

Litter fall, decomposition and nutrient release in three semi-arid forests of the Duero basin, Spain

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Summary

The production of litter, the weight loss dynamic of forest litter decomposition, and the dynamics of bioelement loss during leaf litter decomposition were determined in three forest ecosystems located in a semi-arid zone of the Duero basin, Province of Zamora, Spain, over 2 years. The three ecosystems were a climax evergreen oak (*Quercus rotundifolia* Lam.) woodland, a paraclimax stone pine (*Pinus pinea* L.) forest, and a disclimax maritime pine (*Pinus pinaster* Sol.) forest. The mean total production of litter in the oak forest was 2320 kg ha⁻¹ year⁻¹, quite similar to the *P. pinea* pine forest, at 2400 kg ha⁻¹ year⁻¹ and higher than that of the *P. pinaster* pine forest at 1728 kg ha⁻¹ year⁻¹. Leaves and needles accounted for most of this total production (78, 89 and 96 per cent, respectively). No significant differences were found among the different leaf decomposition processes, except for the oak leaves introduced in the pine ecosystems. A relationship between time (independent variable) and the remaining leaf weight was found, which followed a negative exponential curve, $DM \text{ (dry matter)} = A + B \exp(-Ct)$. About 30 per cent of the weight was lost during the first 4 months. This indicates that climate (semi-arid conditions) speeds decomposition in the short term. The decomposition indices were determined for leaves only and for total litter. Considering total litter and leaves separately, several relations were established for K , K_o and K_d decomposition indices. K and K_o in natural conditions decrease in the following order: evergreen oak > stone pine > maritime pine. The *Q. rotundifolia* woodland potentially returns a greater amount of N and Ca than both *Pinus* forests. A litter-bag method was used for the determination of the dynamics of the decomposing leaves. A progressive loss of P and Mg in the decomposing oak leaves and pine needles, and a sharp loss of K were observed: in contrast, a tendency to retain N and Ca was also seen. *Pinus pinaster* forest had the lowest annual N and P returns.

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 above-ground and root litter (Gosz

et al., 1976). Above-ground 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. This is particularly

important in the nutrient budgets of forest ecosystems on nutrient-poor soils, where the vegetation depends in large part on the recycling of the nutrients contained in the plant detritus (Singh, 1978).

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 (Ehwald, 1957). Root biomass and turnover are difficult to estimate, owing to the difficulty of measuring them (Vogt *et al.*, 1986).

In a forest ecosystem, litter production is mainly expressed as a massive contribution of dead organic matter that accumulates on the ground (Mangenot and Toutain, 1980). This accumulated leaf litter on the soil surface, together with the contribution made by root decomposition (McClaugherty *et al.*, 1982), 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 (Rapp and Leonardi, 1988).

The release of nutrients from decomposing litter is an important internal pathway for nutrient flux in forested ecosystems. Nutrients may be released from litter by leaching or mineralization followed by leaching (Santa Regina and Tarazona, 1995; Santa Regina *et al.*, 1997). Nutrient release from decomposing litter affects the primary productivity of ecosystems (Blair, 1988) since these nutrients then 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 nutrient sources. 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 Parkinson, 1976; Heal, 1979; Edmonds, 1980; Moore, 1986; Witkamp, 1966) and soil moisture (Hayes, 1965). Soil fertility is directly related to decomposer activity (Bocock and Gilbert, 1957; Witkamp and Van der Drift, 1961).

The aim of the present work was to quantify the production of litter and the decomposition rate in forest ecosystems subject to the semi-arid climate of the Duero basin (west-central Spain) with a view to gaining further insights into the recycling of above-ground organic matter and associated bioelements.

Materials and methods

Site description

The study area is located in the north-west of the Province of Zamora, on the western boundary of the Tierra de Campos area, in the municipal district of Villalpando, at 41°47'N and 5°26'W.

Three permanent, representative forest plots were chosen, adjacent to each other and within an area of 2500 m², the first in a *Quercus rotundifolia* Lam. climax forest, the second in a paraclimax forest of *Pinus pinea* L. and the third in a disclimax forest of *Pinus pinaster* Ait. The homogeneity of the soil of these plots was checked and confirmed (Hernández *et al.*, 1992).

The soils have developed over conglomerates and red clays from the Miocene. The soil surface has abundant stones and the soils have a clayey B_t horizon. The texture of the epipedon is usually fine sandy-silty, due to allochthonous contributions; the possibility of an Eolian origin cannot be discounted. Soil fertility is poor, with a low content of total N and assimilable P. In short, the soils are classified as Chromic Luvisols (Food and Agriculture Organization, 1989), since their exchange complex is highly saturated (Hernández, 1989).

The climate is clearly of the semi-arid type and is growth limiting (Figure 1). The annual mean precipitation in the area is ~400 mm, with

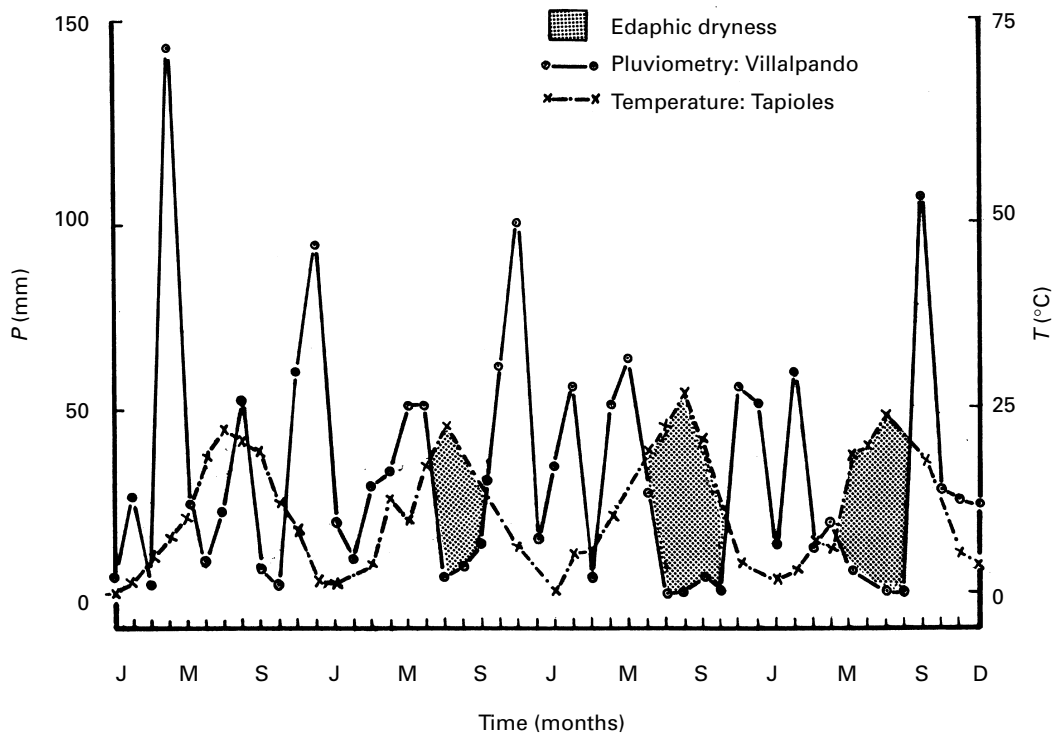


Figure 1. Climatic characteristics at Villalpando and Tapioles, Province of Zamora, Spain. P , annual mean precipitation; T , annual mean temperature.

marked seasonality in the distribution of the rains, almost 3 months being dry (Hernández, 1989). The annual mean temperature is 11.4°C; the mean maximum temperature is 18.2°C and the mean minimum temperature is 3.0°C, with months when the mean temperature drops as low as -3.5°C.

The pine forests were planted after 1950 on former cereal-producing land and vineyards. The plots chosen have an age of ~30 years and have undergone successive thinnings that have reduced the density of the tree cover to ~1000 trees ha⁻¹. In the stone pine (*P. pinea*) forest, the mean height is 4.5 m and the mean trunk diameter at breast height (1.30 m height; d.b.h.) is 22 cm, the crown having a covering of ~6 m². In the maritime pine (*P. pinaster*) forest the mean height is ~6.5 m, the d.b.h. 22 cm, and the mean covering of the crown 5.3 m².

The evergreen oak (*Q. rotundifolia*) woodland forms many dense stands comprising a large

number of trunks and shoots of different ages and diameters; the ground surface covered by the trees is estimated to be 60 per cent of the total, the mean height of the evergreen oaks is 4.5 m. Although in the past felling has been carried out, at present the only exploitation is hunting, with a little usage of the pasture by cattle and sheep.

To collect litter fall, 20 wooden boxes each of 0.14 m² were placed randomly on each plot. Samples were collected monthly over a 3-year period. Each of the constituent fractions was dried in a forced-draught oven at 80°C for 25 h. Some authors have suggested that this temperature should be raised to 105°C (Lemée, 1982; Garay *et al.*, 1986), although in the opinion of the authors this involves the risk of losing organic matter and minerals at such temperatures. Following this, each fraction was weighed separately.

The 'other remains' component was discarded because of its scarcity; such remains

corresponded to small amounts of resin, fragments of arthropods, mesofaunal excrement and other undetermined elements that were sometimes so small that they passed through the mesh.

Significant differences among the means of the data obtained from the different populations were determined using Student's *t* test.

In order to follow the process of release of bioelements during decomposition, 1-mm mesh bags, containing evergreen oak leaves or pine needles, were placed in the plots (litter-bag method); in the case of the stone pine, given the fineness of its needle, the mesh was smaller (0.5 mm) in order to avoid losses. The surface of each bag was 525 cm². Fifty-five bags of each kind were placed in each forest in similar conditions and were initially deposited on top of the leaf litter and under trees. Each month, six bags with leaves of the same species were removed, two for each ecosystem in which they were placed. In the laboratory they were carefully cleaned with a brush (since the use of water could cause the loss of soluble bioelements). Subsequently, the bags were dried in an oven at 80°C for 24 h. The sampling period lasted for 2 years. After each organic residue had been weighed, its N, Ca, Mg, P and K contents were determined. Traditional analytical methods were used: total N by a micro-Kjeldahl Abouat/Afora, total P by spectrophotometry using the vanadate-molybdenum yellow method, Ca and Mg by atomic absorption spectrophotometry, and K by flame photometry (Martín *et al.*, 1995).

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 litter fall (to measure this, all the material of the holorganic horizon contained in a 0.5 × 0.5 m frame was collected. Fifteen samples per plot were taken).

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.

The decomposition coefficient (*K*_o) (Olson, 1963) is:

$$K_o = A/F$$

with *A* and *F* as defined above.

The parameter *K*_d, a coefficient of accumulation of leaf litter, and total litter, was also determined:

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

The ANOVA and Kruskal-Wallis statistical methods of analysis of variance were used to determine whether there were any significant differences in the evolution of each bioelement in each type of leaf, and whether that variance depended on the type of forest in which they were deposited.

Results

Litter production in the three Mediterranean forests

Table 1 shows the results of the annual litter production for the three forest ecosystems considered (kg ha⁻¹) together with the percentage of each fraction with respect to total litter fall. In the three forest stands the contribution of litter to the soil is continuous throughout the year, as expected for a perennial species, although a strong seasonal variation is present which can be observed in its contribution.

Litterfall was greatest in the *Pinus pinea* stand, only marginally less in the *Quercus rotundifolia* and notably lower beneath *P. pinaster*. In each case leaves were by far the greatest component, followed by fruit and flowers in the oak and bark fragments in the pines.

Decayed organic matter

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:

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

Table 1: Annual litter production in the three forest ecosystems studied (kg ha^{-1}) and percentage of each fraction with respect to the total amount shed (— means not significant)

| Forest stand | Organs | Years | | | | | | Annual average | |
|-----------------------------|----------|----------------|------|----------------|------|----------------|------|----------------|-----|
| | | 1 | | 2 | | 3 | | M | % |
| | | M \pm SE | % | M \pm SE | % | M \pm SE | % | M | % |
| <i>Quercus rotundifolia</i> | Leaves | 1630 \pm 340 | 69 | 2510 \pm 85 | 84 | 1400 \pm 390 | 88 | 1850 | 80 |
| | Branches | 390 \pm 71 | 16 | 250 \pm 62 | 8 | 190 \pm 49 | 11 | 280 | 12 |
| | Flowers | 90 \pm 82 | 4 | 170 \pm 125 | 6 | 5 \pm 3 | — | 90 | 3.8 |
| | Fruits | 250 \pm 135 | 11 | 60 \pm 20 | 2 | 3 \pm 3 | — | 100 | 4.2 |
| | Total | 2360 | 100 | 2990 | 100 | 1600 | 100 | 2320 | 100 |
| <i>Pinus pinea</i> | Leaves | 2500 \pm 645 | 88 | 1430 \pm 350 | 88 | 2460 \pm 775 | 90 | 2130 | 89 |
| | Branches | 20 \pm 5 | 0.5 | 10 \pm 6 | 0.6 | 40 \pm 30 | 1.3 | 20 | 0.8 |
| | Bark | 310 \pm 85 | 11 | 180 \pm 27 | 11 | 210 \pm 21 | 8 | 230 | 9.6 |
| | Flowers | 20 \pm 10 | 0.5 | 5 \pm 3 | 0.3 | 10 \pm 5 | 0.5 | 10 | 0.4 |
| | Fruits | 2 \pm 2 | — | 4 \pm 3 | — | 5 \pm 4 | 0.2 | 3 | 0.2 |
| Total | 2850 | 100 | 1630 | 100 | 2725 | 100 | 2400 | 100 | |
| <i>Pinus pinaster</i> | Leaves | 2340 \pm 820 | 97 | 1190 \pm 375 | 94 | 1470 \pm 300 | 96 | 1670 | 96 |
| | Bark | 36 \pm 15 | 2 | 7 \pm 3 | 0.5 | 7 \pm 2 | 1 | 17 | 1 |
| | Branches | 3 \pm 1 | — | 59 \pm 50 | 5 | 18 \pm 12 | 2 | 26 | 2 |
| | Flowers | 2 \pm 2 | 1 | 8 \pm 8 | 0.5 | 13 \pm 8 | 1 | 15 | 1 |
| | Fruits | 3 \pm 2 | — | — | — | — | — | 1 | — |
| Total | 2405 | 100 | 1264 | 100 | 1508 | 100 | 1728 | 100 | |

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 litter fall peak.

The decomposition indices were determined for leaves only and for total litter (Table 2). Considering both total litter and leaves separately, several relations were established for K , K_o and K_d decomposition indices.

A relationship between time (independent variable) and the remaining leaf weight (dry matter) was found, which followed a negative exponential curve $DM = A + B \exp(-Ct)$, where DM is the residual, A the fraction of the initial organic matter which is difficult to decompose, B the fraction with low stability, C the decomposition constant, and t the decomposition period (Figure 2).

Dynamics of bioelements during leaf decomposition

Table 3 gives the chemical composition of the *Q. rotundifolia* leaves and the *P. pinea* and *P.*

pinaster needles that had recently fallen; this corresponds to the initial composition of those placed in the decomposition bags.

Table 4 shows the results of the analysis of variance of the nutrient dynamics for the three types of leaves placed in the same forest, or the same leaves placed in the three ecosystems.

Table 5 shows the minimum bioelement values yielded from decomposing leaves after both 12 and 24 months (litter-bag method), and total bioelements (potential return) in both leaf litter and leaves.

Discussion

Litter production

The three species studied have several characteristics in common: they are sclerophilous, perennial and Mediterranean, such that a convergence would be expected in the adaptive response to a common habitat with a scarcity of nutrients, and

Table 2: Litter and leaf decomposition indexes

| Forest stands | A | F | A + F | K | K_o | P | K_d |
|-----------------------------|----------|----------|----------|------|-------|-----|-------|
| Litter | | | | | | | |
| <i>Quercus rotundifolia</i> | 236 ± 66 | 188 ± 10 | 424 ± 65 | 0.56 | 1.25 | 132 | 0.44 |
| <i>Pinus pinea</i> | 240 ± 67 | 638 ± 26 | 878 ± 53 | 0.27 | 0.38 | 65 | 0.73 |
| <i>Pinus pinaster</i> | 173 ± 60 | 530 ± 39 | 703 ± 22 | 0.25 | 0.33 | 43 | 0.75 |
| Leaves | | | | | | | |
| <i>Quercus rotundifolia</i> | 185 ± 58 | 172 ± 12 | 357 ± 67 | 0.52 | 1.08 | 96 | 0.48 |
| <i>Pinus pinea</i> | 213 ± 61 | 609 ± 15 | 822 ± 71 | 0.26 | 0.35 | 55 | 0.74 |
| <i>Pinus pinaster</i> | 167 ± 60 | 482 ± 30 | 649 ± 88 | 0.26 | 0.35 | 43 | 0.74 |

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

Table 3: Initial chemical composition of the leaves and needles

| Element | <i>Q. rotundifolia</i> | <i>P. pinea</i> | <i>P. pinaster</i> |
|---------|------------------------|-----------------|--------------------|
| N | 0.92 (0.19) | 0.98 (0.19) | 0.76 (0.10) |
| P | 0.07 (0.01) | 0.13 (0.01) | 0.08 (0.01) |
| Ca | 0.58 (0.09) | 0.36 (0.08) | 0.50 (0.09) |
| Mg | 0.13 (0.01) | 0.22 (0.01) | 0.20 (0.02) |
| K | 0.26 (0.02) | 0.25 (0.03) | 0.20 (0.02) |

Values are in percentage dry weight; values in parentheses are standard deviations.

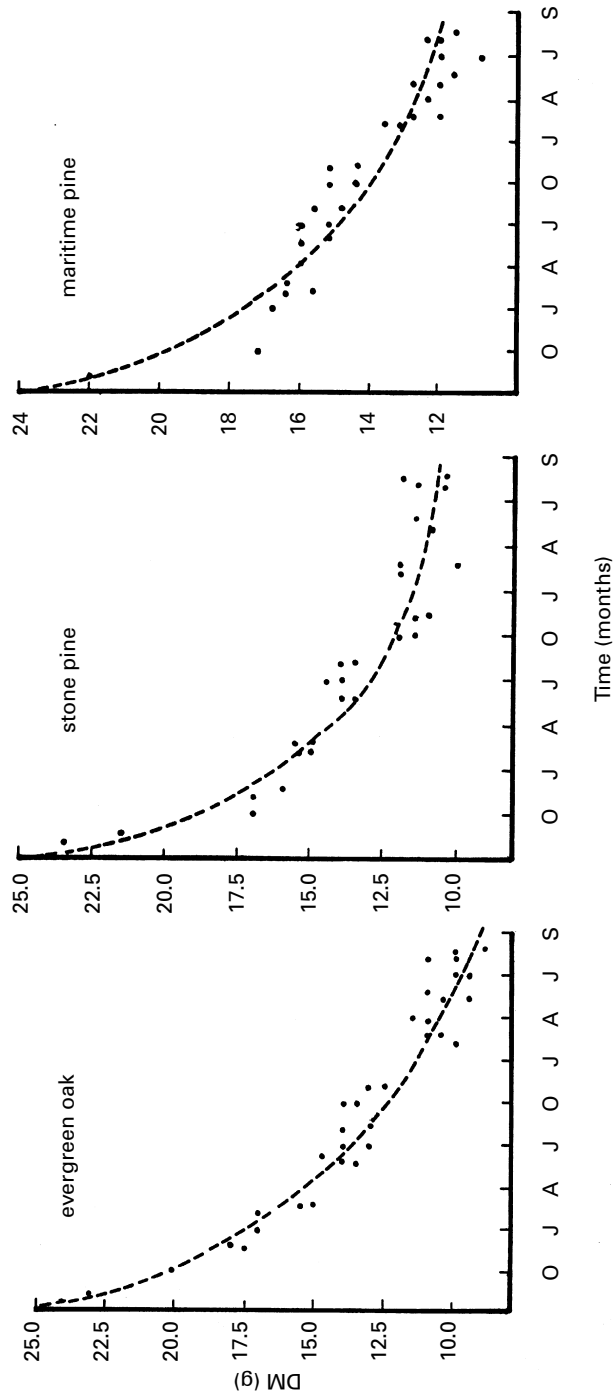


Figure 2. Monthly loss in weight of decomposing leaves (g dry matter, DM) of the three studied stands.

Table 4: Student's *t* values of analysis of variance statistics applied to the dynamics of the release of nutrients in decomposing leaves of needles placed in their own ecosystem

| Element | <i>Q. rotundifolia</i> (<i>n</i> = 36) | <i>P. pinea</i> (<i>n</i> = 37) | <i>P. pinaster</i> (<i>n</i> = 35) |
|---------|--|-------------------------------------|--|
| N | 0.0005 | 0.0005 | 0.0005 |
| P | 0.0004 | 0.0089 | 0.0005 |
| Ca | 0.0005 | 0.0005 | 0.0005 |
| Mg | 0.0005 | 0.0001 | 0.0002 |
| K | 0.2127* | 0.5136* | 0.1663* |

n, Number of samples.

*Significant differences for $\alpha = 5\%$.

Table 5: Minimum bioelement values yielded from decomposing leaves after both 12 and 24 months in both leaf litter and leaves

| Ecosystem | Content (kg ha ⁻¹) | | | | |
|--------------------------------------|--------------------------------|------|------|------|------|
| | N | P | Ca | Mg | K |
| <i>Quercus rotundifolia</i> | | | | | |
| Total leaf litter | 27 | 1.7 | 17 | 4.5 | 5.2 |
| Leaves | 22 | 1.2 | 12 | 2.4 | 3.8 |
| Yield | | | | | |
| First year | -2.0 | 0.3 | 3.5 | 1.0 | 3.0 |
| Second year | 4.0 | 0.2 | 0 | 0.3 | 0.3 |
| Total minimum yield | 2.0 | 0.5 | 3.5 | 1.3 | 3.3 |
| Total minimum yield/potential return | 0.09 | 0.42 | 0.29 | 0.54 | 0.84 |
| <i>Pinus pinea</i> | | | | | |
| Total leaf litter | 14 | 2.2 | 9.9 | 4.8 | 3.3 |
| Leaves | 14 | 2.1 | 9.0 | 4.5 | 3.2 |
| Yield | | | | | |
| First year | -1.5 | 0.8 | 0.8 | 2.1 | 2.5 |
| Second year | 4.0 | 0.5 | 1.0 | 0.8 | 0.2 |
| Total minimum yield | 2.5 | 1.3 | 1.8 | 2.9 | 2.7 |
| Total minimum yield/potential return | 0.18 | 0.62 | 0.20 | 0.64 | 0.84 |
| <i>Pinus pinaster</i> | | | | | |
| Total leaf litter | 8.4 | 0.8 | 9.3 | 4.7 | 3.3 |
| Leaves | 8.1 | 0.8 | 9.0 | 4.5 | 3.2 |
| Yield | | | | | |
| First year | -1.8 | 0.1 | 3.3 | 2.0 | 2.5 |
| Second year | 2.0 | 0.3 | 0.3 | 1.2 | 2.5 |
| Total minimum yield | 0.2 | 0.4 | 3.6 | 3.2 | 2.6 |
| Total minimum yield/potential return | 0.03 | 0.50 | 0.40 | 0.71 | 0.81 |

are subject to a double climatic stress; namely, the summer drought and the winter cold.

The magnitude of the shedding is intimately related to primary production (Bray and Gorham, 1964), from which it may be inferred that productivity will be low in the three plots and that

this, owing to the high percentage of leaves in the production, will hinder them from reaching maturity.

The production by fractions was compared using Student's *t* test, obtaining the values shown in Table 6. In the case of the leaves component

there were no significant differences in the contributions among the three forests and neither were there any significant differences for the twigs between *P. pinea* and *P. pinaster*. However, significant differences did appear regarding the contribution of twigs from the oaks and those of the two species of pine, release to the humus being much more abundant in the former. This means that, with respect to the shedding of twigs, the action of meteorological agents (wind, snow) is not very important in the ecosystems studied. Finally, significant differences can be observed in the shedding of bark between the two pine forests, that of *P. pinea* being more important.

Regarding the phenology of the three ecosystems, there was a definite similarity particularly when comparing the two pine forests, which is undoubtedly due to their genetic proximity (Hernández *et al.*, 1995).

A common observation for all three forests was that the greatest litter fall occurred in the third year and that in this year, shedding was concentrated in the first 2 months. This points to a converging physiological response to the pronounced summer drought of that year which, according to Rapp (1984) triggers the early senescence of plant organs. Jensen (1974) has reported that the occurrence of a dry period increases the fall of litter; that is, within the genetic framework in which the phenology of the shedding depends it would be possible to speculate in terms of the influence of environmental factors, among which humidity and temperature would be decisive.

Decay organic matter

K , K_0 and K_d indices were obtained for total litter rather 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 by Bock (1963), Edmonds (1980) and O'Connell (1987). The values reported by Maheswaran and Attiwill (1987) were higher and those of Gallardo and Merino (1993) were lower.

The litter bags may have hindered free access to the mesofauna (Joergensen, 1991) 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 (Meentemeyer, 1978) and low in N (Berg, 1988). It is possible to observe 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 (Meentemeyer, 1978; Melillo *et al.*, 1982).

An almost complete halt in decaying occurs during the dry summer periods, reflecting in part that the litter dries before the soil, and also dampens before the soil because of the dew effect, with mineralization continuing when humidity is

Table 6: Student's t -test comparing the production by different fractions

| Vegetal organs | Levenes F | Student's t |
|--|-------------|---------------|
| Evergreen oak <i>v.</i> Mediterranean pine | | |
| Leaves | 0.6192 | 0.5197* |
| Branches | 0.0005 | 0.0005 |
| Evergreen oak <i>v.</i> maritime pine | | |
| Leaves | 0.7479 | 0.7995* |
| Branches | 0.0005 | 0.0005 |
| Mediterranean pine <i>v.</i> maritime pine | | |
| Leaves | 0.3706 | 0.3503* |
| Branches | 0.3655 | 0.7071* |
| Bark | 0.0009 | 0.0005 |

high despite the lower temperatures. In this case, a temperature increase of a few degrees in the wet period has significant effects (Shanks and Olson, 1961). The effect of the dry period on leaf decay has been addressed in depth by Martín *et al.* (1993). During the late decay phases, the effect of dry periods is not detectable. As a result, in these forest ecosystems, leaf-litter decay is linked above all to humidity itself (Beyer and Irmeler, 1991), with mineralization slowing down when the leaf litter is dry (the soil may continue to be moist to a depth of >40 cm). Toutain (1981) stressed, however, that there are physical and physicochemical processes of decay in summer (losses of dry matter by animals, water or winds, could be limited).

The winter temperature does not appear to be a first-order limiting factor, under Mediterranean conditions; rather, the seasonality of humidity (necessary for biological activity) and of rainfall (necessary for washing and the removal of solutes, micelles and microparticles towards the mineral horizons of the soil) is responsible. Climate has a strong influence in the first phases of decay and, as mentioned earlier, an increase in temperature of just a few degrees during the wet period may have significant effects (Shanks and Olson, 1961).

Kononova (1966) stated that, initially, autumnal rains leach the hydrosoluble substances, facilitating the action of the soil microorganisms. Following this, the presence of residual chemical substances (lignin) decreases the loss of organic matter in the decomposing forest litter. In addition, the summer dryness reduces the microbial activity.

The sequence of the indices found here does not follow the rainfall gradient, indicating that it is not the total amount of rain that governs the greater rate. Perhaps the greatest effect comes, at least in the early stages of decay, from the distribution of the rainfall throughout the year together with air temperature, aeration and soil texture, humidity and the temperature of the surface horizon of the soil. Moreover, both the specific characteristics of the site and the chemical composition of the litter govern the nature of the heterotrophic community (Kögel-Knaber *et al.*, 1990) and its presence and activity are linked to the physicochemical characteristics of the substrate (Toutain, 1981).

The resulting regression equations for decomposition are as follows:

Quercus rotundifolia ($n = 44$).

$$R = 8.86 + 15.5 \exp(-0.10t)$$

Pinus pinea ($n = 44$).

$$R = 10.8 + 13.3 \exp(-0.15t)$$

Pinus pinaster ($n = 44$).

$$R = 10.7 + 11.7 \exp(-0.08t)$$

A similar model of $DM = A + B \exp(-Ct)$ has been used by Olson (1963) and Berg and Lundmark (1987).

What does seem clear is that using the litter-bag technique gives decay indices for the first year that are below the true values, since the technique prevents the important role of comminution (Bocock, 1964) and that of microbiological insemination (Dommergues and Mangenot, 1970) by the mesofauna, and that fact probably explains why, compared with other published data (Martín *et al.*, 1997), the asymptotic values given here are relatively high.

Dynamics of bioelements during leaf decomposition

Table 3 shows that *P. pinaster* recovers more of the leaf N before abscission. Table 5 shows that there are striking differences between the rates at which N is cycled through litter in the three ecosystems, which may be an indication of greater demand (*Q. rotundifolia*) or frugality (*P. pinaster*). The *P. pinaster* is observed to cycle little P, whereas *Q. rotundifolia* moves more Ca than the conifers. There are no significant differences between the three ecosystems in relation to the K and Mg put into circulation. Rapp and Cabanettes (1980) and Lemoine *et al.* (1988) estimated potential returns of N, P, Ca, Mg and K in *P. pinea* that were higher than those obtained in our study of pine needles. However, Rapp (1971) estimated a greater potential return of N, Ca, and K through leaves in *Q. ilex*, that of P and Mg being slightly lower. When compared with temperate deciduous formations, it is obvious that, in the latter, we will find a greater potential return (Duvigneaud and Denaeyer-De Smet, 1964), although this is not so clear for P (Hernández *et al.*, 1995).

Duchaufour (1984) postulated that the relationship between the total amount of a bioelement and that yielded after decomposition can

give an idea of whether chemical washing or biological fixing predominates in an ecosystem. If ratios are made between the minimum amount returned and the potential or total amount of each bioelement (Table 5), it is easy to separate the bioelements that undergo intense biological immobilization (N, Ca in *Q. rotundifolia* and *P. pinea*), moderate immobilization (P, Ca in *P. pinaster*), and heavy washing (K).

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