Residence time and decomposition rate of Pinus pinaster needles in a forest floor from direct field measurements under a Mediterranean climate

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Abstract

Pinus pinaster (Soland) litter was sampled from a Mediterranean forest floor in order to study decomposition kinetics under natural conditions. Needles were divided into five distinct and successive compartments L, F1a, F1b, F2a, F2b, according to their morphology. The methods of Kendrick (Kendrick, W.B., 1959. The time factor in the decomposition of Coniferous leaf litter. Canadian Journal of Botany 37, 907–912) and Gourbière, (Gourbière, F., 1981. Vie, sénescence et décomposition des aiguilles de sapin (Abies alba Mill.) Part I: Méthodologie et premiers résultats. Acta oecologica, Oecologica Plantarum 2, 223–232) were used to determine the mass loss of each compartment. On the forest floor, the total needle compartment represented 39% of the total decomposing litter mass and the five distinct compartments had similar mass values of 2.8–3.1 t ha⁻¹ ash-free material. The decomposition rate of each compartment was calculated from the mass compartment, its mass loss and the litter-fall in the site. The remaining mass in relation to calculated time was described by a single first-order decay model with a decomposition rate (k) of 0.135 year⁻¹ (R² = 0.86) or by an asymptotic model with k = 0.180 year⁻¹ and the asymptote at 83.2% (R² = 0.87). The first-year mass loss equalled 13%, and after 5.1 years it reached 50% for both models. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Studies on litter decomposition rate are very important for understanding the way a forest ecosystem functions. Indeed, decomposition controls the nutrient release rate, and therefore, the availability to plants of soil nutrients. A small proportion of the nutrients used for the primary production (N, P, S, Ca, Mg) comes from releases of minerals from parent material. The largest proportion comes from the mineralisation by micro-organisms of the organic material fallen on the floor (Swift et al., 1979). Litter decomposition rates also determine the soil organic matter accumulation rates on the forest floor. The balance between litter production and its decomposition controls the size of the carbon reservoir within the soil. A good knowledge of these processes in field conditions and without experimental artefacts is essential to predict the fate of this carbon reservoir in response to climate changes.

Only a few studies have been conducted on decomposition under Mediterranean climates (Escudero et al., 1987; Ferran and Vallejo, 1992; Stamou et al., 1994). In particular, conifers have been little studied. One paper deals with Pinus pinaster (Soland) in southern Tuscany (Italy) (van Wesemael and Veer, 1992), others with P. ponderosa (Hart et al., 1992) in
California, *P. halepensis* in Catalonia (Spain) (García-Plé et al., 1995; Rovira and Vallejo, 1997) and *P. pinea*, *P. laricio* and *P. sylvestris* in Italy (Virzo de Santo et al., 1993). This paper concerns the decomposition of *P. pinaster*, a coniferous tree common in warm Atlantic and Mediterranean climates, on acid parent material in the South of France.

Most studies on litter decomposition have been conducted in litterbags (Gloaguen and Touffet, 1980; Moore, 1984; Taylor et al., 1991; Berg et al., 1993) or microcosms (Gillon et al., 1994). Several authors (Wittkamp and Olson, 1963; Rapp, 1971; Virzo de Santo et al., 1993; Fioretto et al., 1998) have shown significant discrepancies between results coming from these kind of experiments and from direct observations of litter decomposition processes. It was generally observed that confining litter in bags increased the moisture content (Tanner, 1981; Hutchinson et al., 1990). This increase led to faster decomposition rates under a Mediterranean climate or in dry sites (Rapp, 1971; Hutchinson et al., 1990; Virzo de Santo et al., 1993) whereas, under wet conditions no differences were evident (Lemée and Bichaut, 1973; Tanner, 1981).

The aim of this paper is to propose a field method, based on the studies of Kendrick (1959) and Gourbière (1981, 1982), to investigate the decomposition kinetics of coniferous leaf litter without the bias of artificially enclosing material. This method allows us to determine the mass loss and the age of in situ conifer litter, and to build a predictive model of decomposition with time, using direct observations from the forest floor. The method may not be suitable for broad-leaf litters.

2. Materials and methods

2.1. Description of the forest stand

The study site, called Thézan, is a 100 years old maritime pine (*P. pinaster*) forest located near Lézignan in the South of France (43°07′N; 2°45′E) on a leached red sandy Mediterranean soil (chromic luvisol, FAO). No fire has been observed within the last 100 years. The mean annual temperature based on a 30-year average is 14.4°C, with a mean temperature of 7°C for January and 23.2°C for July. The mean annual precipitation is 580 mm with a maximum in October. Almost half of the annual precipitation takes place from October to January. The potential and actual evapotranspiration and the water deficit were calculated with a program (WATERBUD) designed by Sharpe and Prowse (1983). The soil moisture storage was fixed at 300 mm to be comparable with previous works (e.g. Meentemeyer, 1984; Dyer et al., 1990; Berg et al., 1993). A soil water deficit usually appears during four months in the summer from June to September, and reaches a total of 187 mm per year (Fig. 1). The annual actual evapotranspiration (AET) equals 580 mm. The climate is classified as wet Mediterranean.

Pines cover 50% of the stand area, the main other species being *Erica scoparia* (15% of the area), *Juniperus oxycedrus* (15%) and *Ulex parviflorus*, *Quercus coccifera* and *Calluna vulgaris*. The depth of the needle compartment of the floor averages 7 cm.

2.2. Litter-traps

Litter-fall was collected in 990 cm² litter-traps (plastic buckets with small holes to evacuate rainwater) placed at 1.50 m from the soil. Fifteen litter-traps were randomly set up on a 30 × 30 m plot, and were sampled four times a year in 1993 and 1995. The litter was air dried and weighed. The material other than pine needles was sorted out. The debris and the needles were separately weighed.

2.3. Litter preparation

During winter 1996, seven 30 × 40 cm undisturbed soil blocks including all the organic profile and the upper part of the mineral soil were randomly sampled in the plot.

The litter was dried to constant weight at 45°C. Three distinct needle compartments were sorted out according to the morphological criteria described by Kendrick (1959) and Gourbière (1981); (L) surface light-brown needles, still intact and smooth, (F1) entire dark-brown and black needles with a porous appearance, and (F2) broken black needles with a porous appearance (Table 1). The F1 and F2 compartments were subdivided into two sub-compartments F1a, F1b and F2a, F2b, according to their state of decomposition. The difference between the entire and broken needles was attributed to decomposition although some needles may have been broken by animal or
human trampling. Nevertheless, the extent of disturbance was low by these factors and the appearance of the needles which were artificially broken was easy to recognise. In addition, the compartments occur in distinct superimposed layers in undisturbed conditions; nevertheless, the sorting was done on a morphological basis because perturbations can occur during transport, and also because the long *P. pinaster* needles (12–14 cm) often cross different compartments. The stems, the cones, the scales and the flowers were also sorted out from each sampled litterblock and weighed.

### 2.4. Mass loss determination

One meter of needles placed end to end was weighed to determine the linear mass \( l_i \) of each compartment. This measurement was expressed in mg m\(^{-1}\). The linear mass was measured with five replicates on each compartment. The relative needle mass loss (ML\(_i\)) of decomposing needles from each compartment was calculated from Eq. (1), where \( l_0 \) represents the linear mass of needles sampled in litter-traps:

\[
ML_i = (l_0 - l_i)/l_0
\]

(1)

The mass loss determination from the linear mass measurement postulates that decomposition processes did not affect the length of the needles except by breaking. Needle fragments could also be exported by macrofaunal consumption or could be transported by the macrofauna to other places or other compartments, and are therefore, not included in the measure which only takes microbial processes into account.

The weight was expressed ash-free because the mineral contamination was increasing with depth. Ash content was determined gravimetrically after 6 h at 550°C.

### 2.5. Determination of the fluxes between the compartments and the residence time

Considering that the five compartments, \( S_1, S_2, \ldots, S_5 \), are successive and are fed by an input flux \( F(t) \), the variation of their size \( S_1(t), S_2(t), \ldots, S_5(t) \) follows the equations

\[
dS_1(t)/dt = F(t) - k_{11}S_1(t)
\]

(2)

\[
dS_2(t)/dt = k_{21}S_1(t) - k_{22}S_2(t)
\]

(3)

\[
\ldots
\]

\[
dS_i(t)/dt = k_{i,i-1}S_{i-1}(t) - k_{ii}S_i(t) \text{ for } i = 2, \ldots, 5
\]

(4)

where \( k_{ii} \) are the kinetic coefficients of the output flux from \( S_i \) and \( k_{i,i-1} \), the kinetic coefficients of the transfer from \( S_{i-1} \) to \( S_i \). Because there is a mass loss as \( CO_2 \), \( k_{i,i-1} < k_{i-1,i-1} \) and the partition coefficient to the next compartment is

\[
p_{i,i-1} = k_{i,i-1}/k_{i-1,i-1}, \text{ for } i = 2, \ldots, 5
\]

(5)

with \( 0 \leq p_{i,i-1} \leq 1 \).

If \( F(t) \) is constant through time \( (F(t) = F_{10}) \), then \( S_i(t) \) can be represented by a sum of five exponential functions, following the general theorems about differential equation systems:

\[
S_1(t) = c_{10} + c_{11} \exp(-K_{11}t) + c_{12} \exp(-K_{21}t) + \cdots + c_{15} \exp(-K_{51}t)
\]

(6)

\[
S_2(t) = c_{20} + c_{21} \exp(-K_{12}t) + c_{22} \exp(-K_{22}t) + \cdots + c_{25} \exp(-K_{52}t)
\]

(7)

\[
\ldots
\]

\[
S_5(t) = c_{50} + c_{51} \exp(-K_{15}t) + c_{52} \exp(-K_{25}t) + \cdots + c_{55} \exp(-K_{55}t)
\]

(8)

In the long-term, this system tends to be stationary, the derivatives \( dS_i/dt \) converge to 0 and the size of the compartments \( S_i \) becomes constant.

\[
S_i = F_{i,i-1}/k_{ii} \text{ for } i = 1, \ldots, 5
\]

(9)
where \( F_{i, i-1} \) represents either \( F_{10} \) or the flux from the compartment \( i - 1 \) to the compartment \( i \)

\[
F_{i, i-1} = k_{i, i-1}S_{i-1}
\]  
(10)

Hence

\[
F_{i, i-1} = p_{i, i-1}F_{i-1, i-2}
\]  
(11)

In a stationary system, the partition coefficients are directly related to the observed linear mass

\[
p_{i, i-1} = l_{i}/l_{i-1} \quad \text{for} \quad i = 2, \ldots, 5,
\]  
(12)

so that all fluxes can be computed from \( F_{10} \) and \( l_i \),

\[
F_{i, i-1} = (l_i/l_{i-1})F_{i-1, i-2} \quad \text{for} \quad i = 2, \ldots, 5
\]  
(13)

The input flux of the compartment 1 (\( F_{10} \)) is related to the initial flux of falling leaves by the function (14)

\[
F_{10} = (l_1/l_0)F_0
\]  
(14)

which is similar to Eq. (13).

In this stationary cascade system, each compartment \( i \) is fed with a single constant flux \( F_{i, i-1} \). The corresponding residence time \( (t_{r_{i}}) \) is given by

\[
t_{r_{i}} = 1/k_{ii} = S_{i}/F_{i, i-1}
\]  
(15)

The cumulated residence time \( t_{c_{i}} \), i.e. the residence time of a needle atom being successively in all compartments from 1 to \( i \), is equal to the sum of each elementary residence times

\[
t_{c_{i}} = \sum_{i=1}^{i=n} t_{r_{i}}
\]  
(16)

This cumulated residence time was taken as an estimation of the decomposition time associated with each compartment, i.e., the average time at which each compartment is decomposed.

2.6. Determination of the initial chemical composition of needles

Six replicates of needles sampled in litter-traps were chemically analysed. C and N analyses were performed on a CHN analyser (Carlo Erba, EA 1108).

2.7. Data processing

Exponential model fits, two-way ANOVA and Newman–Keuls tests (Dagnelie, 1975) were calculated using Graphpad PRISM software version 2.00, from Graphpad Software.

In order to compare the decomposition rate of \( P. \) pinaster needles with published data, three parameters were taken from tables and graphs: the decomposition rate (\( k \)) from exponential decay curve \( RM = A e^{-kt} \) (Olson, 1963) (where \( RM \) is the remaining mass and \( A \) the initial mass), and/or time necessary to reach 50% of decomposition (half-life), and/or mass loss percentage after one year of decomposition. These values were compared to those obtained in this study. All averages are given with their standard deviations.

3. Results

3.1. \( P. \) pinaster litter quantity and quality

The mean annual needle fall (without ash correction) was 3.46 t ha\(^{-1}\) year\(^{-1}\) in 1994 and 3.89 t ha\(^{-1}\) year\(^{-1}\) in 1996. The mean total litter-fall for 1994–1996 was 4.64 ± 0.72 t ha\(^{-1}\) year\(^{-1}\). The largest needle fall usually occurred in summer in July, August and September which constituted 60–80% of the annual fall. After needle fall, the nitrogen concentration was 0.40 ± 0.06% and the carbon 49.11 ± 0.38%.

The total litter mass of the forest floor was 43.1 ± 12.0 t ha\(^{-1}\). The needle compartment was the largest, representing 39% of the total decomposing litter mass followed by cones, stems and vegetal debris (Fig. 2). The inflorescence and bark fractions were negligible. Among the needles, the mass of the five compartments (L, F1a, F1b, F2a and F2b) ranged from 2.8 to 3.1 t ha\(^{-1}\) ash free (Fig. 3).

3.2. Linear mass variability

The determination of the mass loss from a compartment was based on the linear mass of newly-shed litter (\( I \): initial linear mass of the litter). Consequently, it

![Fig. 2. Litter composition. (Error bars represent the standard deviation \( n = 7 \)).](image-url)
was important to know the variability of this parameter in order to estimate the reliability of the method. The linear mass of newly-shed needles (without ash correction) varied from 879 \pm 249 to 943 \pm 263 mg m\(^{-1}\) as a function of sampling date and from 859 \pm 8 to 1000 \pm 35 mg m\(^{-1}\) as a function of litter-trap position.

A two-way ANOVA, testing the effect of three sampling dates (6 July and 30 Aug. 1995, and 5 Sept. 1996) and the effect of litter-trap position (13 positions) on the linear mass of newly-shed needles, showed a significant effect of both factors (\(P < 0.01\)). The litter-trap effect could be due to the heterogeneous distribution of the trees with various ages and sizes in a forest where regeneration was allowed and to the distribution of the throughfall and the local radiation. The date effect can be attributed to the seasonal variation of the litter quality, and also, to the effect of leaching in litter-traps between two sampling occasions. There was no statistical interaction between the two factors. Finally, the initial linear mass was calculated from the mean of the 39 values (13 replicates \times three dates), weighted for the mass of needles trapped on each of the three sampling dates. It equalled 926 mg m\(^{-1}\) or 849 mg ash-free m\(^{-1}\).

The average linear mass and the average remaining mass (expressed as a percentage of the initial mass) exhibited a significant decrease (Newman–Keuls test, \(P < 0.05\)) along the successive compartments discriminated by morphological criteria (Table 2). These results indicate that these morphological criteria have a biological significance and that the separation of F1 and F2 compartments into two sub-compartments was justified (Table 1).

### 3.3. Decomposition time

The estimated decomposition time for a mass loss of 67.8 \pm 5.7\% for the oldest compartment was 8.05 \pm 2.59 years (Table 2). Newman–Keuls tests between groups showed that the ages of the L–F1a and F1a–F1b compartments were not statistically different. This was mainly caused by the large spatial variability of the needle compartment mass in the field (Table 2). The fluxes are represented in Fig. 3. The residence time in each compartment, \(t_r\), increased with depth, from 1.10 \pm 0.35 years for compartment L, to 2.59 \pm 1.86 years for compartment F2b. The size of the compartments was similar. The annual mass loss as CO\(_2\) release ranged from 0.3 to 0.6 t ha\(^{-1}\) year\(^{-1}\), the annual output flux from a compartment to the next decreased with depth from 2.96 \pm 0.18 t ha\(^{-1}\) year\(^{-1}\) from the compartment L to 1.09 \pm 0.19 t ha\(^{-1}\) year\(^{-1}\) from the compartment F2b. This last output represented the input of organic matter from the litter to the humus (Oh layer). These estimations did not include the amount of material exported by the macrofauna, and therefore, the decomposition time was underestimated.

### 3.4. Decomposition model

The remaining needle mass (RM) was plotted against the estimated decomposition time \(t_{ci}\) in Fig. 4.

![Decomposition models](image)
The double exponential decay with
\[ \text{RM} = A e^{-kt_{\text{a}}} + B e^{-kt_{\text{b}}} + C \] (17)

often reported in the literature in experimental conditions (Berg and Ågren, 1984; Gourbière and Corm, 1987; Gillon et al., 1994) overfitted the data. The best fits were obtained with a single asymptotic model
\[ \text{RM} = A e^{-kt_{\text{a}}} + B \] (18)

with \( R^2 = 0.87 \), where \( A \) represents the percentage of material decomposing at rate \( k \), and \( B \) the proportion of material decomposing with a rate equal or close to zero \( (A + B = 100) \), and with the exponential model
\[ \text{RM} = A e^{-kt_{\text{a}}} \] (19)

which gave a similar fit with \( R^2 = 0.86 \), but gave lower confidence intervals of \( A, k \) and half-life mean values because of the lower number of variables (Table 3). Both models were fitted to four replicate data (Table 3) and validated with three other independent replicates (Fig. 5). The linear regression slope between measured and predicted data when the intercept was forced to zero, was \( 1.01 \pm 0.01 \) \((R^2 = 0.95)\) and \( 0.99 \pm 0.01 \) \((R^2 = 0.94)\) for the exponential and the asymptotic model, respectively. The decomposition rate \( (k) \) was \( 0.13 \pm 0.01 \) year\(^{-1}\) for the exponential model and \( 0.18 \pm 0.06 \) year\(^{-1}\) for the asymptotic model. After one year of decomposition, the needles lost 12.6% of their initial mass according to the exponential model, and 13.7% according to the asymptotic model. The needle litter spent 5.1 years to reach 50% of decomposition in both models (Fig. 4).

4. Discussion

The choice between the asymptotic and the exponential model to describe the time-course of mass losses is based on the underlying processes of decomposition and organic matter dynamics. An exponential model implies that all organic matter will be eventually decomposed in an ecosystem at steady state where the input balances the output and the quantity of material on the forest floor shows long-term equilibrium. A true asymptotic model predicts a continual increase in the soil organic matter in the forest floor. This pattern of accumulation is not observed in stable (mature) systems indicating that the model only takes into account continuous processes and ignores discrete events, e.g. mechanical breakdown and exportation by soil fauna or invasion by white rot fungi. Berg et al. (1996) also suggested possible explanations for this limit value for decomposition and underlined the influence of nutrient composition on the community of microbial decomposer. Our models were fitted on data that reached a maximum of 78% of mass loss for an estimated decomposition time of 11 years for a plant material of

<p>| Table 2 |
| Decomposition of P. pinaster needle litter in each compartment on ash-free data basis(^a) |</p>
<table>
<thead>
<tr>
<th>Compartment</th>
<th>( n )</th>
<th>Linear-mass (mg m(^{-1}))</th>
<th>ML (% initial mass)</th>
<th>Age (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>31</td>
<td>849 (24) a</td>
<td>15.1 (5.2) a</td>
<td>1.10 (0.35) a</td>
</tr>
<tr>
<td>L</td>
<td>7</td>
<td>721 (44) b</td>
<td>24.2 (6.2) b</td>
<td>2.32 (0.61) ab</td>
</tr>
<tr>
<td>F1a</td>
<td>7</td>
<td>644 (52) c</td>
<td>37.4 (6.4) c</td>
<td>3.65 (0.90) b</td>
</tr>
<tr>
<td>F1b</td>
<td>7</td>
<td>531 (54) d</td>
<td>50.3 (6.3) d</td>
<td>5.46 (1.41) c</td>
</tr>
<tr>
<td>F2a</td>
<td>7</td>
<td>422 (53) e</td>
<td>67.8 (5.7) e</td>
<td>8.05 (2.59) d</td>
</tr>
<tr>
<td>F2b</td>
<td>7</td>
<td>274 (48) f</td>
<td>87.3 (5.8) f</td>
<td>11.3 (3.5) d</td>
</tr>
</tbody>
</table>

\(^a\) Standard deviations are in parenthesis. Means with different letters are significantly different \((P < 0.05, \text{Newman–Keuls test)}\); \( n \) is the number of replicates. Age represents the cumulated residence time.

<p>| Table 3 |</p>
<table>
<thead>
<tr>
<th>Parameters of the asymptotic and exponential models (Confidence intervals of the fits are given in italic, ( P = 0.95 ))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calibration model, ( n = 4 )</td>
</tr>
<tr>
<td>( A )</td>
</tr>
<tr>
<td>79.9</td>
</tr>
<tr>
<td>25.7</td>
</tr>
<tr>
<td>( k )</td>
</tr>
<tr>
<td>0.108</td>
</tr>
<tr>
<td>( \text{Half-life} )</td>
</tr>
<tr>
<td>( d_f )</td>
</tr>
<tr>
<td>( R^2 )</td>
</tr>
</tbody>
</table>
which the structure is still preserved. The fit of this relationship allows speculation on the further decomposition which takes place in the Oh horizon or deeper in the profile. It reached 22% (i.e., 100 – 78%) and 4% (i.e., 82 – 78%) according to the exponential and the asymptotic model, respectively. Since the linear mass method described mainly the basic microbial processes and did not include casual events, we consider that the asymptotic model is the best descriptor of the measured data. The 16.8% of organic matter which is not supposed to decompose according to the asymptotic model would disappear either by faunal transfer to deeper horizon (Howard and Howard, 1974) or by the occasional and local invasion of micro-organisms which are able to degrade recalcitrant organic matter (e.g. a burst of activity of white-rot fungi as it is shown by the well-known patchy distribution of bleached litter (Gourbière, 1981)). Nevertheless, the $k$ values of both models are needed in order to compare our results with the literature.

There are few decomposition studies based on direct measurements of the forest floor. Songwe et al. (1995) used a direct method for studying decomposition in a tropical forest. They sampled monthly 50 × 50 cm quadrats of forest floor and monthly litter-fall. The decay was calculated from the difference between the weight of the samples and the weight of the litter that fell during the following month and the weight of the samples in the next month. This method cannot be generally applied because of the high spatial variability of the forest floor mass. In a tropical climate, the decomposition rates are very high and sometimes can outweigh spatial variability.

Other authors have earlier placed leaves which were tethered with a nylon thread, directly on the soil to avoid them from being confined in bags (Anderson, 1973; Lousier and Parkinson, 1976) but mass loss was overestimated due to leaf breakage. Gourbière (1981, 1982), measuring linear mass, found that needles of *Abies alba* preserved their structural shape for a maximum of about eight years. At this stage, the mass loss in the F2 compartment was 40% of the initial needle mass. For *P. pinaster*, we defined two sub-compartments in the F2 compartment. F2a and F2b compartments reached in average 5.46 and 8.05 years of age with a mass loss of 50.3 and 67.8% of the initial needle mass, respectively. This means that *P. pinaster* at Thézan had a higher decomposition rate than *Abies alba* at Tarentaise (Mont Pilat, Massif Central, France). This difference may be species dependent, but it may also be due to the climate differences, especially the lower mean annual temperature of the *Abies alba* site compared to Thézan.

The decomposition rate that we found for *P. pinaster* with the exponential model ($k = 0.13 \text{ year}^{-1}$) meant a first year mass loss of 12.6% and a half-life of 5.1 years. Our decomposition rate values were lower compared to other field results in a Mediterranean climate. Nevertheless, using the $k$ value as calculated by van Wesemael and Veer (1992) by dividing the annual litter-fall by the total litter forest floor mass, we found a $k$ value of $0.23 \pm 0.06 \text{ year}^{-1}$ compared to the value of $0.17 \pm 0.03 \text{ year}^{-1}$ for *P. pinaster*, found by these authors in a similar stand to Thézan. Virzo de Santo et al. (1993), measuring linear mass on three coniferous species incubated in containers (*P. pinea*, *P. laricio* and *P. sylvestris*) in two sites, found a first year mass loss of organic carbon of 18 and 28% for all litters, despite differences in litter quality (except for *P. pinea* in one site which was only 4%). Similar results were found by Fioretto et al. (1998). These higher values can be explained by the higher precipitation of the Italian

![Fig. 5. Linear regression between measured and predicted remaining mass (RM) using the exponential model (A), and the asymptotic model (B).](image-url)
sites (960 and 1225 mm) compared to our site (580 mm). In these studies where litter were exchanged from one site to the other and vice-versa, the lack of a difference between species can be due to the influence of the native litter, which can outweigh the litter quality effect (Chadwick et al., 1998).

Most of the literature data are based on litter-bag studies. Virzo de Santo et al. (1993) and Fioretto et al. (1998) comparing litter-bags to linear mass method showed that in dry conditions, enhanced decomposition appeared in litter-bags, which preserve a higher moisture level. In Mediterranean region where summer drought is important, the relevance of this discrepancy should be taken into account. Aerts (1997), compiling literature, gave a mean $k$ value of 0.35 year$^{-1}$ for the Mediterranean region and a plot of $k$ versus AET corresponding to a value of 0.28 year$^{-1}$ for an AET = 580 mm. Similarly Berg et al. (1993) plotted data on the first-year mass loss of a standard *P. sylvestris* litter incubated in 1 mm mesh size litter-bags and in a large number of coniferous sites along a N–S transect against AET. The linear regression allowed them to predict a first-year mass loss of 32% for an AET of 580 mm. If the regression only includes Mediterranean, Central European and North American sites, the prediction decreases to 28%. However, lower values were found by Hart et al. (1992). They studied the *P. ponderosa* needle decomposition using litter-bags of 3–4 mm mesh size in two forests of different ages. They reported $k$ rate constants of 0.08 year$^{-1}$ in the 100-year old forest and 0.19 year$^{-1}$ in a 20-year old forest under a wet Mediterranean climate in California. Rovira and Vallejo (1997) found a slightly higher decomposition rate compared to our exponential model with a first year mass loss of 18% in litter-bags at a depth of 5 cm for *P. halepensis*, under similar climatic conditions which can be attributed to moist conditions when litter is buried.

The linear mass-loss method only takes into account needles that have retained their structure and excludes litter that was consumed and/or exported by the fauna. Consequently, if we suppose that the fauna consumption occurred in all compartments, the residence time of the litter in each morphological compartment is underestimated, except for the L compartment. Indeed, David et al. (1991) demonstrated in a beech forest that saprophagous animals did not feed, or fed very little, on litter that had been lying on the ground for less than one year. After an average of 65% of mass loss, no needles with an intact structure remained and the deeper compartment was either an Oh horizon or directly an A1 horizon. The loss of structure was partly due either to the extreme fragility of the organic matter or to the massive consumption of this highly decomposed material by the fauna.

The linear mass-loss method measures decomposition that proceeds in contact with several other species that are present in the site. In fact, several works showed that when litters of different quality were mixed, the resulting decomposition rate can differ from the mean decomposition rates of the different species (Blair et al., 1990; Ineson and McTiernan, 1992; Briones and Ineson, 1996).

In addition to the present study, the linear mass method was used with different coniferous species: *A. alba*, *P. pinea*, *P. laricio*, *P. pinaster* and *P. sylvestris* (Gourbière, 1981, 1982; Virzo de Santo et al., 1993; Fioretto et al., 1998) in various natural sites, and therefore, we assume that it could be applied to other needle litter too. For broad leaves’ a method based on the mass loss of the leaves’ specific area could be suggested but it would be difficult to implement because of the fragility of the material.

The present method has the following advantages:

1. It measures decomposition directly as it occurs in the field without the potential artefact of litter enclosure.
2. It does not modify the moisture regime and it takes into account the moisture gradient through the profile from dryer compartments close to the surface to moist compartments in the deep horizons.
3. The contact with other litter species is maintained.
4. It needs only one sampling occasion which can be done at any time of the year.
5. It includes long-term decomposition data (up to 10 years); and finally,
6. It provides information on the influence of climate in the long-term on decomposition rate.

Nonetheless it also presents some disadvantages:

1. The sorting out of the litter is time consuming.
2. There is a high variability of forest floor mass which results in a large variability in the estimated age of the litters; and lastly,
3. The mass loss due to animal exportation cannot be measured.

5. Conclusions

Direct observation allows us to measure the real mass loss of *P. pinaster* needles observed in the field. The subdivision of F1 and F2 compartments into F1a, F1b, F2a, F2b was completely justified according to the Newman-Keuls’ groups, especially when the remaining mass data was tested (Table 2). The calculation of estimated decomposition time on the basis of the mean annual flux from one compartment to another showed that the *P. pinaster* mineralisation
process in a Mediterranean climate follows an asymptotic model: $RM = A e^{-kt} + (100 - A)$.

The decomposition rates observed in the literature for $P.\ piniaster$ and several other species using different decomposition measuring methods were usually greater, especially when the confined litter was under dry conditions.

We conclude that the present method is more reliable for the long-term dynamics of conifer litters and it also reduces experimental artefacts produced by the litter enclosure method.

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