trunk biomass in relation to the DBH for individual trees of beech and pine.

Figures of 98.6 $Mg \cdot ha^{-1}$ are obtained for deciduous forest and 115.1 $Mg \cdot ha^{-1}$ for evergreen forest.

On estimating trunk biomass in relation to the DBH (*figure 6*) greater productivity is seen for beech, with correlation coefficients of $r^2 = 0.99$ in both cases.

The regression equations for the DBH/trunk biomass ratio are as follows (*table VI*):

$Y = 0.08935\ x^{2.4679}$ for the beech forest

$Y = 0.06807\ x^{2.3393}$ for the pine forest

The branch fractions behave in a manner similar to the trunks (*tables IV* and *V*); mean percentages of 23.1 and 19.7 % were obtained for the beech and pine forests, respectively, obtaining 30.7 $Mg \cdot ha^{-1}$ for the deciduous species and 30.0 $Mg \cdot ha^{-1}$ for the evergreen species.

On exploring the biomass of branches with respect to DBH index (*figure 7*), the productivity of the beech trees was seen to be greater than that of the pines. However, some of the r^2 correlation coefficients are poorer than those found for the previous fraction (trunks) $r^2 = 0.98$ for the beech forest and $r^2 = 0.93$ for the pine forest.

The regression equations obtained from the DBH/branch biomass ratio are as follows (*table V*):

$Y = 0.0317\ x^{2.3931}$ for the beech forest

$Y = 0.5653\ e^{0.1433x}$ for the pine forest

A divergence can be seen in the determination of the biomass of leaves. In the beech forest, the contribution of the leaves to total biomass is 2.3 % with 4.5 $Mg \cdot ha^{-1}$ (*table IV*); in the pine forest these figures have values of 4.6 % and 7.0 $Mg \cdot ha^{-1}$, with r^2 correlation coefficients 0.97 for the beech and 0.88 for the pine (*table V*).

However, on establishing leaf biomass with respect to the DBH parameter (*figure 8*), the greatest productivity is also obtained for the beech forest.

The regression equations for the leaf biomass/DBH ratio are as follows (*table VI*):

$Y = 0.0145\ x^{1.9531}$ for the beech forest

$Y = 81.478\ e^{1.384x}$ for the pine forest

Table VI. DBH/biomass relation in the different compartments of the trees.

		Regression equations	r^2
Beech forest	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
Pine forest	DBH-total biomass	$y = 1.9410\ x^{0.238}$	0.99
	DBH-trunk biomass	$y = 0.0681\ x^{2.3393}$	0.99
	DBH-branch biomass	$y = 0.5653\ e^{0.1433x}$	0.93
	DBH-leaf biomass	$y = 81.4780\ e^{1.384x}$	0.97

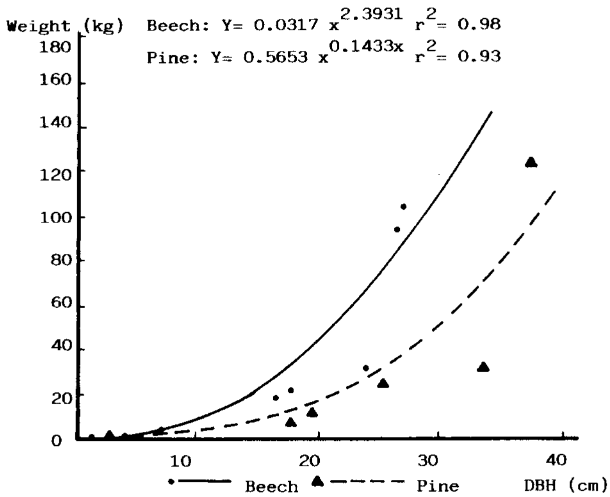

Figure 7. Branch biomass in relation to the DBH for individual trees of beech and pine.

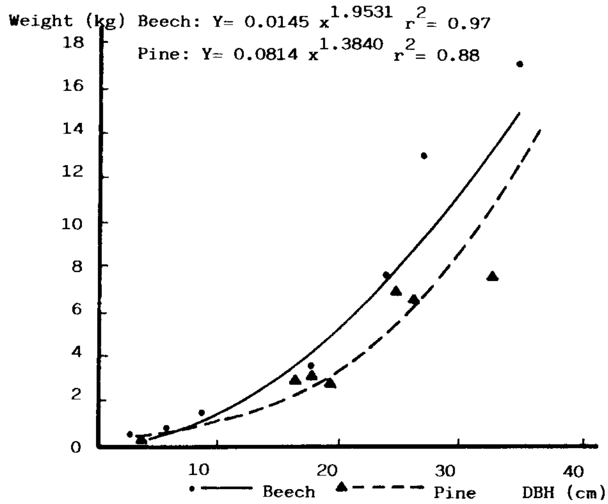

Figure 8. Leaf biomass in relation to the DBH for individual trees of beech and pine.

3.2. Litter fall

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

Leaf litter production was very similar in both forests while litter production was more important in the pine forest.

The differences appearing between the estimated leaf biomass and the leaf litter are mostly in relation to the date of biomass sampling. Canopy leaf mass varies during the season. If the biomass estimate occurs in summer, at the peak of leaf growth, this could explain the differences between leaf litter amounts. In addition, leaf litter was only sampled from September to December, underestimating some possible earlier leaf and litter fall.

Table VII. Litter and leaf decomposition indexes.

	Beech		Pine	
Litter fraction	$Kgha^{-1}y^{-1}$	%	$Kgha^{-1}y^{-1}$	%
Leaves	2897	61.9	2917	50.4
Branches	823	17.6	1766	30.5
Fruits	576	12.3	776	13.4
Flowers	35	0.7	220	3.8
Others	351	7.5	112	1.9
Total	4682	100.0	5791	100.0

3.3. Litter decomposition

The decomposition indices were determined for total litter in each forest ecosystem and for leaves only of both stands (*table VIII*). 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 to 0.37 and 0.46 (*table VIII*).

4. Discussion

The procedure most commonly used to estimate the biomass in forest ecosystems involves destructive techniques in combination with the application or regression equations to manage the data. The best fitted model is the allometric model $Y = X^b$, where Y is biomass and X tree diameter at a height of 1.30 m. It should be stressed that this model is quite complex; indeed some authors [2, 3, 47] have proposed corrections with a view to avoiding under estimations of the true values. This method has been used by several authors [37, 45].

On comparing biomass according to diameter classes, much higher in the beech forest, it may be seen that it

Table VIII. Litter fall amount returning yearly to the soil (kg·ha^{-1}·year^{-1}).

Ecosystem	A	F	A + F	K	K_O	P	K_d
			Litter				
Beechwood	5386	9069	14455	0.37	0.59	1992	0.63
Pinewood	5791	6796	12587	0.46	0.82	2664	0.54
			Leaves				
Beechwood	2906	7229	10134	0.29	0.40	843	0.71
Pinewood	2418	5395	7813	0.31	0.45	750	0.69

A, annual production; F, litter or leaves accumulated on the soil surface; K, Jenny's index; K_o, Olson's index; P, annual loss of produced 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.

would not be very suitable to reforest land appropriate for beech with pine, as confirmed by the contents in C and N in the different tree fractions [45]. Thus, if the total number of trees in each ecosystem is known, figures of 132.7 and 152.1 Mg·ha^{-1} for the beech and pine stands, respectively, are obtained; this is because the distribution in the latter sites follows the Gaussian bell-shaped curve, with few trees belonging to the extreme classes, while in the first site many trees were found in the lower classes and no sampling in the upper classes.

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 *Fagus sylvatica* forest Calamini et al. [8] established an aboveground biomass of 319 Mg·ha^{-1}, Ovington [34] at 50 years old, reported 164 Mg·ha^{-1} and Reiners [39] 124 Mg·ha^{-1}; in gymnosperms of 50-year-old communities Green and Grigal [17] described a range of 92–169 Mg·ha^{-1} while Tappeiner and John [49] reported 102–136 Mg·ha^{-1} in stands of 50–90 years old.

For trunk biomass Calamini et al. [8] obtained 89.1 % with respect to total aboveground biomass, whereas for branch biomass they obtained values of 29 Mg·ha^{-1} or 9.1 % with respect to total biomass, and Grier et al. [18] reported 65 % in *Pinus edulis*. For leaf biomass the literature reports different values: in *Fagus sylvatica* Calamini et al. [8] calculated 2.7 Mg·ha^{-1} or 0.8 % of leaves; Lemée [23] reported 3.5 Mg·ha^{-1} and Lemée and Bichaut [24] 3.1 Mg·ha^{-1}. In *Juniperus occidentalis*, Gholz and Fisher [15] indicated 20 % of needles; in *Pinus sylvestris*, Rodin and Bazilevich [41] established values of 9.6 and 5.5 % of needle biomass with respect to the total forest aboveground biomass.

4.1. Litter fall

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

As in the case of most forest systems, the leaves comprise the most important fraction, representing 61.9 and 50.4 % of the total contribution in the beech wood and pine forest, respectively. This shows that the forest systems in question are immature, since according to Kira and Shidei [21], especially the beech stand, maturity is reached when leaf shedding tends towards 50 % of the total.

Leaf abscission displays a seasonal behaviour, which coincides with that described for the overall production. The formation of tissues triggers a mobilisation of nutrients towards those from older organs, which in turn leads to the abscission of older leaves and twigs [22].

In other resinous species, maximum leaf litter fall occurs later, as in the case of *Pinus sylvestris*: in October and November [1, 7] and in *P. elliotti* [15]. 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 Rapp [36] triggers the early senescence of plant organs.

Branches occupy the second most important place in the amount of aboveground biomass, within the whole set of litter components (823 kg·ha^{-1}·year^{-1} in the beech plot and 1 766 kg·ha^{-1}·year^{-1} in the pine plot, representing 17.6 and 30.5 %, respectively (*table VII*).

The fall or bark contributes to the formation of humus which conserves the humidity of the soil; the late maximum can be related to meteorological factors, rain and wind that are typical of this season. These findings suggest that there could be two alternative possibilities at the moment of the retranslocation of nutrients towards structures in formation.

The fraction corresponding to the fruits displays a period of maximum return. The fraction represents the same proportion in the two stand (12.3 % in beech and 13.4 % in pine). One explanation of this difference can be sought in the different distribution of auxins in apical meristems from one year to another [35].

The flowers and other fractions represent a small proportion with respect to total litter fall.

4.1. Litter decomposition

In both forest ecosystems, greater K and K_o indices were obtained for total litter than for leaves alone. It is possible that the mean soil humidity was not a limiting factor in the decomposition process and 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. Similar values have been reported [6, 10, 31]. The values reported by Maheswaran and Attiwill [25] were higher and those of Gallardo and Merino [13] lower.

The litter bags may have hindered free access to the mesofauna [20] 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 small sizes are involved. F had fairly low values that cannot be entirely explained by the presence of twigs and barks rich in lignin substances [29] and low in N [4, 27].

A similar type of behaviour was observed in both ecosystems, but with occasional divergences. During the first 3 months of the 2 year cycle, 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, 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. This was more pronounced in the beech forest.

Lemée and Bichaut [24] reported an annual weight loss between 15 and 40 % in *Fagus sylvatica* and *Pinus sylvestris*. Berg and Lundmark [5] reported values of 31 % and Santa Regina [42] a value of 27 %.

It is possible to see that the leaf litter decomposition constants are lower than the total litter decomposition constants; nevertheless the total litter includes more wood lignin (twigs, branches) than the leaves or needles alone [29, 30].

5. Conclusions

On comparing biomass according to diameter classes, much higher in the beech forest, it may be noted that it would not be very suitable to reforest land appropriate for beech with pine.

On exploring the biomass of trunks and branches with respect to the DBH index, the productivity of the beech forest is seen to be greater than that of the pine stand. However, some of the r^2 correlation coefficients are similar in both cases for the trunks $r^2 = 0.99$ and the correlation coefficients are $r^2 = 0.89$ for the beech forest and $r^2 = 0.93$ for the pine forest.

A divergence can be seen in the determination of the biomass of the leaves; 2.3 % with respect to total biomass in the beech forest and 4.6 % in the pine forest with r^2 correlation coefficients of 0.92 and 0.88 for the beech and pine, respectively.

As in the case of most forest ecosystems, the leaves comprise the most important fraction of the total litter fall, representing 61.9 and 50.4 % in the beech forest and pine forest, respectively.

During the decomposition cycle, the loss of dry matter was 40 % in the beech forest and 42 % in the pine forest. It is likely that the effect of precipitation during the period of decomposition was not decisive, since its distribution over the time period was similar for both forests.

The decomposition indices of leaves when confined to litter bags were lower than those obtained under natural conditions.

Acknowledgements: We thank the ground staff who have collaborated with us. Field assistance was provided by C. Relaño. The English translation was supervised by N. Skiner.

References

[1] Aussenac G., Production de litiére dans divers peuplements de l'Est de la France, Acta Oecologica, Oecol. Plant. 4 (1969) 225–235.

[2] Baskerville G.L., Use of logarithmic regression in the estimation of plant biomass, Can. J. For. 2 (1972) 49–53.

[3] Beauchamp J.J., Correction for bias in regression estimates after logarithmic transformation, Ecology 54 (1973) 1403–1407.

[4] Berg B., Dynamics of nitrogen (15 N) in decomposing Scots pine (*Pinus sylvestris*) needle litter: Long-term decompo-

sition in a Scots pine forest. VI, Can. J. Bot. 66 (1988) 1539–1546.

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

[6] Bocock K.L., Changes in the amount of nitrogen in decomposing leaf litter of sessile oak (*Quercus petraea)*, J Ecol. 55 (1963) 555–566.

[7] Bray J.R., Gorham E., Litter production in forests of the world, Adv. Ecol. Res. 2 (1964) 101–157.

[8] Calamini G., Gregori E., Hermanin L., Lopresti R., Manolacu M., Studio di una faggeta Dell'Appennino pistoiese: Biomassa e produzione primaria netta epigea, Estratto. Anali XIV, 1983, pp. 1–21.

[9] Duvigneaud P., La productivité primaire des écosystémes terrestres. Problèmes de productivité biologique, Manson et Cie, Paris, 1967.

[10] Edmonds L.R., Litter decomposition and nutrient release in Douglas fir, red alder, and Pacific silver fir in western Washington, Can. J. For. Res. 10 (1980) 327-337.

[11] Ehwald E., Über den Nahrstoffkreislauf des Valdes, Dtsch. Akad. Landwirts. Berlin 6 (1957) 1–56.

[12] F.A.O., The Legend F.A.O./Unesco: Soil Map of the World, F.A.O. Rome, 1973.

[13] Gallardo A., Merino J., Leaf decomposition in two Mediterranean ecosystems of south-west Spain: Influence of substrate quality, Ecology 74 (1993) 152–161.

[14] Gholz H.L., Structure and productivity of *Juniperus occidentalis* in Central Oregon, Am. Midl. Nat. 103 (1980) 251–261.

[15] Gholz H.L., Fisher R.F., Nutrient dynamics in slash pine plantation ecosystems, Oecologia 66 (1985) 647–659.

[16] Gosz J.R., Likens G.E., Bormann F.H., Organic matter and nutrient dynamics of the forest and forest floor in the Hubbard Brook forest, Oecologia 22 (1976) 305–320.

[17] Green D.C., Grigal D.F., Jack pine biomass accretion on shallow and deep soils in Minnesota, Soil Sci. Soc. Am. J. 43 (1979) 1233–1237.

[18] Grier Ch. C., Elliot K.J., McCullough D.G., Biomass distribution and productivity of *Pinus edulis. Juniperus monosperma* woodlands of north-central Arizona, For. Ecol. Manag. 50 (1992) 331–350.

[19] Jenny H., Gessel S.P., Bingham F.T., Comparative study of decomposition rates of organic matter in temperate and tropical regions, Soil Sci. 68 (1949) 419–432.

[20] Joergensen R.G., Organic matter and nutrient dynamics of the litter layer on a forest Rendzina under beech, Biol. Fert. Soils 11 (1991) 163–169.

[21] Kira T., Shidei T., Primary production and turnover of organic matter in different forest ecosystems of the Western Pacific, Jpn. J. Ecol. 17 (1967) 70–81.

[22] Lee K.E., Correl R.L. Litter fall and its relationship to nutrient cycling in a south Australian dry sclerophyll forest, Aust. J. Ecol. 3 (1978) 243–252.

[23] Lemée, G., Structure et dynamique de la hêtraie des réserves biologiques de la fôret de Fontainableau: un cas de complexe climacique de forêt feuillue monospécifique tempérée, Acta Oecol. 10 (1989) 155–174.

[24] Lemée G., Bichaut N., Recherches sur les écosystémes des réserves biologiques de la fôret de Fontainebleau, I.Production de litière et apport au sol d'éléments minéraux majeurs, Oecol. Plant. 6 (1971) 133–150.

[25] Maheswaran J. Attiwill P.M., Loss of organic matter, elements, and organic fraction in decomposing *Eucalyptus microcarpa* leaf litter, J. Bot. 65 (1987) 2601–2606.

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

[27] Martin A., Aportaciones al conocimiento del proceso de descomposición in situ de hojas de *Quercus pyrenaica* y *Pinus pinaster*, Tesis de licenciatura, Universidad de Salamanca, 1992.

[28] McClaugherty C.A., Aber J.D., Melillo J.N., The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems, Ecology 63 (1982) 1481–1490.

[29] Meentemeyer V., Macroclimate and lignin control litter decomposition rates, Ecology 59 (1978) 465–472.

[30] Melillo J.M., Aber J.D., Muratore J.M., Nitrogen and lignin control of hardwood leaf litter decomposition dynamics, Ecology 63 (1982) 621–626.

[31] O'Connell A.A., Litter dynamics in karri (*Eucalyptus diversicolor)* forest of southwestern Australia, J. Ecol. 75 (1987) 781–796.

[32] Ohmann L.E., Grigal D.F., Biomass distribution of unmanaged upland forests in Minnesota, For. Ecol. Man. 13 (1985) 322–331.

[33] Olson J.S., Energy storage and the balance of producers and decomposers in ecological systems, Ecology 14 (1963) 322–331.

[34] Ovington J.D., Flower and seed production. A source of error in estimating woodland production, energy flow, and mineral cycling, Oikos 14 (1963) 148–153.

[35] Rapp M., Production de litière et apport au sol d'éléments mineraux dand des ecosystèmes mediterranéens : La fôret de *Quercus ilex* L. et la garrigue de *Quercus coccifera* L., Oecol. Plant. 4 (1969) 377–410.

[36] Rapp M., Cycle de la matière organique et des éléments minéraux dans quelques ecosystèmes mediterranéens, CNRS, París, 1971, pp. 184.

[37] Rapp M., Ed Derfoufi E., Blanchard A., Productivity and nutrient uptake in a holm oak (*Quercus ilex* L.) stand and during regeneration after clearcut, Vegetatio 99–100 (1992) 263–272.

[38] Rapp M., Leonardi S., Evolution de la litière au cours d'une année dans un taillis de chêne vert (*Quercus ilex*), Pedobiology 32 (1988) 177–185.

[39] Reiners W.A., Structure and energetics of three Minnesota forest, Ecol. Monogr. 42 (1972) 71–94.

[40] Rivas Martínez S., Memoria del mapa de series de vegetación de España 1:400.000 I.C.O.N.A. Madrid, 1987.

[41] Rodin L.E., Bazilevich N.I., Production and mineral cycling in terrestrial vegetation, Oliver and Boyd, Edinburgh, 1967, 288 pp.

[42] Santa Regina I., Contribución al estrudio de la dinámica de materia orgánica y bioelementos en bosques de la Sierra de Béjar, tesis doctoral, Universidad de Salamanca, Salamanca, Spain, 1967, 464 pp.

[43] Santa Regina I., Gallardo J.F., Rico M., Martín A., Gallego H.A., Moreno G., Cuadrado S,. Datos preliminares sobre biomasa aérea, producción y características edafoclimáticas de ecosistemas forestales de *Quercus pyrenaica* (Sierra de Gata, Salamanca), Studia Oecológica 8 (1991) 147–158.

[44] Santa Regina I., Tarazona T., Dynamics of litter decomposition in two Mediterranean climatic zone forest of the Sierra de la Demanda, Burgos, Spain, Arid Soil Res. Reab. 9 (1995) 201–207.

[45] Santa Regina I., Tarazona T., Calvo R., Aboveground biomass in a beech forest and a Scots pine plantation in the Sierra de la Demanda area of northern Spain, Ann. Sci. For. 54 (1997) 261–269.

[46] Singh K.P., Litter production and nutrient turnover in deciduous forest of Varanasi, Proc. Symp. Rec. Adv. Trop. Ecol. 1978, 655–665.

[47] Sprugel D.G., Correcting for bias in log-transformed allometric equations, Ecology 64 (1983) 209–210.

[48] Stanek W., State D., Equations predicting primary productivity (biomass) of trees, shrubs, and lesser vegetation based on current literature, Res. Rep. Can. For. Serv. Inf. Rep. BC-X-183. 1978, 58 pp.

[49] Tappeiner J.C., John H.H., Biomass and nutrient content of hazed undergrowth, Ecology 54 (1973) 1342–1348.

[50] Vogt K. A., Grier C.C., Vogt D.J., Production, turnover and nutrient dynamics of above and below ground detritus of world forests, Adv. Ecol. Res. 15 (1986) 303–377.

[51] Whittaker R.H., Likens G.E., Carbon in the biota, in: Woodwell G.M., Pecan E. (Eds), Carbon and the Biosphere ABC Symp. Ser. Conf. 720510, Washington, DC. 1973, pp. 281–300.