

## Decomposition of Alder, Ash, and Poplar Litter in a Mediterranean Riverine Area

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**Abstract:** Litter decomposition dynamics of three Mediterranean riverine species [*Alnus glutinosa* (L.) Gaertn, *Fraxinus angustifolia* Vahl., and *Populus x hybrida*] was studied in a 2-year experiment in the province of Guadalajara (Spain) using the litterbag technique. Decay rates of the litter were estimated by fitting a single exponential model to the litter decomposition data. At the end of the experiment (after 485 days), the remaining litter necromass varied in the following order: *Populus x hybrida* > *Alnus glutinosa* > *Fraxinus angustifolia*. Litter of the three species was fast degraded; ash litter was almost totally degraded at the end of the experiment. Alder had the highest concentrations of total nitrogen and ammonium in litter, and its pattern of degradation and release to the system was different to the other two litters. This could influence the soil nutrient contents in each system as was indicated by the soil nutrient values.

**Keywords:** *Alnus glutinosa* (L.), Gaertn, ammonium, C/N ratio, *Fraxinus angustifolia* Vahl, litter quality, *Populus x hybrida*

### INTRODUCTION

Decomposition of tree litter is a key process of nutrient cycling in terrestrial ecosystems (Vitousek et al. 1994; Aerts and de Caluwe 1997). On the forest floor, leaf litter acts as an input–output system for nutrients, serving as a

Received 29 November 2004, Accepted 3 October 2005

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temporary sink for nutrients such as nitrogen (N), sulfur (S), and phosphorus (P). Litter also functions as a “slow release” nutrient source for plants and microorganisms. Because of this key role of litter decomposition, factors influencing litter quality and production have important implications for long-term productivity of forest ecosystems (Adams and Angradi 1996).

Litter decomposition involves two simultaneous and fundamental sets of processes (Coûteaux, Bottner, and Berg 1995): 1) the mineralization and humification of lignin, cellulose, and other compounds by the action of a succession of microorganisms and 2) the leaching of soluble compounds into the soil profile. Mineralization of litter nutrients is often referred to a three-stage process: first, nutrients in soluble form are leached from the litter; second, nutrient immobilization occurs; and finally, net nutrient litter mineralization takes place, thereby making nutrients available for plant uptake again (Aerts and Chapin 2000).

Litter production and quality are regulated by stand floristic composition, age, tree management, abiotic factors, and, when grazing is taking place, stocking levels (Finner 1996). Litter decomposition is regulated by three interacting group of factors: 1) the physicochemical soil environments and the chemical properties of the organic matter acting through their regulation of the decomposer community species composition and activity (Swift, Heal, and Anderson 1979; Beare et al. 1992); 2) comminution by which there is a physical reduction in particle size and often selective redistribution of chemically unchanged litter; and 3) leaching, which causes transport down the profile or removal from the system of labile resources in either changed or unchanged form (Heal, Anderson, and Swift 1997). All these factors in turn also alter decay and nutrient turnover rates. For instance, climate has a direct effect on litter decomposition through the regulation of microorganism activity. However, as a result of the climate control of soil formation and nutrient cycling (Vitousek and Sandford 1986; Lavelle et al. 1993), climate must also have an indirect effect through the climatic effects on litter chemistry (Swift and Anderson 1989). Dominant functional tree type also influences litter timing, quantity, quality, and thus the litter decomposition rate (Wedderburn and Carter 1999). Riverine systems are defined as the ecosystems that occupy areas adjacent to the natural watercourses and are characterized for being biogeographical islands with high flora and fauna species richness. The freshwater riverine areas are very productive systems that constitute both an important nexus between terrestrial and aquatic systems (Sánchez Mata and de la Fuente 1985) and a corridor for species and nutrients from the upper to the lower parts of the catchment. Riverine systems are refuges of fragile ecosystems that are extremely sensitive to human activities, for example, deforestation, road building, and industry. Although decomposition processes have been revealed as essential for the maintenance of adequate nutrient supply and diversity in other areas, little attention has been paid to riverine areas, and data are infrequent.

The decomposition rates of plant leaf litter from different functional tree types and their contribution to N input to the soil in a Spanish riverine area were investigated. Quantifying chemical characteristics of the litter and decomposition litter rate were used for this purpose. The study focused on measuring the N and carbon concentration of leaf litter as they influence decomposition and release of N (Berendse, Berg, and Bosatta 1987).

## MATERIALS AND METHODS

### Site Description

The field experiment was conducted at one riverine area in the vicinity of Humanes de Mohernando (Guadalajara, central Spain) (Figure 1). The area can be characterized as belong to the *Populetalia albae* (Clase *Quercus-Fagetea*) and it occupies semipermanent waterlogged soils with the presence of gleyed horizons depending on soil water level. Within the area, three vegetation zones can be distinguished:

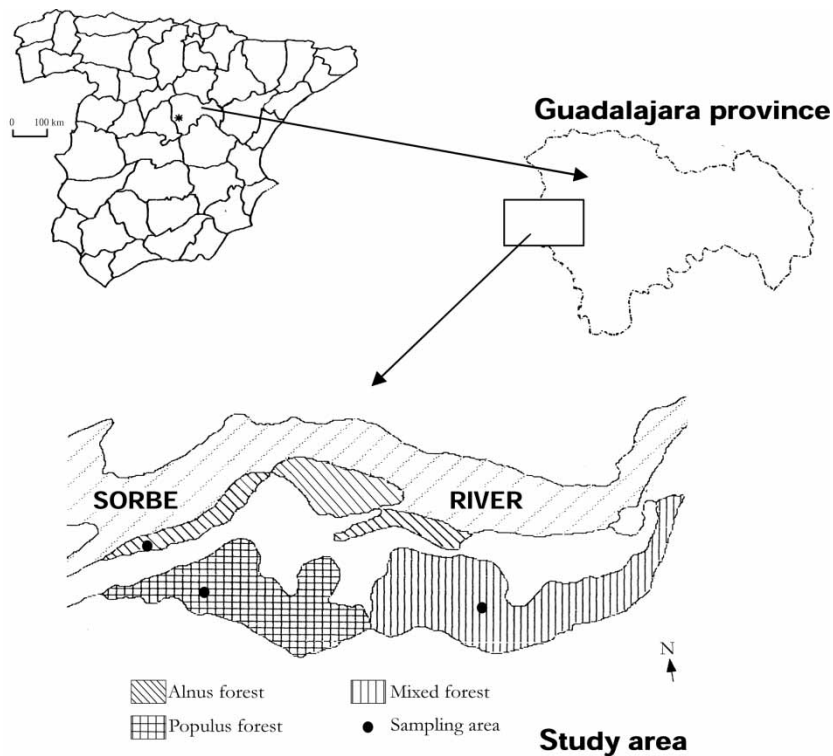


Figure 1. Map of the study area and study sites in central Spain.

1) a monospecific alder forest [*Alnus glutinosa* (L.) Gaertn] with trees ranging between 8 and 20 m in height and a density of  $0.7 \text{ trees} \cdot \text{m}^{-2}$ . The understory was mainly constituted by *Urtica urens* L., *Scirpus holoschoenus* L., and *Geranium robertianum* L.

2) A monospecific planted forest of poplar trees (*Populus x hybrida*) where trees ranged from 4 to 6 m in height and a density of  $0.87 \text{ trees} \cdot \text{m}^{-2}$ . The understory vegetation was dominated by the herbaceous species *Avena sterilis* L., *Bromus hordaceus*, L., *Poa pratensis* L., *Trifolium glomeratum* L., *Medicago minima* Lam., *Melilotus officinalis* Lam., and *Sangisorba minor* Scop.

3) A mixed forest formed by alder, poplar (*P. alba*), ash (*Fraxinus angustifolia* Vahl), and willow trees (*Salix* sp.) with a dense understory dominated by *Rubus ulmifolius* Schott and *Crataegus monogyna* Jacq.

All three zones were free of observable disturbance without evidence of recent cutting, burning, or grazing. A detailed description of the study area is given by Pérez Hernández (1996). In this area three tree species were chosen for the study according to their dominance in the forests. They were alder, poplar, and ash species, which represent two functional types: N-fixing deciduous (alder species) and non-N-fixing deciduous (ash and poplar species).

The three study zones showed a relative uniform climate characterized as mild Mediterranean. The yearly average rainfall was 397.4 mm. Annual average temperature was  $13^\circ\text{C}$ ; the average temperature of the coldest month was  $4^\circ\text{C}$  and the average temperature of the hottest month was  $23^\circ\text{C}$  (Forteza del Rey 1981). The ombroclimatic diagram is shown in Figure 2.

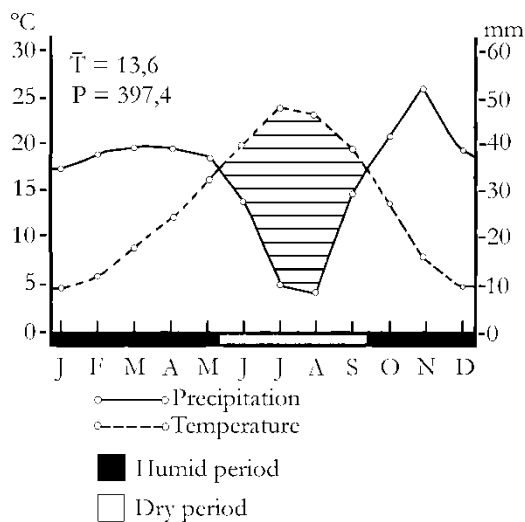


Figure 2. Ombrothermic diagram of the study area.

**Table 1.** Soil parameters in the study area at the beginning of the experiment

Soil parameter	<i>A. glutinosa</i> site	<i>F. angustifolia</i> site	<i>P. x hybrida</i> site
pH	7.94 ± 0.02	8.11 ± 0.02	7.98 ± 0.02
Carbon (%)	4.21 ± 0.16	2.91 ± 0.19	2.58 ± 0.14
Nitrate ( $\mu\text{g} \cdot \text{g}^{-1}$ )	14.50 ± 0.32	18.23 ± 0.25	17.30 ± 0.39
Ammonium ( $\mu\text{g} \cdot \text{g}^{-1}$ )	35.55 ± 1.64	22.39 ± 0.68	20.96 ± 1.03
Total nitrogen ( $\text{mg} \cdot \text{g}^{-1}$ )	4.18 ± 0.24	2.70 ± 0.11	3.00 ± 0.09
C/N	10.09 ± 0.37	10.78 ± 0.65	8.60 ± 0.48

Terrace levels and quaternary alluvial deposits form the soil substrate. The soil texture is sandy loam in all study zones (sand 65.8%, silt 21.0%, and clay 13.2%). The soil is classified as a Zerofluvents developed over the alluvial deposits (MAPA 1986). Soil characteristics are shown in Table 1.

### Litter Decomposition

Leaf litter decomposition rates and patterns of nutrient dynamics in decomposing litter were quantified in the field using the litterbag method (Swift, Heal, and Anderson 1979; Wardle 1993). Newly fallen leaves of ash, poplar, and alder trees were collected from the forest floor in October, in the areas they were present. The collected plant litter was air-dried at ambient temperature until constant weight. Seven grams of air dried litter for each species were put in a polyester litterbag (50 × 20 cm) with a mesh of 0.5 cm. In November, 75 litterbags per species were transferred to the zones where the species were dominant. Within a homogeneous part of each zone, litterbags were buried at 15-cm depth in an area of 25 m<sup>2</sup>.

To observe the decomposition phases (Coûteaux, Bottner, and Berg 1995), litterbags were collected every month during 6 months from the beginning of the experiment and every 2 months from that date until the end of the experiment. At each sampling date, three litterbags per species were randomly harvested from the buried litterbags. The experiment took 14 months. In this way, three replicated bags of each litter type were collected after 0, 31, 63, 91, 119, 154, 182, 238, 302, 360, 427, and 485 days. The litterbags were placed in a plastic bag, which was sealed and transported to the laboratory. Litterbags were examined for soil contamination (none was evident). Plant residues were placed in a paper bag, dried out at 80 °C for 48 h and weighed.

### Litter Analysis

The initial tree litter and the litter from the unburied litterbags were ground and passed through a 2-mm sieve. Samples of each material were analyzed

for total N, nitrate, ammonium, and organic carbon. Total N was determined by Kjeldahl acid digestion and titration of the produced ammonium with an Orion 95-10-00 electrode connected to a mv/pH-meter (Crison digit 501). Nitrate was extracted with a solution containing  $\text{Al}_2(\text{SO}_4)_3$ ,  $\text{H}_3\text{BO}_3$ ,  $\text{Ag}_2\text{SO}_4$ , and  $\text{NH}_2\text{SO}_3\text{H}$  (Milham et al. 1970) and determined with a nitrate selective electrode (Orion 93-07-00). Organic C was determined using the Walkey and Black method.

### Calculations and Statistical Analysis

Annual decay rate constants were calculated from data on the percentage of remaining litter mass, using a single negative exponential decay model proposed by Olson (1963) and Wieder and Lang (1982):

$$\ln\left(\frac{X}{X_0}\right) = -kt$$

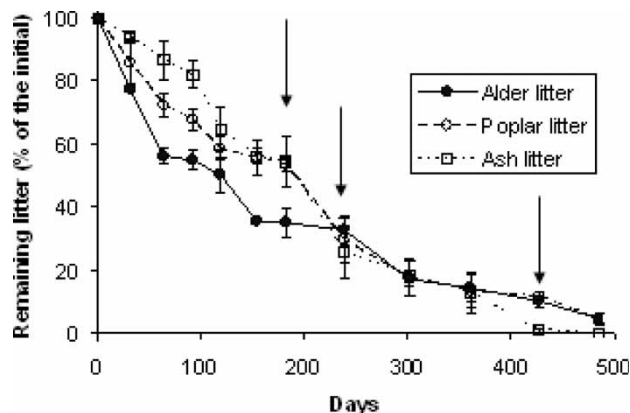
where  $X_0$  is the initial litter mass,  $X$  is the amount of litter remaining after time  $t$ ,  $t$  is the elapsed in years, and  $k$  is the annual decay constant ( $\text{yr}^{-1}$ ). The model was fitted to each of the litterbag sets by least-squares regression of the natural logarithm of the percentage of biomass remaining over time. Half-life of the litter was calculated as  $\ln(0.5)/k$  and turnover as  $1/k$ .

The data were statistically analyzed using one-way and two-way analysis of variance (STATVIEW 1987) to test the main effect of litter type, collection date, and their interaction on various litter chemistry and decomposition parameters. When the differences were significant, a least significant differences test was used to determine differences among means. When data were not homogeneous, they were transformed (arcsine, log). Moreover the temporal evolution of litter decay was adjusted to an exponential regression model (STATVIEW 1987). Climate data were obtained from the closest meteorological station to the study zones.

## RESULTS

### Dry Matter Decomposition

Weight loss in the buried litterbags was fast for all three species (Figure 3). After 427 days of burial, the remaining litter necromass in the litterbags was approximately 10% for alder and poplar species and only 0.71% for ash species. In the alder species, two different phases were differentiated: the first decomposition phase characterized by a very fast loss of biomass litter (approximately until 182 days) and a slower second phase until the end of the experiment. However, the other two species showed a more



**Figure 3.** Temporal variation of remaining biomass in the litter bags for the three tree species (mean  $\pm$  S.E).

regular loss of biomass weight in the litterbags with the faster loss of weight occurring from 182 to 213 days. There was a significant effect of litter type and collecting date and their interaction ( $p < 0.001$ ) on the studied variables, indicating that there were no similarities in collecting date among litter tree species. On the other hand, litter decay dynamics through the study period was fitted to an exponential model (Table 2), showing good regression coefficients (alder 0.87, poplar 0.88, ash 0.72,  $p < 0.0001$ ). Through the study period, the decay constant ( $k$ ) of ash species ( $4.47 \pm 1.13 \text{ year}^{-1}$ ) significantly ( $p < 0.05$ ; Table 3) exceeded that of poplar ( $2.01 \pm 0.15 \text{ year}^{-1}$ ) and alder species ( $2.07 \pm 0.28 \text{ year}^{-1}$ ). Half-life of the litter of ash species was different than those of alder and poplar species, and so for turnover was higher for both *Alnus* and *Populus* than for *Fraxinus*.

### Temporal Variation of Litter Quality

The initial total N concentration in litter of alder and ash species was higher (2.36; 2.13%) than of poplar (0.67%) (Figure 4a). At 427 days, N content of

**Table 2.** Exponential regression equations for the litter remaining of the three species (%)

	<i>A. glutinosa</i>	<i>P.x hybrida</i>	<i>F. angustifolia</i>
Equation	$y = 97.09 e^{-2.17x}$	$y = 117.86 e^{-2.28x}$	$y = 174.69 e^{-3.43x}$
$r^2$	0.87	0.88	0.72
F	237.97	258.30	75.65
P	0.0000	0.0000	0.0000

Note:  $r^2$  = regression coefficient, F = F de Fischer, p = significance level.

**Table 3.** Decomposition constants (k), half-life, and turnover rate of leaf litter from the species studied during a 2-year litter bag study (mean  $\pm$  SE), n = 3

Species	k	Half-life	Turnover
<i>Alnus glutinosa</i>	2.07 $\pm$ 0.28 a	0.35 $\pm$ 0.04 a	0.50 $\pm$ 0.06 a
<i>Populus x hybrida</i>	2.01 $\pm$ 0.15 a	0.35 $\pm$ 0.03 a	0.50 $\pm$ 0.04 a
<i>Fraxinus angustifolia</i>	4.47 $\pm$ 1.13 b	0.17 $\pm$ 0.03 b	0.24 $\pm$ 0.06 b

Note:  $p < 0.05$ . Different letters indicate differences among means (ANOVA and LSD test).

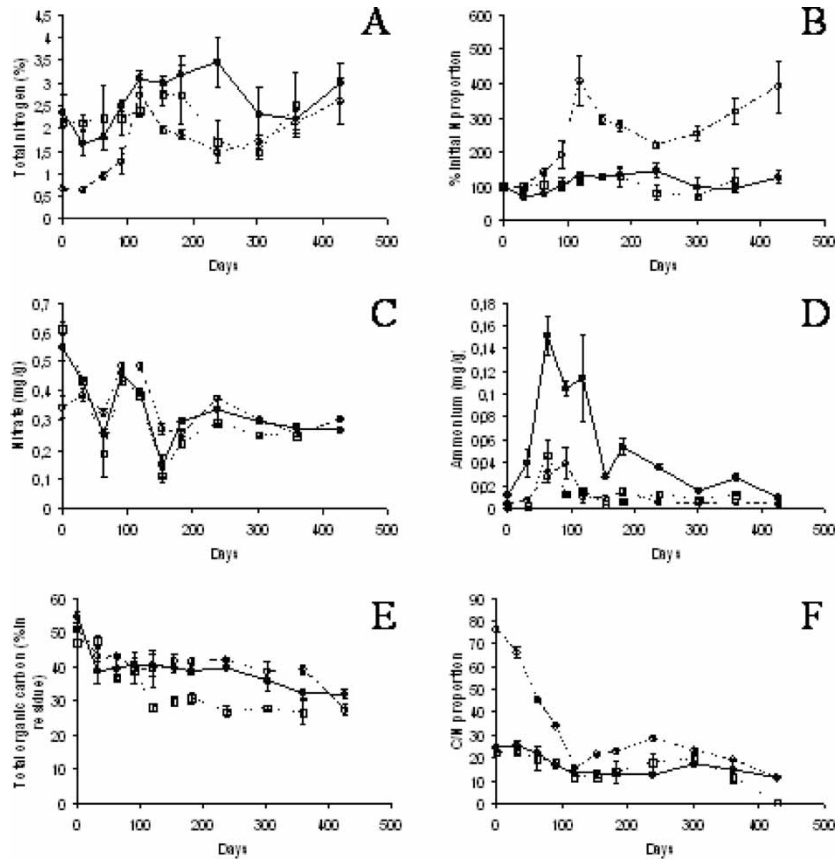
alder was still higher than the poplar. From the second collecting date, N concentrations increased in alder and poplar litter but remained stable in ash litter; N concentration started to decrease from 250 days in alder and from 120 days in poplar species, but at the end of the experiment N raised again. The differences among species or time were significant ( $p < 0.001$ ) and so was the interaction ( $p < 0.05$ ). The N litter content with the respect to the initial one increased with time in the three species. Poplar species showed a higher increase than the other two species (Figure 4b).

There was a significant effect of litter species and time and their interaction on the ammonium–nitrogen concentration ( $p < 0.01$ ). Initial values of alder species were generally higher than for the other two species (Figure 4c). In all cases, ammonium concentration increased initially, but at 427 days of experiment the values were rather similar to the initial ones.

At the third collecting date, the nitrate–nitrogen concentration of the three species followed a similar dynamic with rather similar contents and an irregular temporal pattern (Figure 4d). However, there were remarkable differences between initial concentration of nitrate, with ash and alder species, having a higher content than poplar. Differences among litter type ( $p < 0.01$ ) and time ( $p < 0.001$ ) were significant and so was the interaction ( $p < 0.001$ ).

The initial organic C concentration in the litter of alder significantly exceeded that of ash (Figure 4e;  $p < 0.05$ ), but the poplar species showed the highest content from 150 days until almost the end of the experiment. At the fifth collecting date, ash litter showed the lowest organic C content. There was a significant effect of species, collecting time, and interaction on the organic C content ( $p < 0.01$ ). The decreasing tendency of the organic C percentage through time showed two phases: first, a descendent phase until the fifth (ash species) and fourth (poplar and alder) collecting date and a second phase more stable until the end of the experiment.

C/N initial ratio was higher in poplar than in the other two species ( $p < 0.05$ ), and these values tended to slightly decrease with time (Figure 4f). This was related to the low N content of poplar. Its dynamic descends until 150 days, then increases until 300 days, and finally decreases again. The differences in C/N between time and species were significant



**Figure 4.** Temporal variation of N- and C-related parameters: a) total nitrogen content (%), b) percentage of initial nitrogen, c) ammonium litter content ( $\text{mg} \cdot \text{g}^{-1}$ ), d) nitrate litter content ( $\text{mg} \cdot \text{g}^{-1}$ ), e) the percentage of organic carbon, and f) C/N in the litter (mean  $\pm$  SE).

( $p < 0.001$ ). No relationships were found between initial N and C contents and decompositions parameters.

## DISCUSSION

### Weight Loss and Decomposition Rate

Losses of litter necromass from the bags for alder species were similar to those found by Wedderburn and Carter (1999), who observed that 10% of the necromass remained in the bags after 350 days. Gallardo and Merino (1993), in a Mediterranean area, reported between 60% and 30% of necromass of

ash species remained in the bags after 1 year. They related highest decomposition values to high precipitation average, mild temperature, and well-developed soil. Similar to our results, Cotrufo, Briones, and Ineson (1998) found 14% of ash litter necromass remaining after 1 year under oceanic conditions. Decomposition experiments for *Populus* species such as *P. tremuloides* Michx. and *P. nigra* showed lower loss of litter (Aranda, Serrano, and Bermúdez de Castro 1990; Köchy and Wilson 1997; Prescott, Kabzems, and Zabek 1999) than that found here. Litter decomposition in a Mediterranean area was studied, but it is likely that local abiotic conditions such as closeness to the watercourse could influence these results by provoking local high soil moisture. Mesh size (0.5 cm) could also influence these results but might not have been enough to explain the high decomposition rate. Differences could also be related to chemical composition of the litter.

Because the experiment was carried out in a similar area for the three species, differences in litter decomposition might be related to litter chemical composition, soil microorganism activity, and microclimate differences. In this last case, the distance of the tree species from the watercourse could be an important factor: that is, the *Alnus* species is closer to the watercourse than the other two and thus higher soil moisture could lead to relatively slower decomposition due to expected soil anoxic conditions.

Results showed an increase of the decomposition rate from the middle of the experiment in ash and poplar species. This could be due to the increase in soil temperature and moisture in spring, which likely increases microorganism activity. Despite alder species showing high ammonium content, which could lead to high decomposition, the lack of changes in soil humidity could lead to a delay in decomposition due to low oxygen availability for microorganism activity.

Microbial activity, especially actinomycetes (Rayner, Boddy, and Dawson 1987), also assists in comparing rates of species litter decomposition (Wardle 1993). *Fraxinus* species seems to be one of their favorite trees (Rayner, Boddy, and Dawson 1987). Moreover, some organic compounds such as polyphenols or monoterpenes (complex compounds that are toxic for some microflora) could decrease the decomposition rate of litter; Badré, Nobelis, and Trémolierés, (1998) showed that poplar leaf litter had higher contents of hydrosoluble tannins that are absent in ash leaves.

It has been established that litter mass loss occurs in two sequential phases as the result of the mineralization and humification of litter and the leaching into the soil of soluble compounds (Coûteaux, Bottner, and Berg 1995). The initial phase is faster and dominated by leaching, mineralization, and humification of easily accessible compounds for microorganisms, whereas advanced phases are ruled by mineralization and humification of less accessible compounds (lignin, holocellulose). The present study showed that alder and poplar species could follow that dynamic. Wedderburn and Carter (1999) found similar results for alder species. Nevertheless ash litter was found to decompose in a different way with a rapid similar decay during the whole

study period. These results could be related to the ash litter chemical composition with low recalcitrant compounds such as soluble polyphenols, cutin, and lignin and low toughness (Gallardo and Merino 1999) that allow a continuous decomposition. These results also suggest that the leaching phase of decomposition in the ash litter is irrelevant to determine their long-term decomposition (Moro and Domingo 2000).

### Litter Quality, Nutrient Dynamics, and Decomposition

Initial litter quality in terms of C and N compounds differed significantly among tree species. These differences reflect the combined effect of chemical content in living tissues and the efficiency of retranslocation mechanisms before abscission.

It is known that N-fixer species produce litter richer in N compounds than non-N-fixers (Moro, Domingo, and Bermúdez de Castro 1997; Jamaludheen and Kumar 1999; Wedderburn and Carter 1999). However, the high N concentration in litter of N-fixers does not necessarily lead to a higher decomposition rate, as we found. Ash litter had higher initial total N content (%) than those found by Cotrufo, Briones, and Ineson (1998), Gallardo and Merino (1993; 1999), and Wedderburn and Carter (1999) but are similar to those found by Briones and Ineson (1996). The initial N litter of *Populus x hybrida* species was similar to that of other *Populus* species (Taylor, Parkinson, and Parsons 1989; Prescott, Kabzems, and Zabek 1999) but lower than that of *Populus nigra* (Aranda, Serrano, and Bermúdez de Castro 1990).

Soil nutrient content could not be related to litter decomposition rates, which is in agreement with Prescott (1995) and Aerts and De Caluwe (1997), who have indicated that N availability did not alter litter decomposition rates in forests. These suggest that a small amount of the N release from litter was mineralized by soil microbes (Prescott 1995).

Nutrient release from the decomposing litter followed either a triphasic pattern characterized by an initial accumulation, followed by a rapid release and a final slower phase, or a biphasic pattern that is devoid of the initial accumulation phase (Jamaludheen and Kumar 1999). Results of this research showed that only ammonium content of the litter had a triphasic pattern. However, nutrient dynamics in the litter can only show a potential liberation to the system because accumulation and immobilization can also take place in the soil. When soil and litter nutrient content were compared, the C/N proportions of the three sites were lower in soil than in litter. These results could suggest that N is liberated from litter and taken by plants, thus leading to rapid and efficient recycling.

The initial decrease of total N content of *Alnus* could be related to the primary lixiviation that has been recorded for the Mediterranean (Escudero, Garrido, and Matías 1987) and Tundra ecosystems (Hobbie 1996). Afterward the N content increases were probably due to microbial

immobilization (Tiessen, Stewart, and Hunt 1984). This retention provokes an increase in the N proportion because organic matter is still being lost (Aber and Melillo 1980). Other processes such as degradation of C compounds (carbohydrates) and other easily decomposable compounds took place. The increase of N could be also related to external inputs of N by mean of radical exudates, canopy lixiviates, or leaching. Moreover, the products of the lignin degradation can form stable N compounds, making N less available for decomposing microorganisms (Nömmik and Vahtras 1982; Stevenson 1982).

The initial C concentration in ash litter was similar to those found by Cotrufo, Briones, and Ineson (1998) and Gallardo and Merino (1999) but higher than those found by Wedderburn and Carter (1999). The initial C of *Populus* species was higher than those found by Aranda, Serrano, and Bermúdez de Castro (1990) for *Populus nigra* species. The decrease of C content with time must be related to the degradation of carbohydrates and phenolic compounds at the beginning of the process (Schlesinger 1985), which is also related to mineralization in humid periods (Santa Regina, San Miguel, and Gallardo 1986). Although unburied litter was carefully washed up prior to analysis, the initial decrease of C concentration could also indicate a dilution by mineral soil particles. Differences among species often happens because of different leaf morphologies that induce differences in mineral soil sticking.

Initial decomposition rate is promoted by high N concentration and low C/N proportion (Edmonds 1990 Jamaludheen and Kumar 1999) but N retards long-term decomposition through inhibition of lignin-degrading enzymes and reactions that produce recalcitrant aromatic products (Berg et al. 1996). Moreover, other parameters have to be considered: cellulose, hemicellulose, and P content. An initial lignin content of ash species has been reported between 5.1% and 10.5% (Gallardo and Merino 1993; Cotrufo Briones, and Ineson 1998; Moro, Domingo, and Bermúdez de Castro 1997) and between 20% (Wedderburn and Carter 1999) and 30% (Gillon, Joffre, and Ibrahima 1999) for alder. *P. tremuloides* and *P. balsamifera* (Taylor, Parkinson, and Parsons 1989) have shown 14.1 and 13.6% lignin contents respectively; 21.5% for *P. alba* (Gillon, Joffre, and Ibrahima 1999); 21.4% for *P. grandidentata* (McClagherty et al. 1985). Thus, species with high lignin content have the lower decomposition rate in our experiment. In this sense, litter decomposition rate of alder species have been successfully predicted with lignin values of the litter (Wedderburn and Carter 1999).

Moreover, litter decomposition is affected by morphological leaf characteristics, such as leaf area or toughness. Species with bigger leaves should have lower decomposability because the available area for decomposition is lower. In the present study ash species (small leaves) showed a higher decomposition rate than alder and *Populus* species (big leaves).

Moreover, it has been suggested that, in Mediterranean conditions, lignin or N content were not the best predictors for the rate of decomposability, but

toughness, ratio of toughness/P concentration for the leaching phase, and cutin/N or cutin/P for the postleaching phase were (Gallardo and Merino 1993). Slow-growth deciduous species, as found in the Mediterranean region, contain high concentration of (hemi) cellulose and insoluble sugars, which may lead to low decomposition rates (Aerts and Chapin 2000). The role of P in decomposition rates could be may be related to the secular P deficiency of these Mediterranean areas.

Litter from the three studied species was rapidly degraded. This high speed can have positive consequences for the ecosystem such as the rapid increase of soil nutrients. However, the fast degradation also implies negative consequences. For example, if nutrient recycling is too fast, plants, soil organisms or soil cation and anion exchange sites have no time enough for taking up nutrients, resulting in a high amount of ions in the soil solution and easy loss by percolation. This situation is becoming important at sites close to the river where horizontal movement to the watercourse also exists. If riverine vegetation is removed, loss of nutrients from the system will be higher and equilibrium among production, composition, and species composition will be likely altered.

## REFERENCES

- Aber, J.D. and Melillo, J.M. (1980) Litter decomposition: Measuring relative contribution of organic matter and nitrogen to forest soils. *Canadian Journal of Botany*, 58: 416–421.
- Adams, M.B. and Angradi, T.R. (1996) Decomposition and nutrient dynamics of hardwood leaf litter in the Fernow whole-watershed acidification experiment. *Forest Ecology and Management*, 83: 61–69.
- Aerts, R. and Chapin, F.S., III (2000) The mineral nutrition of wild plants revisited: A reevaluation of processes and patterns. *Advances in Ecological Research*, 30: 1–67.
- Aerts, R. and De Caluwe, H. (1997) Nutritional and plant-mediated controls on leaf litter decomposition of *Carex* species. *Ecology*, 78: 244–260.
- Aranda, Y., Serrano, J.M., and Bermúdez de Castro, F. (1990) Degradación de la hojarasca de *Populus nigra* L. *Revue d'Ecologie et Biologie du Sol*, 27: 395–406.
- Badre, B., Nobelis, P., and Trémolières, M. (1998) Quantitative study and modelling of the litter decomposition in a European alluvial forest. Is there an influence of overstory tree species on the decomposition of ivy litter (*Hedera helix* L.)? *Acta Oecologica*, 16: 491–500.
- Beare, M.H., Parmelee, R.W., Hendrix, P.F., Cheng, W., Coleman, D.C., and Crossley, D.A. (1992) Microbial and faunal interactions and effects on litter nitrogen and on decomposition in agroecosystems. *Ecological Monographs*, 62: 569–591.
- Berendse, F., Berg, B., and Bosatta, E. (1987) The effect of lignin and nitrogen on the decomposition of litter in nutrient-poor ecosystems: A theoretical approach. *Canadian Journal of Botany*, 65: 1116–1120.
- Berg, B., Ekbohm, G., Johnson, M.B., McClaugherty, C., Rutigliano, F., and Virzo de Santo, A. (1996) Maximum decomposition limits of forest litter types: A synthesis. *Canadian Journal of Botany*, 74: 659–672.

- Briones, M.J. and Ineson, P. (1996) Decomposition of *Eucalyptus* leaves in litter mixtures. *Soil Biology and Biochemistry*, 28 (19/11): 10/11: 1381–1388.
- Cotrufo, M.F., Briones, M.J., and Ineson, P. (1998) Elevated CO<sub>2</sub> affects field decomposition rate and palatability of tree leaf litter: Importance of changes in substrate quality. *Soil Biology and Biochemistry*, 30: 1565–1571.
- Coûteaux, M.M., Bottner, P., and Berg, B. (1995) Litter decomposition climate and litter quality. *Trends in Ecology and Evolution*, 10: 63–66.
- Edmonds, R.L. (1990) Litter decomposition and nutrient release in Douglas fir, red alder, western hemlock and Pacific silver fir ecosystems in western Washington. *Canadian Journal of Forest Research*, 10: 327–337.
- Escudero, A., Garrido, M.V., and Matias, M.D. (1987) Decay curves of leaf litter from evergreen and deciduous tree species. *Acta Oecologica/Oecologia Plantarum*, 8 (22): 81–90.
- Finner, L. (1996) Variation in the amount and quality of litterfall in a *Pinus sylvestris* L. stand growing on a bog. *Forest Ecology and Management*, 80: 1–11.
- Forteza del Rey, M. (1981) *Caracterización Agroclimática de la Provincia de Guadalajara*; Ministerio de Agricultura, Pesca y Alimentación: Madrid, España.
- Gallardo, A. and Merino, J. (1993) Leaf decomposition in two Mediterranean ecosystems of south-west Spain: Influence of substrate quality. *Ecology*, 74 (1): 152–161.
- Gallardo, A. and Merino, J. (1999) Control of leaf litter decomposition rate in a Mediterranean shrubland as indicated by N, P and lignin concentrations. *Pedobiologia*, 43: 64–72.
- Gillon, D., Joffre, R., and Ibrahima, A. (1999) Can litter decomposability be predicted by near infrared reflectance spectroscopy? *Ecology*, 80: 175–186.
- Heal, O.W., Anderson, J.M., and Swift, M.J. (1997) Plant litter quality and decomposition: An historical overview. In *Driven by Nature: Plant Litter Quality and Decomposition*; Cadisch, G. and Giller, K.E. (eds.); CAB International: Wallingford, UK, 3–30.
- Hobbie, S.E. (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs*, 66 (4): 503–522.
- Jamaludheen, V. and Kumar, B.M. (1999) Litter of multipurpose trees in Kerala, India: Variations in the amount, quality, decay rates and release of nutrients. *Forest Ecology and Management*, 115: 1–11.
- Köchy, M. and Wilson, S.D. (1997) Litter decomposition and nitrogen dynamics in aspen forest and mixed-grass prairie. *Ecology*, 78 (3): 732–739.
- Lavelle, P., Blanchart, E., Martin, A., Spain, A., Toutain, F., Barois, I., and Schaefer, R.A. (1993) A hierarchical model for decomposition in terrestrial ecosystems: Applications to soils of the humid tropics. *Biotropica*, 25: 130–150.
- MAPA (1986) *Mapa de Cultivos y Aprovechamientos de la Provincia de Guadalajara*; Escala, 1: 200.000. Ministerio de Agricultura, Pesca y Alimentación: Madrid, Spain.
- McClagherty, Pastor, J.C.A., Aber, J.D., and Melillo, J.M. (1985) Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. *Ecology*, 66: 266–275.
- Milham, P.J., Awad, A.S., Paull, R.E., and Bull, J.E. (1970) Analysis of plants, soils and waters for nitrate by using an ion-selective electrode. *Analysis*, 95: 751–757.
- Moro, M.J. and Domingo, F. (2000) Litter decomposition in four woody species in a Mediterranean climate: Weight loss, N and P dynamics. *Annals of Botany*, 86: 1065–1071.
- Moro, M.J., Domingo, F., and Bermúdez de Castro, F. (1997) Flujos de materia orgánica y N en dos arbustos mediterráneos estudiados en una microcuenca de la

- Sierra de los Filabres. XI International Symposium on Environmental Biogeochemistry: Salamanca, Spain, 217–231.
- Nömmik, H. and Vahtras, K. (1982) Retention and fixation of ammonium and ammonia in soils. In *Nitrogen in Agricultural Soils*; Stenvenson, F.J. (ed.); Agronomy Monographs 22, Agronomy Society of America: Madison, Wisconsin, 123–171.
- Olson, J.S. (1963) Energy storage and balance of production and decomposers in ecological systems. *Ecology*, 44: 322–357.
- Pérez Hernández, M.C. (1996) Entradas biológicas de nitrógeno en un bosque ripario. PhD thesis, Universidad Complutense de Madrid.
- Prescott, C.E. (1995) Does nitrogen availability control rates of litter decomposition in forest. *Plant and Soil*, 168–169: 83–88.
- Prescott, C.E., Kabzems, R., and Zabek, L.M. (1999) Effects of fertilisation on decomposition rate of *Populus tremuloides* foliar litter in a boreal forest. *Canadian Journal of Forest Research*, 29: 393–397.
- Rayner, A.D.M., Boddy, L., and Dawson, C.G. (1987) Genetic interactions and developmental versatility during establishment of decomposer basidiomycetes in wood and tree litter. In *Ecology of Microbial Communities*; Fletcher, M., Gray, T.G.R. and Jones, J.G. (eds.); Cambridge University Press: Cambridge, UK, 83–123.
- Sánchez Mata, D. and de la Fuente, V. (1985) *Las Riberas de Agua Dulce*; MOPU, Centro de Publicaciones: Madrid, Spain.
- Santa Regina, I., San Miguel, C., and Gallardo, F.J. (1986) Evolución y velocidad de descomposición de la hojarasca en tres bosques de la Sierra de Béjar (Salamanca). *Anuario CEBAS CSIC Salamanca*, 11: 217–231.
- Schlesinger, W.H. (1985) Decomposition of chaparral shrub foliage. *Ecology*, 66 (4): 1353–1359.
- STATVIEW (1987) *Statistical Package for Macintosh*; SAS, Inc.: Cary, North Carolina.
- Stevenson, F.J. (1982) *Humus Chemistry—Genesis, Composition, Reactions*; Wiley: New York.
- Swift, M.J. and Anderson, J.M. (1989) Decomposition. In *Ecosystems of the World, 14B: Tropical Rain Forest Ecosystems*; Lieth, H. and Werger, M.J.A. (eds); Elsevier: Amsterdam, 547–569.
- Swift, M.J., Heal, O.W., and Anderson, J.M. (1979) *Decomposition in Terrestrial Ecosystems*; Blackwell Scientific Publications: Oxford, UK.
- Taylor, B.R., Parkinson, D., and Parsons, W.F.J. (1989) Nitrogen and lignin content as predictors of litter decay rates: A microcosm test. *Ecology*, 70 (1): 97–104.
- Tiessen, H., Stewart, J.W.B., and Hunt, H.W. (1984) Concepts of soil organic matter transformations in relation to organo-mineral particle size fractions. *Plant and Soil*, 76: 287–295.
- Vitousek, P.M. and Sandford, R.L. (1986) Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics*, 17: 137–167.
- Vitousek, P.M., Turner, D.R., Parton, W.J., and Sandford, R.L. (1994) Litter decomposition on the Manua Loa environmental matrix, Hawaii: patterns, mechanisms and models. *Ecology*, 75: 418–429.
- Wardle, D.A. (1993) Changes in the microbial biomass and MQ during leaf litter succession in some New Zealand forest and shrubland ecosystems. *Functional Ecology*, 7: 346–355.
- Wedderburn, M.E. and Carter, J. (1999) Litter decomposition by four functional tree types for use in silvopastoral systems. *Soil Biology and Biochemistry*, 31: 455–461.
- Wieder, R.K. and Lang, G.E. (1982) A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology*, 63: 1636–1642.

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