Foliar nutrient dynamics and nutrient-use efficiency in *Castanea sativa* coppice stands of southern Europe

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Summary

Chemical and biological aspects of above-ground leaf biomass and nutrient content, redistribution of leaf litter and nutrient return to the soil, seasonal foliar dynamics and nutrient-use efficiency were studied in four *Castanea sativa* Mill. forests of varying ages near Salamanca (Spain), Montpellier (France) and Catania (Italy). From 49 felled, measured and weighed trees, leaf biomass was determined for each tree relative to their diameter at breast height (d.b.h.). It was possible to establish a single regression equation: Biomass = $a(\text{d.b.h.})^b$. Young stands had much lower leaf biomass values: (1600 kg ha^{-1} and 1500 kg ha^{-1}) than the two older stands, (3900 kg ha^{-1} and 4100 kg ha^{-1} respectively). The amounts of the nutrients immobilized in leaf biomass followed the order: N > K > Ca > Mg > P. The amounts of immobilized N, P, K and Mg were less in young stands than old stands; whereas the amounts of Ca were greater in the young stands. N and P translocation to perennial parts followed the same relationship as nutrient immobilization in above-ground leaf biomass, the K translocation differed in the French stand, whereas for Ca, the pattern differed for the two Italian stands. Magnesium does not follow any pattern. The Spanish plot reabsorbed greater amounts of the nutrients considered, except for P, where the greatest amount occurred in an Italian stand. The French site resorbed similar proportions of N as the Italian stands and considerably lower proportions of Mg and K than the other three stands. The two Italian stands resorbed the same proportions of K and Mg, Fossa la Nave greater proportions of Ca, and Piano Porcheria of P.

Introduction

Quality of organic matter is of prime importance for the majority of functional processes in forest soils. Above-ground and root litter are the most important contributions to soil humus (Gosz *et al*., 1976). Above-ground litter plays a fundamental role in nutrient turnover and in the transfer of energy between plants and soil, being the source of the nutrient accumulated in the uppermost layers of the soil. Litterfall is particularly important in the nutrient budgets of forests on nutrient-poor soils, where the vegetation depends largely on the recycling of nutrients in plant detritus (Singh, 1978).

Litter returned to the soil must not be regarded as an independent process. Litter formation is a physiological process, affecting not only the soil but also the growth patterns and nutrition of plants. As is the case for other metabolic functions, it is likely to have adapted via evolutionary forces, that have generated strategies, that vary among plant species and as well as among for the whole ecosystems (Staaf and Berg, 1981).

Studies on foliar nutrient dynamics have been used to estimate the best time during the year for tissue sampling in nutritional studies (Hoyle, 1965), to determine retranslocation and internal cycling in forest ecosystems (Luxmoore *et al*., 1981; Lim and Cousens, 1986; Santa Regina, 1987), to estimate nutrient uptake (Ryan and Bormann, 1982) and to evaluate adaptations of trees to nutrient stress (Boerner, 1985).

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). Retranslocation of nutrients may supply a significant proportion 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 buffering the tree against fluctuations in nutrient availability in the soil and against nutrient losses via litterfall.

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*., 1997).

Sweet chestnut (*Castanea sativa* Mill.) stands are common in the western Mediterranean Basin. Formerly managed as coppices, these stands were regularly clear-cut every 15–25 years according to their productivity under various conditions. However, *C. sativa* coppice management is now more or less abandoned. Fruit production is mostly limited to orchards and the wood is only used for barrels or fuel. Nevertheless, chestnut coppices cover large areas in the Mediterranean mountains of France, Italy, Portugal and Spain.

The aim of the present work was to measure seasonal changes in concentrations and absolute amounts of nutrients in leaves of *C. sativa* forests, in Spain, Italy and France, that differed in climate, especially rainfall or the duration of summer drought, and in soil conditions (poor acid soils and volcanic andosols).

Materials and methods

Study sites

In Italy two *C. sativa* stands were selected around the Etna volcano along an elevational gradient. One stand was situated at 1600 m above sea level (Fossa la Nave) on the southern side of the volcano, while the other (Piano Porcheria) was on the eastern slope at 1000 m above sea level. The two stands were even-aged young coppices, with a density of 1895 and 5668 trees (shoots) ha^{-1} respectively. The distribution of d.b.h. (diameter at breast height) values for each coppice is shown in Figure 1. The basal area was 26.0 m^2 for Fossa la Nave and 28.1 m^2 for Piano Porcheria.

The Spanish stand of San Martín was located in the Sierra de Gata (Cáceres Province, west of Salamanca), at 940 m elevation, with a density of 3970 trees ha^{-1} and 26.0 m^2 basal area.

The French stand of Le Vernet was located at 800 m elevation, in the Cevennes mountains, on the southern part of the Massif Central, about 100 km north of Montpellier, with a density of 2706 trees ha^{-1}. Basal area was 33.5 m^2.

The climatic differences among the sites can mostly be attributed to altitude (Table 1). Soils differed greatly: humic leached brown soils (cambisols) in Spain, acid brown soils in France (cambisols) and volcanic andosols at Etna Volcano (Leonardi *et al*., 1996). The general climate, parent material, forest data and other structural characteristics are shown in Table 1.

Methods

Leaf biomass determination

The d.b.h.s of all trees from a 1 ha area were measured in each experimental plot and their distribution in diameter classes were established.

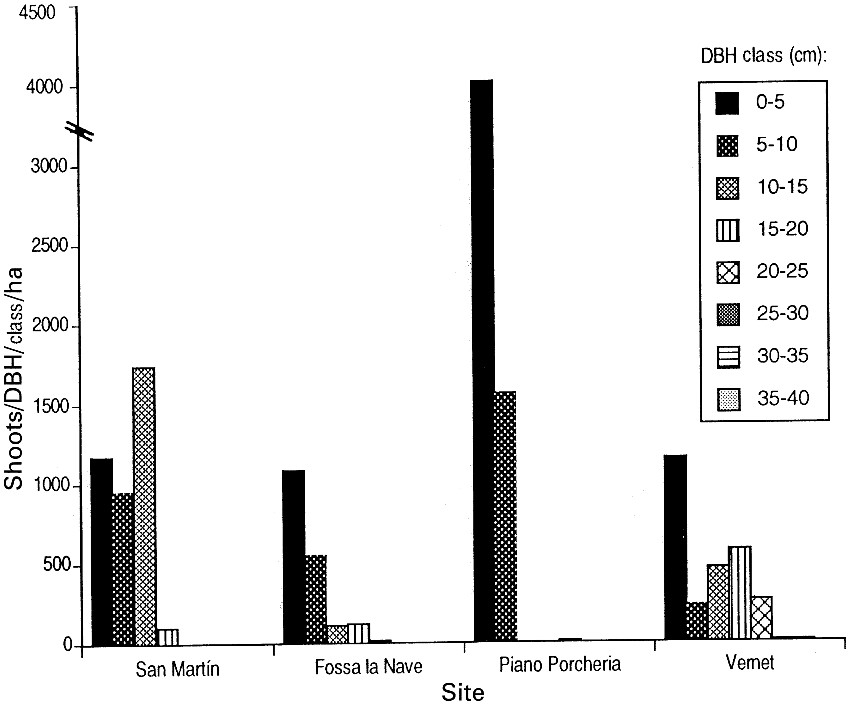

Figure 1. Diameter at breast height (d.b.h.) distribution among classes in the four chestnut forests.

Forty-two representative trees of the different diameter classes were felled to establish their above-ground biomass: 31 in Italy, eight in Spain and 10 in France. Each harvested tree was divided into trunk, branches and leaves, according to their height (0–1.3, 1.3–3, 3–5 and 5–7 m). Total branch mass and individual branches were weighed in the field. Leaf samples were brought to the laboratory for further determination of the moisture content, after drying to constant weight at 80°C. The proportion of leaves per branch and the ratios of branch and leaf weight to the branch diameter were calculated, allowing calculation of leaf weight for each tree. Individual leaf biomass was correlated with d.b.h. using regression analysis. The power regression equation, biomass = $a(\text{d.b.h.})^b$, was the best model.

Leaf litterfall

Thirty litter traps, each with a 0.25 m^2 collection area were distributed randomly at the Spanish and French sites and 40 at the Italian sites. Litter was collected monthly, and subdivided into leaves, reproductive organs, wood and miscellaneous litter, oven-dried at 80°C, and weighed. Results were expressed on an area basis.

Seasonal variation of canopy leaf biomass

Four branches were collected each month during vegetative growth at three heights (lower, medium and upper part of the trees), from nine trees representative of the different d.b.h. classes on each plot. These samples were taken to the laboratory and dried at 80°C for 24 h. The weight per unit and the chemical composition were also determined.

Cycling indexes

Several parameters were calculated for the different compartments and fluxes studied.

Nutrient translocation from leaves to perennial biomass (kg ha^{-1}) was defined as: nutrient content of leaf biomass – nutrient content of leaf litterfall.

Leaf rotation coefficient (percentage): nutrient

Table 1: Site and forest characteristics for the four experimental plots

Site	Altitude (m)	Mean temp. (°C)	Annual rainfall (mm)	Parent material	Soil type	Trees (ha^{-1})	Age (years)	Basal area ($m^2\ ha^{-1}$)	Mean d.b.h. (cm)
Fossa la Nave	1600	7.5	1110	Volcanic ash and lava	Andosol	1895	8	26.0	7.5
Piano Porcheria	1000	13.3	1180	Volcanic ash and lava	Andosol	5668	7	28.1	4.9
San Martín	940	14.2	1180	Granite	Cambisol	3970	25	26.0	10.0
Le Vernet	800	12.7	690	Schist	Cambisol	2706	>30	33.5	10.0

content of litterfall × 100/nutrient content of biomass.

Several definitions of nutrient-use efficiency have been defined for forest species (Bockheim and Leide, 1991). A commonly used indicator is the proportion of foliar resorption, which is estimated as the difference between the maximum and minimum foliar nutrient contents divided by the maximum foliar nutrient content (Chapin and Kedrowski, 1983). This technique ignores canopy leaching and dry deposition during leaf maturation.

Laboratory procedures

Representative subsamples of all tissues collected in the field samplings were ground for chemical analysis. After mineralization of the plant material, Ca, Mg and K were determined using atomic absorption spectrophotometry or flame photometry. Phosphorus was determined colorimetrically using metavanadate (Chapman and Pratt, 1979) and nitrogen by the Kjeldahl method or directly with a macro-N Heraeus device. Weight-basis concentrations of foliar litter nutrients were converted into amounts of nutrients in the leaf biomass or in leaf litter, on a surface-area basis (Leonardi *et al.*, 1996).

Results

Above-ground leaf biomass

From all felled, measured and weighed trees, leaf biomass was determined for each tree, using a single regression equation between d.b.h. and leaf biomass, integrating all 49 trees from the four study sites from the three countries. The global regression equation is as follows:

$$\text{Leaf biomass}_{(\text{kg})} = 0.004\ (\text{d.b.h.}_{(\text{cm})})^{2.296}$$

Leaf biomass in the two younger stands was less than half that of the older two (San Martín and Le Vernet) (Table 2).

The amounts of nutrients immobilized in the leaf biomass were in order: N > K > Ca > Mg > P. Less N, P, K and Mg were immobilized in the young stands than the older stands; whereas more Ca was immobilized in the younger stands.

Leaf litterfall and nutrient return to the soil

The amounts of annual leaf litterfall and its nutrient content are indicated in Table 3. In the two younger stands at Fossa la Nave and Piano Porcheria, the amounts of annual leaf litterfall were: 1230 kg ha^{-1} per year and 1353 kg ha^{-1} per year respectively; compared with the two older stands, where the leaf litter amounts were: San Martín (3429 kg ha^{-1} per year) and Le Vernet (3457 kg ha^{-1} per year). These amounts are in agreement with the values established for the canopy leaf biomass.

The return of nutrients in leaf litterfall reflected patterns of nutrient accumulation in the leaf biomass and amounts of leaf fall (Table 3). For N and K the relationship was: Le Vernet > San Martín > Piano Porcheria ≥ Fossa la Nave; for P and Ca and Mg: San Martín > Fossa la Nave ≥ Piano Porcheria > Le Vernet.

Within year variation of the nutrients in canopy leaves

Table 4 shows the variation in concentration of mineral elements in leaves during a vegetative cycle. For all sites concentrations of N, P and K generally decreased between the emergence and senescence of the leaves and that of Ca increased. Concentrations of Mg did not vary over time.

Translocation of nutrients from leaves to perennial parts is given in Table 5. Amounts of N

Table 2: Leaf biomass and leaf nutrient immobilization (kg ha^{-1})

Site	Organic matter	N	P	K	Ca	Mg
Fossa la Nave	1600 ± 238	21.9 ± 4	3.6 ± 1	16.8 ± 3	18.0 ± 3	5.5 ± 1
Piano Porcheria	1500 ± 201	19.8 ± 3	3.4 ± 1	14.8 ± 3	15.6 ± 3	6.4 ± 1
San Martín	3900 ± 509	59.7 ± 8	9.8 ± 2	35.9 ± 6	12.9 ± 2	9.8 ± 2
Le Vernet	4100 ± 582	67.0 ± 9	–	24.0 ± 4	14.0 ± 3	8.0 ± 2

Table 3: Yearly leaf litterfall and amounts of nutrients returning to the soil (kg ha^{-1} per year)

Site	Organic matter	N	P	K	Ca	Mg
Fossa la Nave	1353 ± 168	10.3 ± 2	1.9 ± 0.3	6.9 ± 1	15.0 ± 3	6.5 ± 1
Piano Porcheria	1230 ± 139	10.4 ± 2	1.8 ± 0.3	7.7 ± 1	10.7 ± 2	6.4 ± 1
San Martín	3429 ± 418	41.5 ± 8	6.8 ± 1.0	15.4 ± 3	18.5 ± 3	11.0 ± 2
Le Vernet	3457 ± 425	43.7 ± 8	–	17.3 ± 3	10.4 ± 2	5.0 ± 1

Table 4: Variation of chemical composition (percentage) of the leaves during a year

Stand	Date	Single leaf dry weight (g)	N	P	K	Ca	Mg
Fossa la Nave	18.06	0.13	1.77	0.35	1.56	0.86	0.39
	06.07	0.24	1.59	0.23	1.15	0.92	0.36
	03.09	0.39	1.31	0.22	1.01	1.08	0.33
	18.09	0.31	1.28	0.26	1.19	1.16	0.34
	29.10	0.28	0.92	0.28	0.90	1.72	0.39
Piano Porcheria	28.05	0.03	2.08	0.54	1.50	0.78	0.44
	21.06	0.15	1.37	0.24	1.03	0.90	0.41
	29.08	0.19	1.04	0.16	0.82	1.16	0.48
	15.09	0.19	0.98	0.17	0.93	1.16	0.47
	24.10	–	0.88	0.22	0.91	1.22	0.43
San Martín	28.04	0.13	2.85	0.28	1.21	0.19	0.27
	25.05	0.13	2.65	0.31	1.24	0.28	0.30
	28.06	0.23	2.20	0.21	1.10	0.31	0.24
	27.07	0.34	2.01	0.24	1.08	0.25	0.27
	25.08	0.40	1.96	0.24	1.00	0.33	0.29
	28.09	0.40	1.59	0.26	1.01	0.34	0.27
	02.11	0.43	0.82	0.24	0.58	0.40	0.27
Le Vernet	21.04	0.08	2.43	–	0.75	0.25	0.20
	06.05	0.11	2.43	–	0.75	0.25	0.22
	07.06	0.21	1.47	–	0.55	0.30	0.20
	01.07	0.27	1.65	–	0.60	0.35	0.21
	27.07	0.33	1.19	–	0.65	0.30	0.20
	07.09	0.39	1.46	–	0.65	0.45	0.20

Table 5: Nutrient translocation to perennial parts (kg ha^{-1}): nutrients in leaf biomass-nutrient in litterfall

Stand	N	P	K	Ca	Mg
Fossa la Nave	11.6	1.7	9.9	3.0	–1
Piano Porchería	9.4	1.6	7.1	4.9	0
San Martín	18.2	3.0	20.5	–5.6	–1.2
Le Vernet	23.3	–	6.7	3.6	3

and P retranslocated were in proportion to the amounts immobilized. For K, retranslocation at Le Vernet was much less than in leaf biomass, for Ca the amounts retranslocated in the two Italian stands were much less than in leaf biomass.

Nutrient-use efficiency

The San Martín plot resorbed greater amounts of the five nutrients considered, except for P, than did the other plots, for which the greatest amount was resorbed in Piano Porcheria (Table 6). Le Vernet resorbed similar proportions of N as Fossa la Nave, and considerably lower proportions of Mg and K than the other three stands. The two Italian stands resorbed the same proportions of K and Mg. Fossa la Nave resorbed a greater proportion of Ca than Piano Porcheria and a lower proportion of P.

Discussion

Above-ground leaf biomass

In the old stands, with trees aged from 12 to >25 years, leaf biomass was directly related to the stand age (Tables 1 and 2). The proportions of leaves to perennial biomass (Fossa la Nave, 20 430 kg ha^{-1}; Piano Porcheria, 22 594 kg ha^{-1} (Leonardi *et al.*, 1995); San Martín, 116 509 kg ha^{-1}; Le Vernet: 149 766 kg ha^{-1} (Leonardi *et al.*, 1996)) were 7.2 per cent at Fossa la Nave, 6.6 per cent at Piano Porcheria, 3.4 per cent at San Martín and 2.4 per cent at Le Vernet. For Le Vernet, the low proportion of leaves may be because high mortality had resulted in a high volume of standing dead trunks.

These findings should be extrapolated with caution since productivity varies considerably within forests owing to variations in geography, soil depth and fertility, substrate, microclimate, age, tree density, silvicultural management, etc. (Cabanettes and Rapp, 1978). Furthermore, extrapolation to other areas will cause a loss of precision in the above-ground biomass estimate (Harding and Grial, 1986; Satoo and Madgwick, 1982).

The amounts of nutrients stored in leaves depends, above all, on leaf biomass. The main differences for the five analysed nutrients lay between the two older Spanish and French stands (San Martín and Le Vernet) and the younger Italian stands (Fossa la Nave and Piano Porcheria). Concerning N and P, the amounts were three times greater in the older stands; potassium was only twice as great. In contrast the Ca contents of the Italian stands seemed higher than that of the two old plots, presumably because they were on more base-rich soils.

Castanea sativa exhibits different features concerning storage and concentration of nutrients in the different parts of the tree as compared with other hardwood species (Jokela *et al.*, 1981; Lemoine *et al.*, 1988; Albert and Prescoller-Tiefenthaler, 1992; Helmisaari, 1992; Saur *et al.*, 1992).

Leaf litterfall and nutrient amounts

Leaf litter production was very similar at Fossa la Nave and Piano Porcheria and lower than at the older stands of San Martín and Le Vernet (Table 3). Comparison of leaf litterfall between the Etna sites (Leonardi *et al.*, 1996) also showed that the leaves lost 18.5 per cent of their weight before litterfall (leaf biomass – leaf litter mass) (Leonardi *et al.*, 1996). The relationship between leaf litterfall and stand age was also very significant: in the two younger coppices of Fossa la Nave and Piano Porcheria, leaf litter amounted to only 1353 (±168) and 1230 (±139) kg ha^{-1} per year,

Table 6: Nutrient-use efficiency index as applied to the four studied stands: maximum foliar nutrient content-minimum foliar nutrient content/maximum foliar nutrient content

Stand	N	P	K	Ca	Mg
Fossa la Nave	0.48	0.37	0.42	0.50	0.15
Piano Porcheria	0.58	0.69	0.45	0.36	0.15
San Martín	0.71	0.32	0.53	0.53	0.20
Le Vernet	0.51	–	0.27	0.44	0.09

respectively, whereas in the two older stands leaf litter observed was similar: 3429 (±418) and 3457 (±425) kg ha^{-1} per year, in the Spanish and French sites, respectively. Similar values are reported by Leonardi *et al*. (1995) and Martín (1995) for other C. *sativa* stands or for other study periods.

Annual litter production is one of the main sources for the annual return of nutrients to the soil. Khanna and Ulrich (1991) indicated that root content of nutrients represents about 20 per cent of the total potential return. According to these authors we estimate that leaf litter is responsible for about 80 per cent of the total amount of nutrients returning to the soil through plant detritus. Because of differences in nutrient concentrations in the leaf litter, the distribution of nutrients did not always follow the pattern established for leaf mass. *Castanea sativa* leaf litter from the Etna volcano contained less N, P and K than those from the San Martín and Le Vernet sites, and it was the opposite for Ca and Mg between the Italian plots and Le Vernet. For these two bioelements, San Martín showed the greatest amounts (Table 3).

The rotation coefficient: nutrients in leaf litterfall × 100/nutrients in leaf biomass indicated interesting values for the four chestnut stands (Table 7). In the two Italian stands N, P and Mg are recycled to the soil in the same proportions. In contrast, the K is recycled more slowly in Fossa la Nave and Ca in Piano Porcheria. Except for K, the other four bioelements were more completely recycled in San Martín than in the Le Vernet site. Generally, the nutrients are more completely recycled in the old stands.

In the present work it appears that nutrient management is related to the availability of nutrients, such as phosphorus and potassium for the trees. Nutrients which are present in lower amounts in volcanic soils (phosphorus) are recycled through the plant–soil system in much higher proportions than other nutrients available in higher quantities in these soils (Leonardi *et al*., 1996).

Seasonal leaf mass and nutrient content variations

The dry weight of current leaves varied within the year. The current leaves had lighter weight in the first months in the two Italian stands. Dry weight increased significantly as the growing season progressed. Seasonal increases in mass of current foliage was reported by Woodwell *et al*. (1975) and Helmisaari (1990).

The vegetative cycle of deciduous forest leaves is subject to three stages of development: rapid growth, maturation and senescence. During the first period, relative concentrations of basic biological and mobile macronutrients N, P and K were the highest, then decreased even by the end of the vegetative cycle in all the plots studied. The decrease would probably occur because the increase in dry weight of the recently matured leaves was faster than the input of nutrients into the leaves (Helmisaari, 1990). These changes have also been attributed by several authors to resorption of nutrients from the foliage into perennial tissues (Luxmoore *et al*., 1981; Ostman and Weaver, 1982; Ryan and Bormann, 1982; Boerner, 1985; Tyrrell and Boerner, 1987). The concentration of Ca, considered to be an immobile element, increases until leaf abscission. A similar pattern was reported by Nable and Loneragan (1984) for the same nutrient. The concentration of Mg remains constant during the vegetative cycle in all the sites considered.

Efficient retranslocation of the most essential nutrients is a typical characteristic of the climax phase of any forest ecosystem (Whittaker *et al*., 1979; Staaf and Berg, 1981; Prescott *et al*., 1989).

Table 7: Leaf rotation coefficients between the four forest stands: nutrients in leaf litterfall × 100/nutrients in leaf biomass

Stand	N (%)	P (%)	K (%)	Ca (%)	Mg (%)
Fossa la Nave	47.0	52.7	41.1	83.3	100.0
Piano Porcheria	52.5	52.9	52.0	68.6	100.0
San Martín	69.5	69.4	42.9	100.0	100.0
Le Vernet	62.5	–	72.1	74.3	62.5

Translocated P and N could supply most of the demand for these nutrients for production of new leaves during the following cycle. This retranslocation, accompanied by a reduction in the nutrient restitution through leaf litter and in requirements, allows the ecosystem to have a certain independence with regard to the soil and the possibility of optimal management of the available elements (Melillo, 1981).

Nutrient-use efficiency

The nutrient-use efficiency index values (proportional resorption) as applied to the four stands suggest that the Le Vernet stand translocated less K and Mg, Fossa la Nave less N, Piano Porcheria less Ca and San Martín less P. The *C. sativa* stands conserve nutrients by having a lower nutrient requirement, investing lower amounts of nutrients in foliage and woody tissues per unit of leaf of production, retaining greater proportions of nutrients in perennial production and returning lower amounts of nutrients in litterfall and fine-root turnover. Similar conclusions were showed by Bockheim and Leide (1991).

Conclusions

The main differences for the five analysed nutrients in leaf biomass were found between the two older stands (San Martín and Le Vernet) and the Italian stands (Fossa la Nave and Piano Porcheria). Concerning N and P, the amounts were three times higher in the older stands. For K, it was only twice as great. In contrast, the Ca contents of the Italian stands seemed higher than in the two older plots.

The relation between leaf biomass and leaf litterfall related to the stand ages was very significant in the two younger coppice stands. Leaf biomass and leaf litter amounted respectively to 1600 kg ha^{-1} and 1500 kg ha^{-1}, 1353 kg ha^{-1} per year and 1230 kg ha^{-1} per year, whereas in the two older plots the leaf litter observed was similar and very much higher, 3429 kg ha^{-1} per year and 3457 kg ha^{-1} per year for 3900 kg ha^{-1} and 4100 kg ha^{-1} leaf biomass, respectively. Because of differences in nutrient concentrations among the leaf litter compartments, the distribution of nutrients did not always follows the pattern established by mass.

It appears that nutrient management is related to the availability of nutrients such as phosphorus and potassium. Nutrients which are in lower amounts in volcanic soils are recycled through the soil–plant system in much higher proportions than other nutrients available in higher quantities in the soil.

The nutrient-use efficiency index values showed that Le Vernet stand translocated less K and Mg, Fossa la Nave less N, Piano Porcheria less Ca and San Martín less P.

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