Biogeochemistry (2011) 106:397–414
DOI 10.1007/s10533-010-9518-2

Thinning affects *Pinus sylvestris* needle decomposition rates and chemistry differently depending on site conditions

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Received: 19 May 2009 / Accepted: 13 August 2010 / Published online: 4 December 2010

Abstract Changes in mass and chemical composition of *Pinus sylvestris* senescent needles were studied over a 5 year period in Mediterranean (MF) and Continental forests (CF) in the Pyrenees under varying levels of thinning (P0: reference, no thinning; P20: removal of 20% basal area, P30: removal of 30% basal area). Decomposition rates were higher in MF ($k = 0.423$ year^{-1}) than in CF ($k = 0.245$ year^{-1}). However, the maximum decomposition limit was higher in CF (87.9%) compared to MF (78.1%). The relative importance and timing of rainfall, and cellulose and lignin abundance on the decomposition process was similar among both sites. However, air temperature and degree-days only affected CF (the colder site) during the initial stages of decomposition, while litter moisture was significant only in MF (the drier site) in the latter stages of decomposition. Nutrient and carbon dynamics showed temporal patterns similar to those reported in higher latitudes (except for Ca), however, indicators of N mineralization such as C/N and lignin/N at the study sites were lower than values reported in the literature. Decreases in decomposition rates after thinning were higher in MF than in CF, indicating that this ecosystem could, in the short term, be more sensitive to human intervention. Thinning had similar temporary qualitative effects at both sites, slowing decomposition, increasing N and P immobilization and decreasing Ca immobilization. However, quantitative effects of thinning were site dependent in that the magnitude of nutrient immobilization was higher in CF. A conceptual model is presented to explain effects of thinning on litter N dynamics. These temporary changes are not trivial as nutrient immobilization and accumulated organic matter losses over a thinning cycle may affect tree growth particularly during short rotations and intensive fast-growing plantations. Under similar nutrient availability conditions, sites where nutrient release occurs faster may show higher post-thinning tree growth rates.

Keywords Leaf litter decomposition · Mediterranean pine forest · Nitrogen mineralization · Nutrient cycling · Thinning

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Introduction

In most temperate forests, forest floor litter is an important nutrient reservoir for tree growth. In addition, the main source of energy for soil microbes and microfauna in forest ecosystems is the decomposition of roots and litter. Nutrients stored within leaf litter are recycled and become available for tree uptake by decomposer organisms, following sequential resource utilization (Heal et al. 1997). Quantification of soil nutrient inputs via litterfall and their subsequent immobilization and release are crucial to understanding trophic dynamics, carbon and bioelement fluxes in forest ecosystems. This knowledge could be key when developing and applying forest management practices that aim to rationally manage nutrient reserves, especially in nutrient-poor environments, fast-growing plantations or plantations on short rotations. One such management practice is thinning, which is commonly used in forestry to reduce inter-tree competition, an important issue arising in nutrient-limited forests where fertilization is not economically or environmentally feasible. Thinning is a very common and recommended practice to manage plantations (Allen 2001) and forest stands in general (Oliver and Larson 1996). However, little is known about the effects of thinning on nutrient release from decomposing litter.

Litter decomposition in unmanaged systems is influenced mainly by climatic variables (Aerts 1997). However, at the local scale, the influence of litter quality plays a significant role, particularly during the most advanced stages of decomposition (Berg and Laskowski 2006). In arid and semi-arid sites, photodegradation could also be an influential factor (Austin and Vivanco 2006). Mechanisms to determine nutrient dynamics during litter decomposition have been extensively studied from biochemical to biogeochemical points of view (Berg and Laskowski 2006, and references therein). However, accurate conceptual models that explain observed differences in nutrient dynamics in decomposing litter among ecosystems or litter types are still missing (Laskowski et al. 1995a, b; Berg and Laskowsky 2006). Models work relatively well for nitrogen (N) and phosphorus (P) in temperate forests, showing concentration increases during the initial stages of leaf litter decomposition, and decreases thereafter. Other elements such as calcium (Ca), magnesium (Mg) and potassium (K), however, have been shown to exhibit variable temporal dynamics (Staaf and Berg 1982; Laskowski et al. 1995a, b; Osono et al. 2006). Recent studies suggest that these other nutrients may be more important in regulating decomposition than had been previously thought (Hobbie 2005; Hobbie and Hobbie 2006). Similarly, timing of nutrient release, particularly for N and P, has been related to different ratios (e.g., carbon/nitrogen (C/N), Lignin/N, among others) and remaining litter mass, with varied success. In the final decomposition stages, litter generally decomposes very slowly (Harmon et al. 2009), and stored nutrients may remain unavailable for plants over long periods (Berg 2000).

Latitude (Berg et al. 1993; Parton et al. 2007) and altitude (e.g., Scowcroft et al. 2000) gradients have been used to elucidate the mechanisms and drivers involved in decomposition rates, nutrient temporal dynamics and/or timing of nutrient release in decomposing litter. Management practices such as clear-cutting and thinning can also be carried out along natural and/or artificial gradients with the same goal. Additionally, by using different thinning intensities, within-site gradients of variables potentially affecting decomposition (e.g., soil microclimate, soil nutrient imports and exports, biota densities and composition) may be created. Degradation of important litter components such as lignin, cellulose and hemicellulose have been correlated to moisture, precipitation and temperature (McTiernan et al. 2003), and consequently may be affected by forest management.

Relative to latitudinal or altitudinal gradient approaches, the within-site gradient approach allows for greater experimental control on drivers of decomposition such as soil type, climate and disturbance history which are similar for all plots. However, isolating the impacts of other variables may not be as straightforward. Because timing of responses of different variables to thinning may vary as the canopy recloses, the interaction between variables may be studied more dynamically than with the latitudinal or altitudinal gradient approaches. Furthermore, timing and magnitude of decomposition drivers after thinning may influence magnitude and timing of leaching, accumulation and release of litter nutrients, informing conceptual models of nutrient dynamics during decomposition. Studies on the influence of clear-cutting on litter decomposition are numerous, and have shown a variety of responses in decomposition rates. These responses are often difficult to anticipate such as increases in decomposition rate (Bachiller et al. 1999), no change (Duchesne and Wetzel 1999) or decrease (Berg 1988). However, decomposition has been relatively unstudied in thinned forests (see Piene and Van Cleve 1978; Kunhamu et al. 2009). Most decomposition studies involving management are usually too short (i.e., 2 years or less) to characterize nutrient dynamics (Berg and Laskowski 2006), as decomposition subprocesses such as nutrient release may start much later. Furthermore, often only N and P are determined, and in most cases lignin and cellulose are not analyzed.

In 1999, our group initiated a long-term study to assess the ecological sustainability of thinning practices on *P. sylvestris* forests within site quality and climate gradients in the western Pyrenees (Spain). Our sites, one mesic and the other more arid, are located close to the south-western distributional limit for this species in Europe, where little information is available on *P. sylvestris* needle decomposition. Nevertheless, the opportunity to compare long-term nutrient dynamics in decomposing litter with similar studies carried out at higher latitudes was possible. On this basis, the objectives of this study were: (1) to compare decomposition rates and maximum accumulated mass losses in two nearby forests with different climates, (2) to determine which are the most influential variables on this process in both forests, (3) to compare temporal dynamics of nutrients and carbon compounds in litter from both forests, and (4) to determine the influence of thinning on decomposition rates, maximum accumulated mass loss and contents of nutrients and carbon compounds. We predicted that the mesic site (CF) would be limited by temperature whereas the more arid site (MF), would be limited by water. Given these conditions, we predicted that opening the canopy through thinning would increase soil temperature in plots at the mesic site, resulting in an increase in the decomposition rate, and would decrease soil moisture in plots at the more arid site (particularly in summer) resulting in a decrease in decomposition rates.

Materials and methods

Study sites and experimental design

Our experimental sites, Garde and Aspurz (Table 1), are located in the western Pyrenees, in the province of Navarre (northern Spain). The study site in Garde (CF) represents an average productive continental *P. sylvestris* forest in Spain. The study location in Aspurz (MF) is a highly productive Mediterranean *P. sylvestris* forest. The most important soil properties are shown in Table 2. Additional information on climate in both locations for the study period can be found in Blanco et al. (2006a). Data were gathered across nine rectangular (30 × 40 m) plots per site. Treatments were implemented by the Government of Navarre according to the guidelines of the International Union of Forestry Research Organizations (IUFRO) in August 1999 (CF) and November 1999 (MF). The experimental design consisted of three treatments replicated three times at each site: P0: control with no thinning; P20: moderately low thinning (20% of basal area removed according to the tree selection method, felled trees were mainly suppressed but included dominant or co-dominant trees with malformed stems); P30: heavy low thinning (30% of basal area removed using the same criteria as in P20). Plots were chosen to fit within the boundaries of public land in each area and close to trails to facilitate access. To avoid edge effects, the same treatments were applied within a 5–10 m strip adjacent to each plot. Stumps were left on the ground, and logs and most branches from the felled trees were left outside the plot limits. No heavy machinery was used to pull or drag the logs in order to avoid litter layer alteration.

Preparation and placement of litter bags

Freshly fallen whole senescent needles were collected in October 2000, and air-dried until constant weight was attained, creating 9 different pools of litter (one from each plot) in each site. We used 1000 litter bags (15 × 20 cm; 1.5 mm mesh size) of fiber-glass coated with polyethylene and filled with 10 ± 0.001 g of needles. The bags were taken to CF and MF on November 17th and 23rd 2000, respectively. Each bag was placed on the soil surface of the same plot where its needles had been previously collected. In each plot we selected five points at random and at each point we placed two groups of five bags tied at the base of two trees with nylon (2 sites × 9 plots × 5 points × 2 trees × 5 bags per tree = 900 bags). Fifty bags per site were placed within sealed plastic bags and returned to the laboratory on the first sampling

Table 1 Site characteristics (mean ± standard error)

Site	ASPURZ Mediterranean forest (MF)	GARDE Continental forest (CF)
Latitude	42°48′50″ N	42°42′31″ N
Longitude	52′30″ W	1°8′40″ W
Altitude (m)	625	1335
Slope (%)	7	40
Soil	Haplic Alisol	Dystric Cambisol
Mean Temperature (°C)	12.0	8.2
Mean precipitation (mm)	912	1268
Climate type (Papadakis, 1970)	Cold wet Mediterranean	Cold wet continental
Other overstory tree species[a]	*Fagus sylvatica* L. *Quercus humilis* L.	*Fagus sylvatica* L.
Dominant understory species[b]	*Pteridium aquilinum* (L.) Kuhn *Rubus ulmifolius* Schott	*Deschampsia flexuosa* L. *Pteridium aquilinum* (L.) Kuhn
Tree stand before thinning		
Site index at stand age 80 years (m)	29	23
Age (years)	32	37
Density (stems ha^{-1})[c]	4040 ± 326	3230 ± 162
Dominant height (m)[d]	15.1 ± 0.4	14.3 ± 0.2
Mean DBH (cm)[e]	11.7 ± 0.5	13.8 ± 0.3
Volume (m^3 ha^{-1})	270.7 ± 11.9	290.1 ± 10.5
Basal area (m^2 ha^{-1})	41.2 ± 0.9	47.8 ± 1.6
Fraction of live canopy (%)[f]	40.8 ± 1.2	54.6 ± 1.7

Stands descriptors from Puertas (2001) and Iriarte and Puertas (2003)

[a] Eighteen and ten tree species identified in Aspurz and Garde, respectively

[b] Sixty-six and fifty-two shrub and herb species identified in Aspurz and Garde, respectively

[c] Trees with DBH > 7.5 cm

[d] Measured averaging ($n = 100$) the height of the thickest dominant trees per hectare

[e] Measured by double cross measurement

[f] Percentage of canopy (from the lowest dead branch to tree top) occupied by branches with green leaves

day to calculate handling losses. Starting in December 2000, three random samples per plot were collected monthly during the first 3 months, then bimonthly from April 2000 to October 2002, and finally yearly to complete a study period of 5 years ending in October 2005. Fresh and oven-dry weights were measured in the lab in order to calculate leaf litter moisture. When collecting the litterbags, soil moisture (soil moisture probe Delta-T Thetaprobe ML2X; moisture meter HH2, Delta-T) and soil temperature (thermometer Hanna Inst.) were measured in horizon A near the bag. A total of 845 samples (bags) were collected in this study: 3 bags per plot × 3 treatments × 3 replicates × 2 sites × 16 sampling dates = 864 samples minus 19 samples that were not found during the last sampling date (however, there was always at least one bag per plot).

Chemical analyses of leaf litter

Leaf litter samples were ground to powder with an electric mill (Frisch, Pulverisette 14, Idar-Oberstein, Germany). Ash-free dry matter of leaf litter was calculated after drying a subsample until a constant weight was reached at 70°C and then combusting it at 525°C overnight. Nitrogen was analyzed using the Kjeldahl method along with analysis for total ammonium content (Horwitz 1980). To determine P, K, Ca and Mg concentrations, samples were digested with wet oxidation using a nitric-perchloric acid solution

Table 2 Soil chemical and physical properties in the study sites

Site/ Horizon	Depth cm	Clay %	Silt %	Sand %	pH 1:2.5 H_2O	Density[a] g cm^3	CEC meq 100 g^{-1}	O.M. %	C mg g^{-1}	N mg g^{-1}	P mg g^{-1}	K mg g^{-1}	Ca mg g^{-1}	Mg mg g^{-1}	C/N
ASPURZ (MF)															
A	0–10	7.2	50.5	42.3	5.45	0.96	14.2	**11.69**	**67.8****	**3.05****	**0.029**	**0.098*****	**1.94****	**0.213*****	**22.6**
B	10–45	14.2	33.3	55.5	5.55	1.31	7.2	1.14	6.6	1.503	0.011	0.043	0.980	0.142	4.4
GARDE (CF)															
A	0–10	23.3	30.8	45.8	5.48	0.76	23.3	**9.88**	**57.3**	**2.67**	**0.026**	**0.145**	**2.20**	**0.273**	**22.0**
B	10–45	25.7	34.5	39.4	6.00	1.26	19.7	3.05	17.7	2.310	0.007	0.055	2.872	0.170	7.7
C	45–60	26.5	31.7	41.8	6.40	0.71	22.6	1.88	10.9	1.602	0.014	0.043	3.732	0.212	6.8

Between-site comparisons in horizon A (bold case) are shown for organic matter (O.M.) and organic C (defined as in Walkley and Black (1934)), Kjeldahl N, available P (defined as in Bray and Kurtz (1945)), exchangeable K, exchangeable Ca, exchangeable Mg and C/N ratio. Data from Blanco (2004). Horizon A data are averages of bimonthly samples taken from April 2001 to April 2003 ($n = 13$), as described in Blanco (2004)

CEC cation exchange capacity

[a] Density: apparent density

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

(Zasoski and Burau 1977; M.A.F.F. 1986). Total P was determined using the phosphomolibdo-vanadate method, with a UVICOM spectrophotometer (Kontron Instruments) at 340 nm. Calcium and Mg were analyzed by atomic absorption spectrophotometry and K was analyzed by flame photometry (VARIAN, model SpectrAA-250 PLUS, SPS5). Percentage acid-detergent fibre (ADF), percentage acid-detergent cellulose (ADC), and percentage acid-detergent lignin (ADL) were determined following Horwitz (1980). A one gram tared sample (P1) was first digested with cetyltrimethyl-ammonium bromide and the resulting residue (P2) was digested with 72% H_2SO_4. The final residue (P3) was ignited at 500°C to yield P4. ADF = P2–P4, ADC = P2–P3 and ADL = P3–P4. The lignin fraction also includes humic substances produced during decomposition. Finally, total organic C was analyzed by an infrared gas chromatographer (Carlo Elba EA-1108).

Statistical analyses

Global decomposition rates (k) were calculated using Olson's (1963) model: $W_t/W_0 = e^{-kt}$; where W_t is the weight of needles remaining in the bags at time t and W_0 is the weight at the beginning of the study. Decomposition rates were also calculated for the periods November 00–December 01 (Year 1), February 02–October 02 (Year 2), October 02–October 03 (Year 3), October 03–October 04 (Year 4) and October 04–October 05 (Year 5). We calculated the rates for each year using the first data of remaining weight for that year as the "initial mass" and we applied Olson's model using only the data for that given year. Although this is one of the simplest models of decomposition (Berg and Laskowski 2006), its wide use makes it easier to compare results than those of more complicated models. Differences in Olson's k values among treatments were tested using a repeated measures ANOVA, with the main factors being site, thinning intensity and time. Linear contrasts were used to test for pair-wise differences between thinning intensities separately for each year. Maximum decomposition levels were calculated with an asymptotic nonlinear model: $1 - W_t = m\ (1 - e^{-kt/m})$ (Berg 2000), where m is the asymptotic level that the accumulated mass loss will ultimately reach. The parameters for this model were estimated by nonlinear regression. Differences in m were tested with a two-way ANOVA with the factors being site and thinning intensity.

Repeated measures ANOVAs (factors: site, thinning intensity and time) were used to analyze soil temperature and moisture, and contents of nutrients, carbon, cellulose and lignin in decomposing litter. Yearly differences found among thinning intensities in contents of nutrients and carbon compounds were tested using linear contrasts. Two-way ANOVAs (factors: site and thinning intensity) were also used to analyze different indicators of N release. It was assumed that the end of N accumulation occurred when contents of N in the remaining biomass reached a maximum value (Berg and Staaf 1980). At that time, the following estimated ratios were determined: C/N, C/P, lignin/N, lignin/P, lignin/(lignin + cellulose) (or LIC), along with the remaining organic matter and years since the beginning of the study. If a significant interaction between site and thinning intensity was found, Tukey H.S.D. analysis between the thinning intensities were carried out separately for each site.

The relationship between changes in selected variables and changes in remaining organic matter mass during decomposition was assessed using multiple regressions. Percentages of organic mass loss (dependent variable) were calculated for periods between two consecutive sampling dates. The independent variables were the relative change (in percentage) between two consecutive sampling dates of: lignin mass, cellulose, C, N, P, K, Ca, and Mg, along with the ratios of C/N, lignin/N, lignin/P and LIC; soil and air temperature besides the litterbags at the time of collection, soil and leaf litter moisture, rainfall, accumulated rainfall and degree-days over 5°C (Government of Navarre 2006) were also independent variables. A preliminary outlier analysis was carried out to remove potential extreme values (a total of 5 out of the 288 data values), given the high sensitivity of multiple regressions. To select variables to be included in the multiple regression analysis, the first step was to test for significant individual regressions for each variable in relation to the dependent variables. The second step was to reduce the correlation between variables by selecting only one of each group of variables containing similar information (i.e., carbon compounds masses, temperatures or precipitation), based on the individual *r* values obtained in the first step. Tolerance values for selected variables were in all cases above 0.10 (the limit for significant collinearity, Quinn and Keough 2002). The third step was to test for temporal autocorrelations of variables selected with the Durbin-Watson test, which did not detect any significant autocorrelation. The fourth and final step was to carry out stepwise regressions, with the probability of 0.2 for a new variable entering into the model. Best regression models were selected using the adjusted r^2, Mallow's Cp and the Akaike information coefficient (AIC). These multiple regressions were carried out first with data from the entire study period and then separately for every phase observed during the decomposition process. These phases were defined as follows: Phase 1 ended when fast initial N and P losses ended (end of leaching losses stage as defined by Berg and Ekbohm 1991); Phase 2 lasted until the remaining mass, as calculated by the exponential model, equaled the average of the remaining biomass as measured with the litterbags (Aber et al. 1990). Finally, Phase 3 was considered, with very low mass loss. When needed, data were transformed to logarithms or arcsine (percentage data) to achieve homogeneity of variances and normal distribution; these assumptions were evaluated with residual plots and the Shapiro–Wilk test. All statistical analyses were carried out using JMP v.5.0.1 (SAS Institute, NC, USA).

Results

Objective 1: Differences between sites in decomposition rates and maximum accumulated mass loss

Olson's single exponential model provided a good fit to mass loss (Fig. 1). In MF (Aspurz) global Olson's *k* for the 5-year period were 0.470 ± 0.007 ($R^2 = 0.912$), 0.414 ± 0.020 ($R^2 = 0.825$) and 0.397 ± 0.010 year^{-1} ($R^2 = 0.873$) in P0, P20 and P30, respectively. In CF (Garde) *k* values were 0.263 ± 0.016 ($R^2 = 0.852$), 0.237 ± 0.007 ($R^2 = 0.895$) and 0.863 ± 0.016 year^{-1} ($R^2 = 0.912$) in P0, P20 and P30, respectively. These values showed that pine leaf litter decomposed faster in MF than in CF ($p = 0.011$, Fig. 1), and that relative to P0, decomposition rates in P30 decreased by 15.5% in MF and by 10.3% in CF. Maximum accumulated mass loss in CF (87.96% ± 0.03) was significantly higher than in MF (78.14% ± 0.03; $p = 0.047$).

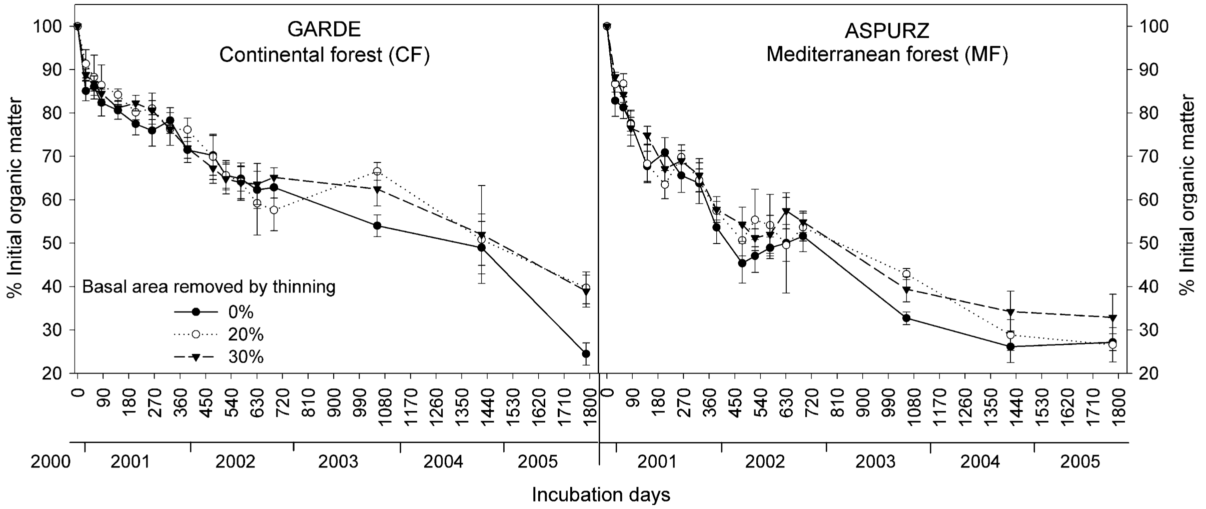

Fig. 1 Mass loss in decomposing needles during 5 years of study (mean ± standard error, $n = 9$)

Objective 2: Regressions of organic mass loss versus climatic and leaf litter quality variables

Dynamics of organic matter losses over time in Phases 1 and 2 were better explained by selected variables in CF than in MF (Table 3). In Phase 1 the multivariate models explained 71% and 79% of the variance of litter mass change in MF and CF, respectively. In MF, this model included changes in N and cellulose masses, whereas in CF the variables selected were changes in cellulose mass, lignin/P and rainfall. In Phase 2, three variables (changes in lignin mass, LIC ratio and litter moisture) explained 17% of the variance in MF and also three variables explained 24% of the variance in CF (changes in N and lignin masses and lignin/P ratio). When the total study was considered, the best model in MF included four variables (changes in lignin mass, LIC ratio, accumulated rainfall and soil moisture), explaining 29% of the variance in litter mass change. In CF, 21% of the variance was explained with a two-variable model (changes in lignin mass and soil moisture) (Table 3). Additionally, simple linear regressions in MF showed significant positive correlations of litter mass with rainfall in Phase 1, and with degree days, accumulated rainfall and soil moisture in Phase 2. Likewise, litter mass loss in CF was positively related to degree days, air temperature and accumulated rainfall in Phase 1, and to degree days and accumulated rainfall in Phase 2 (Table 3). Changes in nitrogen and phosphorus contents showed significant negative correlations with mass losses in Phase 1 (MF) and Phase 2 (MF, CF only for N), while P was positively correlated in Phase 2 in CF.

Objective 3: Temporal changes in contents of nutrients and carbon compounds

Initial chemical properties of litter are presented in Table 4. Initial litter content of lignin was significantly higher in CF than in MF ($p = 0.009$), whereas N content was higher in MF ($p = 0.029$), and there were not significant differences between sites for P, K, Ca, Mg, C and cellulose. Generally, content values of P, Ca and Mg in CF and Ca in MF (Figs. 2, 3) at the end of the 5-year study period were similar or higher than those of initial litterfall. Nevertheless, a clear leaching phase was observed at both sites for N, P and K, but was absent for Ca and Mg (Figs. 2, 3). The net release of N started at the end of the second year in MF, and during the third year in CF. Net release of Ca started at the end of the first year in MF and during the second year in CF. However, although the net release of P was observed in MF at the end of the second year, it was never observed in CF over the duration of the study (Fig. 2). Potassium content showed an initial phase of fast decrease and a late phase of increase more accentuated in CF than in MF.

Table 3 Regressions of changes in remaining organic mass versus changes in litter quality and climate variables

Variable	Phase 1 (1 to 84 days)		Phase 2		Total study (1 to 1785 days)	
	Aspurz (MF)	Garde (CF)	Aspurz[a] (MF)	Garde[b] (CF)	Aspurz (MF)	Garde[b] (CF)
N mass	**−<0.01**	ns	−0.51	**−0.06**	−0.32	−0.82
P mass	−0.68	ns	−0.79	+	−0.92	ns
K mass	–	–	ns	ns	ns	ns
Mg mass	ns	–	ns	ns	ns	ns
C mass	**–**	–	**–**	**–**	**–**	**–**
Lignin mass	ns	ns	**−0.05**	**−0.10**	**−<0.01**	**−<0.01**
Cellulose mass	**−<0.01**	**−0.05**	–	–	–	–
Lignin/P	ns	**+0.12**	–	**−0.02**	−0.20	ns
LIC[c]	+0.32	ns	**−0.02**	ns	**+<0.01**	ns
Degree days	ns	+	+	+	ns	+0.81
Air temperature	ns	+	ns	ns	ns	–
Soil temperature	ns	ns	–	ns	ns	ns
Accumulated Rainfall	ns	**+**	+0.53	+0.61	**+<0.01**	+
Rainfall	+	**+<0.01**	ns	ns	ns	−0.42
Soil moisture	−0.91	ns	+	ns	**+0.10**	**−0.08**
Litter moisture	ns	ns	**+0.02**	ns	ns	ns
R^2 adjusted	0.71	0.79	0.17	0.24	0.29	0.21
Cp	1.27	4.00	3.28	3.26	5.07	0.64
AIC	−196.6	−115.3	−338.8	−554.2	−638.3	−442.5

Four types of variables are included in the table: (1) variables without significant correlation with mass losses, denoted as "ns"; (2) Variables with significant ($p < 0.05$) correlations but not included in the stepwise multiple regression, denoted as "−" or "+"; (3) Variables with significant correlations and included in the multivariate analysis but not selected for the final model, denoted with "+" or "−" followed by the associated p-value of the *F*-test that its effect on the multivariate model is zero in plain case, and (4) Variables with significant correlations selected for the final multivariate model, denoted by "+" or "−" followed by their associated *p*-values in bold case. See text for rules on including variables in the multivariate model. Values of R^2, Cp and AIC for the final multivariate model provided at the bottom

[a] Phase 2 ended in Aspurz after 1053 days

[b] Phase 2 had not finished in Garde after 1785 days (the end of this study)

[c] LIC = [Lignin]/([lignin] + [cellulose])

An increasing trend was observed for Mg after the first year of incubation in CF (Fig. 3).

Total C and cellulose decreased in both sites within the study period (Fig. 3). Total C dynamics resembled those for organic matter, especially in the MF. Differences in cellulose dynamics between sites were mainly caused by a faster loss of weight in MF during the first 7 months. Lignin in CF exhibited a small increase at the beginning of incubation, reaching a plateau during the first year and showing a declining trend afterwards (Fig. 3). In MF, however, the increase in lignin content was larger than in CF, and the decrease started at the end of the second year in P20 and P30, and after the end of the third year in P0 (Fig. 3). The length of the N leaching period showed less among-plot variability than the number of incubation days needed for the onset of N mineralization. Although net N release started significantly earlier in MF than in CF, no significant differences between sites were found for the percentage organic mass remaining, C/N, Lignin/N and LIC ratios at the time N mineralization started (Table 5, Fig. 3). However, at this initiation point the values for C/P and Lignin/P were significantly higher in MF.

Table 4 Initial chemical composition of senescent needles. All values in mg g^{-1} (mean ± SE, $n = 3$)

Site	Aspurz			Garde		
	Mediterranean forest (MF)			Continental forest (CF)		
Basal area removed	0%	20%	30%	0%	20%	30%
C	483.13 ± 0.15	483.91 ± 0.23	483.13 ± 0.11	486.61 ± 5.61	483.52 ± 3.23	483.54 ± 3.32
Cellulose	259.83 ± 2.91	260.52 ± 3.30	255.64 ± 4.01	261.11 ± 4.71	263.63 ± 6.11	257.34 ± 5.92
Lignin	182.21 ± 28.12	246.82 ± 35.51	190.41 ± 27.83	235.43 ± 9.81	256.52 ± 0.92	237.70 ± 4.92
N	11.22 ± 0.43	13.34 ± 1.54	11.01 ± 0.74	8.63 ± 0.92	9.40 ± 1.12	10.71 ± 0.72
P	0.70 ± 0.03	0.92 ± 0.12	0.76 ± 0.01	0.80 ± 0.07	0.84 ± 0.07	0.86 ± 0.12
K	4.90 ± 0.30	4.52 ± 0.22	4.29 ± 0.14	4.55 ± 0.53	4.41 ± 0.59	3.42 ± 0.25
Ca	3.44 ± 0.58	5.05 ± 0.81	4.77 ± 0.36	5.06 ± 0.80	5.34 ± 1.51	3.59 ± 0.99
Mg	0.84 ± 0.04	1.19 ± 0.25	0.87 ± 0.04	1.05 ± 0.04	1.12 ± 0.03	0.94 ± 0.05

Significant differences between sites were only found for lignin and N (ANOVA, $p < 0.05$). For within site comparisons significant differences were only found for K in Garde (P0 > P30, $p = 0.043$, linear contrast). The latter result was probably due to differences among thinning intensities in throughfall reaching senescent litter, before litter collection

Objective 4: Effects of thinning on soil temperature and moisture, decomposition rates and litter chemical contents

No significant changes in soil temperature ($p = 0.948$) or soil moisture ($p = 0.628$) were detected after thinning. Thinning did not affect leaf litter decomposition at any site during the first year ($p = 0.257$). Second year decomposition rates in MF were significantly higher in P0 than in P20 and P30 ($p = 0.003$), but no significant differences were found between P20 and P30 ($p = 0.480$). No thinning effect was found in CF ($p = 0.796$) during the second year. In the third year, however, both sites showed significant differences in decomposition rates between P0 and P20 and between P0 and P30, but not between P20 and P30 ($p = 0.054$). No significant effect to thinning was found in the 4th and 5th years (4th year: $p = 0.134$; 5th year: $p = 0.979$).

Thinning caused more chemical changes in the litter in CF than in MF (Figs. 2, 3). Thinning effects in CF generally appeared sequentially, first nutrients and cellulose and then total C and lignin. A similar pattern was observed in MF, but significant effects on cellulose were not found, and the effects on lignin and C lasted less than in CF and were detected earlier. When significant effects were detected, N and P increased with thinning intensity in CF, and P30 had the highest values for P in MF (Fig. 2). Calcium, however, was generally lower in P30, both in MF and CF. Thinning effects on Mg content lasted more in CF (4 years) than in MF (1 year) and although a clear gradient was not observed, Mg values were generally lower in P0 (Fig. 3). Potassium effects were mainly observed immediately after the experiment began, and at this time K contents were significantly higher in P30 than in P20 and P0 (Fig. 2). Finally, C/P and Lignin/P at the time N mineralization started were significantly reduced in P30 relative to P0 in CF (Table 5).

Discussion

Our results show that both main effects (site and management) clearly influenced litter decomposition, although the effects of management changed over time. Warmer conditions at the Mediterranean site caused faster mass loss and chemical changes compared to the cooler continental site. However, these differences disappeared over time as the litter quality for decomposers was reduced, and after 5 years both sites had similar remaining litters. The influence of local climate on litter decomposition was exacerbated by thinning. Removing part of the forest cover reduced litter moisture and litter inputs to the soil, and increased light, altering the decomposer community and therefore reducing decomposition rates. A detailed discussion of our results in relation to our objectives and their implications for management follows below.

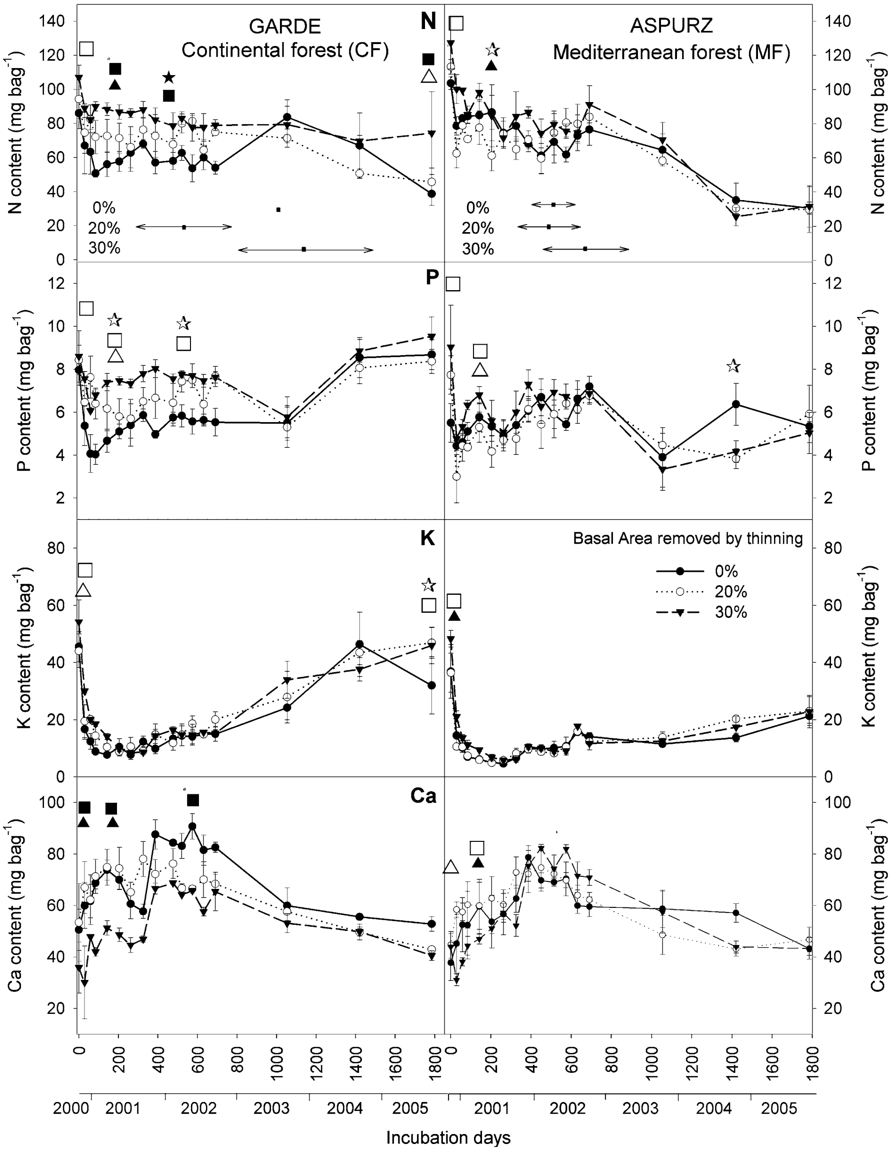

Fig. 2 Nutrient content (N, P, K, Ca) in decomposing needles (mean $\pm$ standard error, $n = 9$). Significant differences on a year basis resulting from linear contrasts are represented as follows: star P0 $\neq$ P20, square P0 $\neq$ P30, triangle P20 $\neq$ P30; solid symbols $p < 0.01$, empty symbols $p < 0.05$. Black dots at the bottom of the N panel mark the average and arrows the range (standard error) of the onset of net N release in each treatment. No among-plot variability was found for Garde 0%

Objectives 1 & 2: Differences between sites and variables affecting decomposition rates

The *k* value for MF was higher or similar to those reported for *P. sylvestris* in other Mediterranean sites (e.g., Fioretto et al. 1998; Santa Regina and Tarazona 2001), and the *k* value for CF was similar to other continental sites (e.g., Pausas 1997; Belchansky et al. 1998). Differences between sites in stem density were probably not important, because the site with the higher number of trees (MF) also had thinner trees with smaller canopies (Table 1).

During the first decomposition stage, rainfall removed organic matter from litter by leaching away the more soluble carbon compounds at both sites, which explains the high proportion of mass loss decrease, especially in MF. The negative correlation between mass losses and N and P in MF may simply be due to the fact that mass losses increased when leaching losses of labile carbon compounds were also high. It is likely that temperature was involved in determining decomposition rates, at least in CF (the colder site). Indeed, Phase 1 took place during the winter months and the limiting effects of temperature

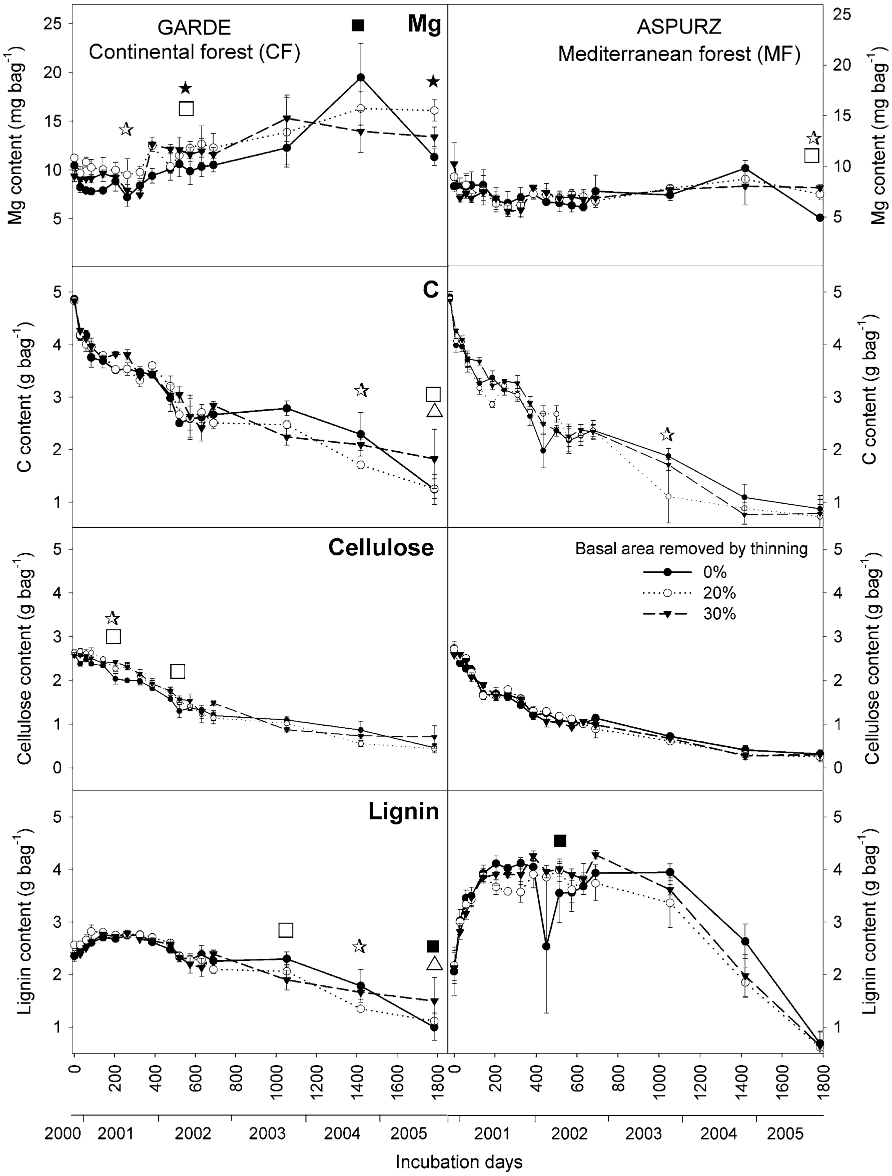

Fig. 3 Nutrient (Mg) and organic compounds content (C, cellulose, lignin) in decomposing needles (mean ± standard error, $n = 9$). Significant differences on a year basis resulting from linear contrasts are represented as follows: star P0 ≠ P20, square P0 ≠ P30, triangle P20 ≠ P30; solid symbols $p < 0.01$, empty symbols $p < 0.05$

were likely enhanced in CF relative to MF. Cellulose mass was one of the critical variables at this period in both sites, probably as a consequence of its role as an easy energy source for decomposers.

During the second phase of decomposition, climate was still important at both sites, but changes in mass losses were mainly related to changes in carbon content, especially lignin. Negative correlations between mass losses and N might also indicate the suppressing effect of N on lignin degradation (Berg and Laskoswski 2006), which could be due to reductions in the activity of the phenol-oxidase enzyme (Waldrop et al. 2004). Other variables in the best model were site-specific: changes in litter moisture in MF and changes in the nutrient content in CF. This fact might indicate that decomposers followed different strategies at each site. The significant positive relationships in MF between mass losses and accumulated rainfall and changes in soil and litter moisture support the hypothesis that, at this site, faster decomposer activity may be limited by climate, specifically soil moisture. Organic mass losses were relatively slower in summer coinciding with low water contents and higher temperatures

Table 5 Mean ± standard error of different variables at the time net release of N started

Site	Thinning intensity	Time[a] (years)	Initial O.M. (mass%)	C/N	Lignin/N	C/P	Lignin/P	LIC
Aspurz (MF)	Control	1.45 ± 0.30a	55.88 ± 4.59a	35.04 ± 6.69a	28.74 ± 4.42a	831.66 ± 159.09a	683.06 ± 106.97a	0.62 ± 0.02a
	Removal 20% BA	1.39 ± 0.42a	57.88 ± 5.06a	34.75 ± 4.97a	28.48 ± 4.03a	857.51 ± 116.15a	704.00 ± 97.20a	0.64 ± 0.01a
	Removal 30% BA	1.89 ± 0.58a	52.18 ± 9.36a	30.74 ± 6.62a	25.92 ± 5.31a	928.82 ± 97.71a	787.60 ± 59.43a	0.66 ± 0.02a
Garde (CF)	Control	2.89 ± 0.00A	55.35 ± 2.41a	33.94 ± 2.44a	27.99 ± 2.00a	832.37 ± 87.47A	687.04 ± 74.48A	0.68 ± 0.02a
	Removal 20% BA	1.61 ± 0.64A	70.15 ± 5.31a	39.54 ± 4.85a	32.15 ± 2.62a	629.02 ± 49.97AB	514.01 ± 28.64AB	0.57 ± 0.03b
	Removal 30% BA	3.22 ± 0.88A	47.08 ± 12.56a	27.25 ± 3.09a	23.02 ± 2.77a	504.56 ± 63.22B	428.09 ± 61.58B	0.67 ± 0.01a

Different letter cases indicate significant differences between sites and different letters indicate differences among treatments ($p < 0.05$) with Tukey's H.S.D.

[a] Time: years after the beginning of the study

BA Basal area

(Fioretto et al. 1998), but losses were higher in spring and fall when rainfall increased.

A third phase was observed only in MF, characterized by small mass losses apparently controlled by leaf litter chemical composition (Berg 2000). However, maximum decomposition limit was significantly higher in CF, implying that in the long term organic mass loss in CF could be larger than in MF. This could explain the observed higher C accumulation in horizon A at MF. The higher N concentration in needles and soil in MF and the increase in recalcitrant lignin-like compounds agree with the mechanism suggested by Berg (2000) to explain the lowering of the limit value in *P. sylvestris* litter. Furthermore, remaining organic mass after 5 years was similar in both sites, despite the fact that Phase 2 had not finished in CF. It has been reported that high-N needle litter or N-fertilized needle litter (Berg 2000; Sjöberg et al. 2004) starts to decompose faster, but decelerates later on. From a management perspective, in stands under long rotations, it may not matter if N initially accelerates litter decomposition if, at the same time, it retards decomposition in the long run (Prescott et al. 2004).

Objective 3: Temporal changes in contents of nutrients and carbon compounds

Lower nutrient contents in MF decomposing litter may imply higher release of nutrients due to higher decomposer activity at the site with higher evapotranspiration, supporting the hypothesis by Berg and Laskowski (2006). Considering the 5-year period as a whole, there was no net release of P, Ca and Mg in CF and Ca in MF. Therefore, nutrient immobilization was higher in the continental stand for P and Mg. Nitrogen, P and K exhibited an initial phase with decreasing nutrient content, mainly due to leaching losses. Then, a second stage with increases in nutrient content was observed for N, P, and Ca. The increase in nutrient content was likely caused by fungi importing N, P and maybe Ca to overcome nutrient limitation (Berg and Laskowski 2006). Potassium showed a slow asymptotic increase after the initial content decrease, likely a consequence of being immobilized by the most stable organic fractions or by saprotrophic fungi (Laskowski et al. 1995b). The stands studied here seem to differ from most temperate pine forests whose Ca litter content decreases over time (Staaf and Berg 1982;

Laskowski et al. 1995a, b) although Ca increases have also been reported in some studies (Klemmedson 1985; Kainulainen and Holopainen 2002). Magnesium showed little initial change after leaching and an increase as decomposition proceeded (mainly in CF), a pattern previously described (Berg and Laskowski 2006). The initial increase in lignin content at both sites appears to result from lignin-related substances (such as humic acids) formed during decomposition (Berg and McClaugherty 1987). A conceptual model for N dynamics emerged from our results with the phases of leaching, accumulation (i.e., immobilization) and release (Berg and Laskoski 2006), the magnitude of the immobilization phase increasing with nutrient limitation due to thinning, and the timing for release phase depending on initial N litter (Fig. 4).

Litter values of C/N, lignin/N, LIC and mass loss were similar at the onset of N release in both stands, despite the fact that CF took twice as long to reach the end of N accumulation relative to that of MF (Table 5). For litter C/N, this convergence of values (i.e., 33.3) appears to be due to physiological constraints of microbes which have narrow ranges of biomass C/N ratios which are stoichiometrically related to litter C/N ratios (Sterner and Elser 2002). Furthermore, the inverse relationship between the time required to initiate net N release and initial litter N observed in our sites (MF > CF) has also been reported on a global scale (Parton et al. 2007). It appears that at the time N accumulation ended, our stands had lower values of C/N and lignin/N, higher values of mass loss and similar or longer incubation times than those reported for *P. sylvestris* in more northern latitudes (Staaf and Berg 1977; Berg and Laskowski 2006).

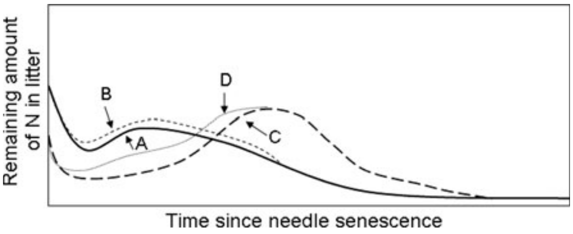

Fig. 4 Conceptual model of N release in decomposing leaf litter emerging from our results. (A) Litter with higher initial N concentration in unthinned plots, (B) Litter with higher initial N concentration in thinned plots, (C) Litter with lower initial N concentration in unthinned plots, (D) Litter with lower initial N concentration in thinned plots. All curves show phases of leaching, accumulation (i.e., immobilization) and release (Berg and Laskowski 2006). N immobilization increases with thinning intensity (B > A and D > C) although different results might be expected depending on thinning effects on litter quality and/or microbial C/N ratios (see main text). N immobilization is higher in lower-N litter than in higher-N litter both in unthinned (C > A) and thinned (D > B) plots, because microbes need to input more N from litter surroundings to utilize the available carbon. Higher-N litter (A, B) takes less time to initiate N release than lower-N litter (C, D). Thinning, however, has no effect on initiation time of N net release. Our litters have intermediate initial N concentrations according to Parton et al. (2007). A higher relative increase in N immobilization in response to thinning would be expected for low-initial N litter and extremely-low initial N litter

All things considered, the use of nutrient/C ratios to predict the onset of nutrient release should be taken with caution. These nutrient/C ratios are highly influenced by local conditions, and they do not take into account the quality of C, N or P constituents in the litter, which is more important than the relative amounts of nutrients or lignin (Berg and Laskowski 2006). Nitrogen release generally starts when lignin breakdown begins, as appears to have been the case in MF (Fig. 3). Usually, net P release starts when it ceases to limit decomposers growth, an event that in our study seems to have occurred only in some plots in MF. Lignin/P ratios on both sites were within the limits of the critical range proposed by Osono and Takeda (2004), but there was no clear relationship between this ratio and the time when P release started, indicating that this index is not useful to predict P mobilization at our sites. In the case of Ca, its net release in MF started before that of N and P and appears to be related to decomposition of structural compounds where it is confined (Laskowski et al. 1995a).

Objective 4: Effects of thinning on litter quality and decomposition rates

Reduction in decomposition rates due to thinning started after 2 years in the Mediterranean site and after 3 years in the continental site, coinciding with the time when more significant relationships were found between mass loss and content of carbon compounds. However, this reduction in decomposition rates was apparently not caused directly by changes in soil temperature, and it contradicts the possible effect of UV radiation on decomposition rates in the thinned plots (Austin and Vivanco 2006).

A parallel study carried out at our sites showed that the decrease in litter moisture after thinning (a phenomenon also described by Gurlevick et al. 2003) was associated with a decrease in mesofauna densities on leaf litter and decomposition rates (Blanco 2004; Garay 2004). Reduction of mesofauna abundance may also be related to increased light levels in the thinned plots (negatively affecting luciphobous species) and increasing polyphenol concentrations in leaf litter thereby inhibiting microbial growth (Covelo and Gallardo 2002). Reduction in microarthropod densities after thinning has been previously reported (Bird et al. 2000). In light of these results we reject our hypothesis regarding decomposition increases in CF due to soil temperature increases after thinning, but do not reject the prediction of decomposition decreases in MF due to decrease in soil water after thinning.

In addition, significant differences between thinning intensities in decomposition rates occurred 1 year after differences in microarthropod densities and nutrient immobilization of N, P and Ca were detected (Blanco 2004; Garay 2004). These results suggest a combined action of microarthropods and microorganisms which accelerate decomposition. Lower microarthropod taxa richness could also explain reduced decomposition rates. Lower diversity of microarthropods results in consumption of a smaller variety of litter fractions, leaving other types untouched (González and Seastedt 2001), leading to a decrease in decomposition rate and nutrient release. Indeed, taxa richness generally decreased in thinned plots relative to control plots in MF (first and second year) and CF (second half of first year and second year) (Garay 2004). Similar changes in fungal and bacterial density and diversity could have occurred in response to changes in leaf moisture, although this type of data was not collected during this study.

Soil biota immobilized nutrients in these stands in response to nutrient limitations, triggering increases in N, P and Ca contents in the thinned plots at CF during the first 2 years of incubation. Thus, N and P contents increased with thinning intensity ($P0 < P20 < P30$) while Ca contents were lower in P30, suggesting that two functional types of microorganisms may be involved in the immobilization process. The increase for N and P may be related to a reduction in cellulose degradation, with cellulose contents in P20 and P30 higher than in P0 (Fig. 3). Calcium is the principal ion deposited by atmospheric means at our sites, with a bulk deposition of 24.5 kg Ca ha^{-1} $year^{-1}$ (Blanco et al. 2005). Although we do not have data on dry deposition of Ca to these sites, we hypothesize that the lower Ca content in decomposing litter in the thinned plots could have resulted from lower dry deposition of Ca to the thinned canopies of those plots and therefore lower Ca in throughfall that could be incorporated into the litter (Baeumler and Zech 1997). Nutrient increases in MF, particularly for P and Ca, were generally similar to those of CF but their magnitude was smaller and their duration shorter, likely because canopy closure occurred faster at this site.

Changes in N and P immobilization with thinning may have been caused by two factors: (1) changes in C/N and C/P ratios of litter, and (2) changes in C/N and C/P ratios of microbial biomass. The first factor may be ruled out as there were no significant differences among thinning intensities for N and P concentrations in litter, and for litter C/N and C/P ratios when incubation started (Table 4). Furthermore, except for N litterfall concentration in Aspurz ($P20 < P0$), N and P concentrations in litterfall showed no significant differences among thinning intensities in a parallel study carried out in the same experimental sites (Blanco et al. 2008). Regarding the second factor, if thinning did not affect litter quality, a decrease in C/N and C/P ratios of microbial biomass would have been expected in order to observe an increase in N and P immobilization in litter after thinning. These microbial C/nutrient ratio changes imply a change in soil microbial community structure. This phenomenon has been observed or predicted after litter removal (Sayer 2006) and after increases of carbon inputs to soils (Fontaine et al. 2003; Chigineva et al. 2009; Nottingham et al. 2009). In this context, the change in microbial community structure in our study would have been triggered by decreases in C, N and P inputs in total litterfall with thinning intensity ($P0 > P20 > P30$) during peaks of litterfall production (Blanco et al. 2008), although the decrease in litter moisture might also be involved. Finally, the magnitude of immobilization increases was higher in CF than in MF which is in accord with significantly lower N litterfall concentrations in CF than in MF (Blanco et al. 2008). However, P litterfall concentration was significantly higher in CF than in MF which contradicts the phosphorus immobilization pattern, and indicates that factors other than C/nutrient ratios might be involved. Lower N and P immobilization in MF than in CF is not surprising as MF is an ecosystem more productive than CF (Blanco et al. 2005). Given that the available P concentration in soil is similar at both sites, there are several facts indicating that competition for P between trees and microorganisms may be greater in CF: (1) P concentrations in *P. sylvestris*' branches and needles was higher in CF than in MF (Blanco et al. 2006b); (2) trees retained P for longer periods of time in CF (Blanco et al. 2009); (3) no net P release in decomposing litter occurred on average in CF over 5 years; (4) P was positively correlated with mass losses in Phase 2 in CF; and (5) thinning reduced litter C/P and lignin/P ratios at the onset of N release in CF, suggesting changes in P assimilation efficiency of decomposers (Chapin et al. 2002) and that P was still limiting decomposition at this point in time, more so in the thinned plots.

All things considered, studies on the influence of thinning or clearcutting on litter decomposition are scarce and frequently contradictory. For example, in agreement with our study, Hendrickson et al. (1985) reported a decrease in decomposition rates of *P. resinosa* litter in a whole-tree removal plot relative to an uncut plot, but unlike our study they also observed a decrease in N, P, K and Mg litter after whole-tree removal. On the other hand, Kunhamu et al. (2009) described accelerated decomposition rates in *Acacia mangium* stands with high thinning intensities, but no changes under medium and low intensities. As our results show, conflicting observations may be the result of management activities affecting litter decomposition differently, depending not only on the type and intensity of disturbance but also on site characteristics (e.g., soil type, climate, plant species, and site history). In agreement with our results, Berg (1988) showed a decrease in decomposition rates and a concomitant increase in N concentration and content after clearcutting. Gurlevick et al. (2003) also reported slower decomposition and lower release rates of N and P in *P. taeda* litter after reducing vegetation cover by clear-cutting.

Timing of nutrients and carbon release may be important in management of stands under short rotations because thinning effects on tree growth occur mainly within the first years after tree removal (Oliver and Larson 1996). If everything else is equal, sites where nutrient release occurs faster may show higher post-thinning tree growth rates. Hence, despite convergence and probably reversal of mass loss rates, higher and faster release of nutrients in MF during this 5-year period suggests relatively stronger thinning effects on tree growth at this site. These short-term and temporal changes could be even more important in management of fast-growing plantations for fiber or biomass (which could be as short as 7 or 10-year rotations, depending on the species, climate and management objectives) (Mboukou-Kimbatsaa et al. 1998; Weih 2004).

It is important to highlight that quantitative effects at our sites were site dependent, with the magnitude of nutrient changes higher in CF, likely reflecting greater N and P limitation for decomposers at this site. On the other hand, decreases in decomposition rates in response to thinning were higher in MF, indicating that this ecosystem could be more sensitive to human intervention in the short term, which agrees with similar conclusions obtained by analyzing other ecosystem processes at this site (Blanco et al. 2005, 2008, 2009). This result may imply that the effects of thinning on decomposition limiting factors other than N and P were stronger in MF than in CF. If another thinning is carried out in these sites resulting in a significantly reduced stand density, it might increase solar radiation to the soil and cause changes in temperature and moisture levels in the A horizon of the soil, in addition to changes in litter moisture observed during the first thinning. This might induce more long-lasting changes in decomposition rates and nutrients, which may cause management failure with reduced tree competition being balanced out with decreased nutrient availability as a consequence of both slower litter decomposition and a reduction in nutrient mineralization. Further, decreases in decomposition rates in thinned plots would probably not counterbalance decreases in soil C storage due to reduced litterfall.

Acknowledgments Thanks are due to the Government of Navarre for financial support and setting up the experimental plots. Special thanks to Fernando Puertas, Carmen Traver and Ana Iriarte for assistance at several stages of this work. Juan A. Blanco had financial support from a fellowship granted by the Spanish Ministry of Science and Technology. We thank Susana García, Pablo Pujol and staff at SAI for chemical analyses. Thanks are also due to Gary M. Lovett and two anonymous reviewers whose comments helped to greatly improve this paper. Last but not least, we thank Tanya Seebacher for her English grammar review.

References

Aber JD, Melillo JM, McClaugherty CA (1990) Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. Can J Bot 68:2201–2208

Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79:439–449

Allen HL (2001) Silvicultural treatments to enhance productivity. In: Evans J (ed) The forest handbook, vol 2. Applying forest science for sustainable management, vol 2. Blackwell Science, Oxford, pp 129–136

Austin AT, Vivanco L (2006) Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nature 442:555–558

Bachiller A, Montero G, Ortega C, Cañellas I et al (1999) Aboveground productivity and nutrient dynamics in a reforestation of *Pinus pinaster* Ait. with different intensities of thinning. Investigación Agraria, Sistemas y Recursos Forestales 8:175–206

Baeumler R, Zech W (1997) Atmospheric deposition and impact of forest thinning on the throughfall of mountain forest ecosystems in the Bavarian Alps. For Ecol Manage 95:243–251

Belchansky GI, Petrosyan VG, Douglas DC (1998) Community structure, plant diversity and microclimate of boreal forest types in the Russian Ural. In: Dallmeier F, Comiskey A (eds) Forest biodiversity research, monitoring and modeling. Man and The Biosphere series, vol 20. UNESCO, Paris, pp 101–108

Berg B (1988) Dynamics of nitrogen (15 N) in decomposing Scots pine (*Pinus sylvestris*) needle litter. Long-term decomposition in a Scots pine forest. IV. Can J Bot 66:1539–1546

Berg B (2000) Initial rates and limit values for decomposition of Scots pine and Norway spruce needle litter: a synthesis for N-fertilized forest stands. Can J For Res 30:122–135

Berg B, Ekbohm G (1991) Litter mass-loss rates and decomposition patterns in some needle and leaf litter types-long-term decomposition in a Scots pine forest. VII. Can J Bot 69:1449–1456

Berg B, Laskowski R (2006) Litter decomposition: a guide to carbon a nutrient turnover. Adv Ecol Res 38:1–428

Berg B, McClaugherty C (1987) Nitrogen release from litter in relation to the disappearance of lignin. Biogeochemistry 4:219–224

Berg B, Staaf H (1980) Leaching, accumulation and release of nitrogen in decomposing forest litter. In: Clark FE, Rosswall T (eds) Terrestrial nitrogen cycles. Ecological Bulletin, vol 33. Swedish Natural Science Research Council, Stockholm, pp 163–178

Berg B, Berg MP, Bottner P, Box E, Breymeyer A, Calvo de Anta R, Couteaux M, Escudero A, Gallardo A, Kratz W, Madeira M, Mälkonen E, McClaugherty C, Meentemeyer V, Muñoz F, Piussi P, Remacle J, Virzo de Santo A (1993) Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. Biogeochemistry 20:127–159

Bird S, Coulson RN, Crossley DA Jr (2000) Impacts of silvicultural practices on soil and litter arthropod diversity in a Texas pine plantation. For Ecol Manage 131:65–80

Blanco JA (2004) La práctica del aclareo y su influencia en la estructura y función de dos bosques de pino silvestre del Pirineo Navarro. PhD thesis, Public University of Navarre

Blanco JA, Zavala MA, Imbert JB, Castillo FJ (2005) Sustainability of forest management practices: Evaluation through a simulation model of nutrient cycling. For Ecol Manage 213:209–228

Blanco JA, Imbert JB, Castillo FJ (2006a) Influence of site characteristics and thinning intensity on litterfall production in two *Pinus sylvestris* L. forests in the western Pyrenees. For Ecol Manage 237:342–352

Blanco JA, Imbert JB, Castillo FJ (2006b) Effects of thinning on nutrient pools in two contrasting *Pinus sylvestris* L. forests in the western Pyrenees. Scand J For Res 21:143–150

Blanco JA, Imbert JB, Castillo FJ (2008) Nutrient return via litterfall in two contrasting *Pinus sylvestris* forests in the Pyrenees under different thinning intensities. For Ecol Manage 256:1840–1852

Blanco JA, Imbert JB, Castillo FJ (2009) Thinning affects nutrient resorption and nutrient use efficiency in two *Pinus sylvestris* stands in the Pyrenees. Ecol Appl 19:682–698

Bray RH, Kurtz LT (1945) Determination of total, organic and available forms of phosphate in soils. Soil Sci 59:39–45

Chapin FS, Matson PA, Mooney HA (2002) Principles of terrestrial ecosystem ecology. Springer-Verlag, New York

Chigineva NI, Aleksandrova AV, Tiunov AV (2009) The addition of labile carbon alters fungal communities and decreases litter decomposition rates. Appl Soil Ecol 42:264–270

Covelo F, Gallardo A (2002) Effect of pine harvesting on leaf nutrient dynamics in young oak trees at NW Spain. For Ecol Manage 167:161–172

Duchesne LC, Wetzel S (1999) Effect of clear-cutting, prescribed burning and scarification on litter decomposition in an eastern Ontario jack pine (*P.* banksiana) ecosystem. Int J Wild Fire 9:195–201

Fioretto A, Musacchio A, Andolfi G, DeSanto AV (1998) Decomposition dynamics of litter of various pine species in a Corsican pine forest. Soil Biol Biochem 30:721–727

Fontaine S, Mariotti A, Abbadie L (2003) The priming effect of organic matter: a question of microbial competition? Soil Biol Biochem 35:837–843

Garay I (2004) Influencia de distintas intensidades de aclareo sobre la colonización de microartrópodos de hojarasca en descomposición en dos bosques de *Pinus Sylvestris* del Pirineo navarro. Segundo año. BSc thesis, Public University of Navarre

González G, Seastedt TR (2001) Soil fauna and plant litter decomposition in tropical and subalpine forest. Ecology 82:955–964

Government of Navarre (2006) Meteorología y climatología de Navarra. Available via Government of Navarre. http://meteo.navarra.es/. Cited 20 Oct 2006

Gurlevick N, Kelting DL, Allen HL (2003) The effect of vegetation control and fertilization on net nutrient release from decomposing loblolly pine needles. Can J For Res 33:2491–2502

Harmon ME, Silver WL, Fash B, Chen H, Burke IC, Partons WJ, Hart SC, Currie WS LIDET (2009) Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. Glob Change Biol 15:1320–1338

Heal OW, Anderson JM, Swift MJ (1997) Plant litter quality and decomposition: an historical overview. In: Cadisch G, Giller KE (eds) Driven by nature: plant litter quality and decomposition. CAB International, Wallingford, UK

Hendrickson OQ, Chatarpaul L, Robinson JB (1985) Effects of two methods of timber harvesting on microbial processes in forest soil. Soil Sci Soc Am J 49:739–746

Hobbie SE (2005) Contrasting effects of substrate and fertilizer nitrogen on the early stages of litter decomposition. Ecosystems 8:644–656

Hobbie JE, Hobbie EA (2006) N-15 in symbiotic fungi and plant stimates nitrogen and carbon flux rates in Arctic tundra. Ecology 87:816–822

Horwitz W (ed) (1980) Official methods of analysis of the Association of Official Analytical Chemists, 13th edn. A.O.A.C., Washington, DC

Iriarte A, Puertas F (2003) Thinning experiment in a natural stand of *Pinus sylvestris* L., Aspurz (Navarre). In: Proceedings of IUFRO meeting "Silviculture and sustainable management in mountain forests in the western Pyrenees. Isaba. 15–19 Sep 2003

Kainulainen P, Holopainen JK (2002) Concentrations of secondary compounds in Scots pine needles at different stages of decomposition. Soil Biol Biochem 34:37–42

Klemmedson JO (1985) Needle decomposition and nutrient release in Ponderosa Pine Ecosystems. For Sci 31: 647–660

Kunhamu TK, Kumar BM, Viswanath S (2009) Does thinning affect litterfall, litter decomposition, and associated nutrient release in *Acacia mangium* stands of Kerala in Peninsular India? Can J For Res 39:792–801

Laskowski R, Niklińska M, Maryański M (1995a) The dynamics of chemical elements in forest litter. Ecology 76:1393–1406

Laskowski R, Berg B, Johansson MB, McClauherty C (1995b) Release pattern for potassium from decomposing forest needle and leaf litter. Long-term decomposition in a Scots pine forest. IX. Can J Bot 73:2019–2027

M.A.F.F. (1986) The analysis of agricultural materials (RB427). Ministry of Agriculture Fisheries and Food, London

Mboukou-Kimbatsaa IMC, Bernhard-Reversata F, Loumetob JJ (1998) Change in soil macrofauna and vegetation when fast-growing trees are planted on savanna soils. For Ecol Manage 110:1–12

McTiernan KB, Couteaux MM, Berg B et al (2003) Changes in chemical composition of *Pinus sylvestris* needle litter during decomposition along a European coniferous forest climatic transect. Soil Biol Biochem 35:801–812

Nottingham AT, Griffiths H, Chamberlain PM, Stott AW, Tanner EVJ (2009) Soil priming by sugar and leaf-litter substrates: A link to microbial groups. Appl Soil Ecol 42:183–190

Oliver CD, Larson BC (1996) Forest stand dynamics. Wiley, New York

Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. Ecology 14: 322–331

Osono T, Takeda H (2004) Accumulation and release of nitrogen and phosphorus in relation to lignin decomposition in leaf litter of 14 tree species. Ecol Res 19:593–602

Osono T, Hobara S, Koba K et al (2006) Immobilization of avian excreta-derived nutrients and reduced lignin decomposition in needle and twig litter in a temperate coniferous forest. Soil Biol Biochem 38:517–525

Parton W, Silver WL, Burke IC, Grassens L, Harmon ME, Currie WS, King JY, Adair EC, Brandt LA, hart SC, Fasth B (2007) Global-scale similarities in nitrogen release patterns during long-term decomposition. Science 315: 361–364

Pausas JG (1997) Litter fall and litter decomposition in *Pinus sylvestris* forests of the eastern Pyrenees. J Veg Sci 8:643–650

Piene H, Van Cleve K (1978) Weight loss of litter and cellulose bags in a thinned white spruce forest in interior Alaska. Can J For Res 8:42–46

Prescott CE, Vesterdal L, Preston CM, Simard SW (2004) Influence of initial chemistry on decomposition of foliar litter in contrasting forest types in British Columbia. Can J For Res 34:1714–1729

Puertas F (2001) Sitios de ensayo de claras de masas de pino Silvestre en Navarra (Garde y Aspurz). Servicio de Conservación de la Biodiversidad. Departamento de Medio Ambiente Ordenación del Territorio y Vivienda. Government of Navarre, Pamplona

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

Santa Regina I, Tarazona T (2001) Nutrient cycling in a natural beech forest and adjacent planted pine in northern Spain. Forestry Oxford 74:11–28

Sayer EJ (2006) Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. Biol Rev 81:1–31

Scowcroft PG, Turner DR, Vitousek PM (2000) Decomposition of *Metrosideros polymorpha* leaf litter along elevational gradients in Hawaii. Glob Change Biol 6:73–85

Sjöberg G, Nilsson SI, Persson T, Karlsson P (2004) Degradation of hemicellulose, cellulose and lignin in decomposing spruce needle litter in relation to N. Soil Biol Biochem 36:1761–1768

Staaf H, Berg B (1977) Mobilization of plant nutrients in a Scots pine forest mor in Central Sweden. Silva Fennica 11:210–217

Staaf H, Berg B (1982) Accumulation and release of plant nutrients in decomposing Scots pine needle litter. long-term decomposition in a Scots pine forest II. Can J Bot 60:1561–1568

Sterner RW, Elser JJ (2002) Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton, NJ

Waldrop MP, Zak DR, Sinsabaugh RL, Gallo M, Lauber C (2004) Nitrogen deposition modifies soil carbon storage through changes in microbial enzymatic activity. Ecol Appl 14:1172–1177

Walkley A, Black IA (1934) An examination of the Degtjareff method for determining soil organic matter and a proposed modification of the chromic acid titration method. Soil Sci 37:29–38

Weih M (2004) Intensive short rotation forestry in boreal climates: present and future perspectives. Can J For Res 34:1369–1378

Zasoski RJ, Burau RG (1977) A rapid nitric-perchloric acid digestion method for multielement tissue analysis. Comun Soil Sci Plant Anal 8:425–436