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Litterfall, litter decomposition and associated nutrient fluxes in *Pinus halepensis*: influence of tree removal intensity in a Mediterranean forest

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Abstract

Our knowledge about the influence of silvicultural treatments on nutrient cycling processes in Mediterranean forests is still limited. Four levels of tree removal were compared in an Aleppo pine forest in eastern Spain to determine the effects on litterfall, litter decomposition and the associated nutrient fluxes after 12 years. Removal treatments included clearfelling, two shelterwood intensities (60% and 75% of basal area removed) and untreated controls. Twelve years later, the basal area removed still explained 60% of litterfall mass variance, and 60% of C, 52% of N, 45% of P, 17% of K, 47% of Ca and 60% of Mg return variances. Litter decomposed somewhat more slowly in clearfellings compared to controls (p=0.049), and accumulated more Ca and released less K compared to the other three treatments. This was explained by contamination with mineral particles due to the poorly developed O horizon in clearfellings. We conclude that the management practices reduced the nutrient return via litterfall, but the nutrient release through decomposition seems poorly sensitive to canopy disturbance. In order to accurately quantify the harvesting impacts on nutrient cycling in this Mediterranean forest system, it is necessary to measure the litterfall of the understory layer.

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1. Introduction

In recent years abandonment has been considered a crucial factor influencing Mediterranean forests (Fabbio et al., 2003). Most of these forested areas are pioneer ecosystems that should be managed to increase their ecological value and their resistance to fire and pests (Scarascia-Mugnozza et al., 2000). In the Mediterranean, silvicultural treatments have been postulated as a way to increase tree species richness (Torras and Saura, 2008), to augment water yields (Molina and Del Campo, 2012) or to reduce fire intensity (Alvarez et al., 2012). In this scenario, it is important to take into account how these practices influence ecosystem stability and functioning to ensure sustainable forest management.

A good knowledge of the impacts that harvesting practices have on nutrient cycling processes is needed to evaluate the sustainability of forest management systems (Kimmins 2004). Litter production and its subsequent decomposition constitute the main aboveground path of nutrients to soil. Therefore, they are common components of mathematical models used to forecast the implications of management at the ecosystem level (e.g. Kimmins et al., 1999; Blanco et al., 2005; Petritsch et al., 2007). Silvicultural treatments that reduce the forest canopy are expected to reduce nutrient return to soil through litterfall (Prescott, 2002; Blanco et al., 2008). This could lead to reduced soil nutrient availability in the long term, depending on intensity of treatments and rotation period duration (Blanco et al., 2005). Besides, changes in the litter production-decomposition balance can modify forest floor layer size, which has been considered to be either a nutrient reservoir that gradually provides nutrients or a temporal obstacle to tree nutrient availability due to immobilisation processes (Roig et al., 2005, Jonard et al., 2006). Litterfall and litter decomposition fluxes are especially important for nutrient budgets in ecosystems whose environmental conditions limit tree vegetation growth (Caldentey et al., 2001). This highlights the pressing need for experimental data to optimise management practices in order to prevent nutrient overexploitation in Mediterranean forests, which usually develop on nutrient-poor soils and are submitted to strong water limitations (which are expected to increase in the future due to climate change; Christensen et al., 2013). Paradoxically, such information for these ecosystems is comparatively scarce.

Litter production seems to decrease proportionally with the stand basal area (Hennessey et al., 1992; Kunhamu et al., 2009; Navarro et al., 2013; Trofymow et al., 1991). Nonetheless, the mechanisms behind reduced litter production are not straightforward. According to Blanco et al., (2006), the forest response to management practices is controlled by several factors and their interaction (e.g. tree species, climatic conditions). Hence it is difficult to predict changes in litter production. The same conclusion can be applied to litter decomposition rates. Thus the literature presents contradictory responses of litter decomposition to partial or total canopy removal, with decreases (Blanco et al., 2011; Prescott, 1997; Blair and Crossley, 1988), increases (Caldentey et al., 2001; Bates et al., 2007), or no effect (Lytle and Cronan, 1998; Wallace and Freedman, 1986) in decay rates. Climate has been proposed to be able to explain these different behaviours (Yin et al., 1989). Thus, clearcutting may stimulate decomposition in cold climates because of an increase in soil temperature, whereas decomposition would be inhibited in warm climates as a result of more intense forest floor drying. Although previous studies conducted under Mediterranean conditions coincide with this hypothesis (Cortina and Vallejo, 1994), we should be careful when generalising about this issue (Prescott et al., 2000).

Despite all this being true, the consequences that tree harvesting has on nutrient fluxes can be influenced by other interfering factors beyond litter mass production and the decomposition rates of dry matter. For instance, Guo and Sims (1999) reported that tree density affected P release from decomposing litter, but not N release and mass loss rates. Similarly in a *Pinus densiflora* stand, Kim et al. (2012) reported that partial cuttings significantly reduced the C, N, P and Ca returns to soil via litterfall, but not K and Mg. Moreover, studies have often focused on N and P fluxes as they are most limiting, which means that less information on other macronutrients is available.

Pinus halepensis is a widely distributed tree species in the western Mediterranean basin, but very little information on the impacts of harvesting treatments on its litter production and decomposition nutrient fluxes is available. In a naturally regenerated forest 5 years after a fire, Sardans et al. (2005) reported how nutrient returns through litterfall were affected by removing competing vegetation in an area covering 1 m^2 around trees. Recently, Navarro et al. (2013) analysed the effect of thinning intensity on litterfall mass production in a 15-year-old *P. halepensis* afforestation area. In the present study, we offer experimental data regarding the effects of management intensity on litter production, litter decomposition and the associated transfers of nutrients (C, N, P, K, Ca and Mg) in a 55- year-old *P. halepensis* forest in the eastern Iberian Peninsula. Treatments were carried out in experimental plots (30 m x 30 m), and included two shelterwood intensities (60% and 75% of basal area removed), clearfellings and untreated controls. This study was conducted twelve years after intervention. We hypothesised that: (i) litter production and nutrient returns through litterfall will be proportionally reduced with harvesting intensity given the reduced canopy cover; (2) the litter decomposition rate and concomitant nutrient releases will be inversely related to tree canopy removal as a result of increased water limitations.

2. Material and methods

2.1. Study area and silvicultural treatments

The study area is located closely to the *Alto de la Montalbana* (39°49’26’’N; 1°05’47’’W, 980 m a.s.l.) in Tuéjar, the province of Valencia, eastern Spain. The climate is Mediterranean-type, with dry summers. According to data from the Titaguas station (832 m a.s.l.) for the 1960-1990 period, mean annual temperature is 12.5°C and mean annual precipitation is 457 mm, with a minimum in summer of 45 mm (Pérez Cueva, 1994). The *Pinus halepensis* Mill. forest resulted from natural regeneration of abandoned agricultural fields. Mean tree age was 55 years when management treatments were applied (1998). The understory community is dominated by

Quercus coccifera, Juniperus oxycedrus, Juniperus phoenicea and *Brachypodium retusum,* with the scant presence of suppressed *Quercus rotundifolia.* Soils in the area are Rendzic Leptosols that develop on calcareous rock, with outcrops of Albic Luvisols and Calcaric Regosols (GVA 1995).

In the spring of 1998, an experimental study began to compare different silvicultural systems on this *P. halepensis* stand. The main goal of these silvicultural systems was to convert the stand into a mixed forest of *P. halepensis* and *Q. rotundifolia* to increase its biological diversity and resilience. Treatments were carried out following a randomised block design, with four treatments and three blocks. The distance among the three blocks was less than 3 km. They had a similar slope (<5%), canopy and climatic characteristics, but contrasting soil properties (Table 1). In each block, four experimental square plots (30 m x 30 m) were selected, one per treatment. Treatments were: (i) T0: untreated control reference; (ii) T60: moderate shelterwood with 60% of mean basal area removed; (iii) T75: strong shelterwood with 75% of mean basal area removed; (iv) T100: clearfelling (100% of mean basal area removed). To avoid edge effects, all the treatments were also applied in a strip of 7.5 m around the plots. In all the treatments, stems were removed, and logging residues (branches, needles, cones, etc..) were left in piles in plots. In the shelterwood treatments, no preparatory cuttings were previously performed. Sheltered trees were selected among diameter classes 20 and 25 (DBH, in cm), and were chosen in an attempt to achieve homogeneous spatial distribution in the whole plot. Thus removed trees were mainly suppressed individuals, but some were also dominant. Table 2 summarises the dendrometric parameters that resulted from the shelterwood cuttings.

2.2. Microclimate

Soil temperature (5 cm depth) was measured in all the plots with soil temperature probes (RT-1, Decagon Devices), except the T75 plots of blocks II and III. Understory air temperature (1.5 m height) was also measured in the T0, T60 and T100 plots of block I with temperature probes

(ECT-S, Decagon Devices). Rainfall was measured in the T100 plot of block II with a rainfall recorder (ECH2O rain, Decagon Devices). All the probes were attached to dataloggers (EM50, Decagon Devices), which recorded data at hourly intervals. The monthly temperature average and accumulated monthly precipitation values were obtained. The microclimatic variables were measured during the period covering October 2009-October 2011.

2.3. Litter production

The litterfall traps used in this study were constructed with plastic boxes with an opening of 60 x 40 cm^2 which were 30 cm high, and with a plastic mesh (1.2 mm mesh size) attached to the inside. These shallow boxes, which were deployed directly on the soil surface, were used to ensure also collecting the understory litterfall. Twelve traps were distributed randomly in each plot. Litterfall was collected monthly for 2 years, from November 2009 to October 2011. The material from each litter trap was sorted into six fractions: *needle*, *branch*, *bark*, *cone*, *other organs* and *miscellaneous* (other species than *P halepensis*). Samples were dried in the laboratory at 65ºC for 72 h and weighed.

2.4. Litter decomposition

Litterbags (15 x 20 cm^2) were constructed with fibre glass mesh (1.5 mm mesh) and sewn with nylon. The filling material, freshly fallen intact needles, was collected from the top of the OL layer in each block in July 2009, and was left to air dry in the laboratory. Next 180 litterbags were filled with 10 g of this material per block. In each plot, 45 bags were attached to the surface with metal pins at the beginning of October 2009, and three bags per plot were retrieved at 1, 2, 3, 4, 5, 6, 8, 10, 12, 14, 16, 18, 20, 22 and 24 months after being installed. On each sampling date, the litterbags were transported to the laboratory in sealed plastic bags. Bag content was cleaned of foreign material with a brush and weighed. Then samples were dried at 65ºC for 72 h and weighed again.

2.5. Nutrient content analyses

The monthly dynamics of the litterfall nutrient concentration was obtained for the year 2010. A composite sample was prepared for each month and block for both the *needles* and *miscellaneous* fractions. Another sample was also prepared for each block and season for the other fractions. Additionally, the effect of silvicultural treatments on the litterfall nutrient concentration was evaluated for the *needle* and *miscellaneous* fractions in the summer peaks of litterfall production. Nutrients were analysed for each plot on both the summer peak sampling dates, which corresponded to August 2010 and July 2011. The nutrient concentration was also analysed for the decomposing needles in each plot when litterbags remained in the field for 6, 12, 18 and 24 months. The nutrient content of the initial material (0 months) was also obtained.

The litterfall and litterbag samples were milled and sieved to 500 µm. Total C and total N were determined by a total analyzer (FLASH EA 1112 SERIES-LECO TRUSPEC). The P, K, Ca and Mg contents were determined by inductively coupled plasma optical emission spectroscopy (ICP-OES; ICAP 6500 DUO/IRIS INTREPID II XDL), after acid digestion (HNO_3-H_2O_2 4:1) in a microwave.

2.6. Data analyses

The returns of nutrients to soil through litterfall for 2010 were obtained by multiplying the corresponding mass production (kg ha^{-1}) by the nutrient concentration (kg kg^{-1}), and by adding up all months and fractions.

In relation to needle decomposition, Olson’s (1963) decay rate coefficients (k) were obtained as:

$$W_t=W_0\, e^{-kt}$$

where t is time (year), W_t is dry weight at time t (g), W_0 is the initial dry weight (g), and k the annual decay constant (year^{-1}).

The nutrients release from decomposing needles was also obtained as (Entry et al., 1991):

$N_t = C_0 - [(1- W)\ C_t]$

where N_t is the amount of nutrient released or absorbed at time t (mg g^{-1}), C_0 is the initial nutrient litter concentration (mg g^{-1}), W is weight loss at time t (%) and C_t is the nutrient litter concentration at time t (mg g^{-1}).

The effects of block and silvicultural treatment on litterfall production, nutrient return via litterfall, needle-litter mass loss, decomposing needles moisture, the nutrient concentration of decomposing needles and nutrient release from decomposed needles were tested with repeated measures ANOVAs, where time was the within-subject factor. In the litter decomposition variables, these differences were also tested for each date separately by two-way ANOVAs, where block and silvicultural treatment were the factors. Differences in the *needle* and *miscellaneous* litterfall nutrient concentrations on the summer production peak dates were analysed with three-way ANOVAs, with silvicultural treatment, block and year used as the factors. Differences in Olson's *k* values were analysed with a two-way ANOVA, where block and silvicultural treatment were the factors. In some cases, ln(x+1) transformation was used to achieve homoscedasticity (Levene's test) and approximate normality. When the ANOVAs indicated significant differences between silvicultural treatments, the Tukey's HSD *post hoc* test was used. If Levene's test indicated unequal variances of transformed data, then Tamhane's T2 *post hoc* test was used. All the statistical analyses were performed with SPSS v. 16.

3. Results and discussion

3.1. Microclimate

The precipitation observed during the observations period was 804 mm and 545 mm for year 1 and year 2, respectively (Fig. 1a). The mean annual soil temperature at the 5 cm depth was clearly higher in clearfelling (15.6 °C, Fig. 1b) compared to the other treatments (10.4; 11.3 and

12.0°C in T75, T60 and T0, respectively). These observations contrast with the understory air temperature data, which obtained similar monthly values in the three plots where data were available (Fig. 1c).

3.2. Litter production

Twelve years after the interventions, all the litterfall fractions considered in this study were significantly affected by treatment, whereas block was not a significant factor (Table 3). The *P. halepensis* litterfall production (i.e. total litterfall excluding the *miscellaneous* fraction) decreased compared to the untreated forest by 33.5% for T60, 59.8% for T75 and 95.8% for T100. The reduction effect was observed for all the fractions, except *miscellaneous*. This fraction increased quantitatively with treatment intensity. For total litterfall, we found significant differences among all the silvicultural treatments, but not between the two shelterwood treatments in year 1 (Table 3). Similarly, Navarro et al. (2013) reported a significant drop of *P. halepensis* litterfall production in an intense thinning treatment compared to the control, but no differences among the intermediate thinning intensities tested in their experiment (75%, 60% and 48% of basal area removed) were found. The authors attributed such lack of differences to the broad variability between trees and plots, but only 1 year of litterfall data was analysed (Navarro et al., 2013). In our case, no significant differences were observed between shelterwood intensities, but this was true only for year 1 (Table 3). The different behaviour noted between years can be explained by environmental factors, such as wind or snow, which can modify the year-to-year relationship between stand density and litterfall (Inagaki et al., 2008; Klemmedson et al., 1990). Nevertheless, the analysis of the relationship between basal area removed and the litterfall amount depicted in Fig. 2a proved to be a more appropriate approach to assess this question (Binkley, 2008). Thus the similar slope that we found for both years suggests no appreciable differences between years in the litterfall response to cutting intensity.

The litterfall dynamics throughout the year showed a high peak of total litter production in summer (Fig. 2b), which is the typical pattern of this species (García-Plé et al., 1995; Navarro et al., 2013). In the clearfelling plots, however, a dramatic change in the distribution of fractions occurred, which smoothed the monthly dynamic pattern (Fig. 2b). The importance of the needle fraction in our T100 plots (23% of total weight) was not as strong as the 54% reported by Klemmedson et al. (1990) in clearcuts of Ponderosa pine, probably because of the perimeter trees in our 45x45 m^2 squares (including the buffering zone) having less influence versus their 18-metre wide strips. Interestingly, the modification of the litterfall composition and its monthly pattern attributable to clearfelling was not reflected in deviations in the regression analysis (Fig. 2a). One question that remains unclear is how long this relationship would remain proportional. In clearfelling, we observed the incipient recovering of *P. halepensis*, with some individuals >2 m height, which anticipates major changes in the amount, composition and dynamics of litterfall in the short term.

3.3. Litterfall nutrient content and nutrient return to soil

The nutrient concentrations of senescent *P. halepensis* needles in summer production peaks were more affected by the block factor (i.e., soil type) than by silvicultural treatments (Table 4), and this result coincides with the findings of other authors (Blanco et al., 2008; Inagaki et al., 2008). For N, P and K, lack of differences due to management practices can be explained by the buffering effect of retranslocation from needles to other plant organs before abscission. Calcium was abundant in our study soils, which developed on calcareous bedrocks (Table 1) and was expected, therefore, to be non-limiting. Mg was the only macronutrient to be significantly affected by the treatment factor. The Mg concentration in the T0 plots (1.03 mg g^{-1}; Table 4) was significantly higher than the concentration found in the needles of the treated plots (0.83 mg g^{-1} on average). One possible explanation for this would be an increase in tree nutrient availability as a result of cuttings. For example, magnessium uptake could lower by increased ammonium availability because both cations compete in root uptake (Slovik, 1997). Along these lines, Sardans et al., (2005) reported that N and P fertilisation lowered the Mg concentration of litterfall in *P. halepensis* trees. In light of our Mg results, it is possible that the trees that remained after the shelterwood cuttings, as well as the perimeter trees of the clearfelling plots, were still exposed to fewer nutrient restrictions (lower intraspecific competition) 12 years after implementing the treatments.

Treatments apparently affected the nutrient returns of the year 2010 (shown in Table 5) by controlling litter mass production rather than its nutrient concentration, which coincides with other reports in the bibliography (Blanco et al., 2008; Kim et al., 1996b, Klemmedson et al., 1990). Concomitantly with litter production, no differences between the T60 and the T75 treatments were found in the return of any nutrient for the year 2010 (Table 5). Reductions in nutrient return were also linearly related to treatment intensity (Table 5), which reinforces the first hypothesis of our work. The response to cutting intensity was similar for all the nutrients, and only K showed a remarkably lower sensitivity to harvest (r^2=0.17; Table 5). The effect of canopy removal on K supply was buffered by understory contributions; e.g., in treatment T75, the portion of the yearly K return owing to the needle fraction was 51%, but the portion due to the miscellaneous fraction was as high as 39% (data not shown). In any case, any conclusions that can be drawn from our nutrient return data should be interpreted with caution as we studied it for a year that was particularly wet. Under Mediterranean conditions, Roig et al. (2005) observed that a longer summer drought was associated with a prolonged duration of the litterfall production peak in *P. pinaster* stands. It is possible that the differences between treatments could be intensified in our plots in dry years, but this remains to be confirmed.

3.4. Litter decay rates

In our 2-year study, the decay rate coefficients *k* analyses (Fig. 3a) indicated only lower decomposition in clearfellings in comparison to the untreated plots, but this difference was barely significant (*p*= 0.049). On the contrary, the repeated measures ANOVA of litter mass loss indicated no significant effect of silvicultural treatment, although it was on the limit of significance (*p*=0.050). No differences in mass loss or *k* were attributable to the block. The field litter water content at the time of collection was similar on the majority of the sampling dates for all the silvicultural treatments (Fig. 3b). The main differences were found when litter was obtained at low moisture values, where the highest water contents were encountered in the control plots, and the driest in clearfellings.

The mass loss data of our experiment suggested that clearfelling slowed down the needle decomposition process in comparison to the untreated forest (Fig. 3a), and that litter water content during dry periods was significantly lower in T100 (Fig. 3b). In principle, these results partially support our hypothesis which stated that tree canopy removal would hamper the decomposition process as there would be less moisture on the surface, at least as regards to the T100 treatments. Moreover, the increase in the extremely high soil summer temperatures that we observed (Fig. 1b) has also been suggested as a possible explanation for lower decomposition rates in clearcuts (Whitford et al., 1981). However, changes in microclimate are not the only explanation for our results, as we discuss later.

3.5. Nutrient release through litter decomposition

The shelterwood cuttings did not modify the nutrient concentration dynamics of decomposing needles, although the effect of clearfelling was clearly visible at the end of the study period (Fig. 4). In particular, the needles that decomposed in clearfellings presented a significantly lower C concentration, and also considerably higher K and Ca contents. These differences in concentration were expressed as differences in the nutrient release for K and Ca, but not for C (Fig. 5). As a possible explanation, we hypothesise a massive mineral particle input into the litterbags of clearfellings, which led to a significant portion of these particles to resist our mechanical brush cleaning. In our T100 plots, a naked-eye examination showed that organic horizon was badly lacking. Litterbags were attached directly to the mineral soil surface in most cases, whereas they were fixed on the O horizon in T0, T60 and T75. Therefore, we expected a higher mineral particle input into T100 due to the wind, splash by raindrops or runoff caused by microtopography. This hypothesis is supported strongly by the higher aluminium concentration of decomposed needles in clearfellings (available online as Supplementary Data Fig. 1a). Al content, considered here as an indicator of the proportion of mineral soil in the sample, explains the lower C concentration, Ca absorption and the poorer K release in the litterbags of the clearfelling plots (Supplementary Data Fig. 1b, 1c and 1d).

The key question that arises here is if the slightly lower decomposition rates measured in clearfellings are attributable to differences in microclimate (low water availability) or to mineral soil contamination. The possibility of mineral particles masking an effect prevents us from drawing definitive conclusions about the effects of clearfelling on decomposition mass loss. In fact a slight increase in decomposition is not unconceivable. Almagro and Martínez-Mena (2012) reported a higher decomposition rate of *P. halepensis* litter in an abandoned agricultural field compared with an open forest, with higher plant cover in the latter. They concluded that, due to the recalcitrant chemical composition of Aleppo pine needles, its decomposition was governed mainly by abiotic factors, which were enhanced in the agricultural field. In our study, the T100 treatment increased some abiotic processes associated with higher decomposition rates. We firstly observed a different colour of the needles decomposing in clearfellings (a phenomenon also reported by Kim et al., 1996a), which might be explained by direct exposure to sunlight. In arid and semiarid climates, the role of photodegradation in litter decomposition could be even more important than biological activity (Austin and Vivanco, 2006). Secondly, field observations have revealed that frosts were more common and severe in T100. Therefore, frozen litterbags were collected more frequently in these plots. This could also stimulate decomposition as freeze-thaw cycles may cause physical damage to litter (Taylor and

Parkinson, 1988). In any case, the dynamics of N, P and Mg was not significantly affected by either microclimate or mineral particle input, which suggests that the actual effect of clearfelling on needle decomposition was weak in our experiment.

In general, nutrient release through decomposition was not affected by the block factor except in K (*p*=0.008), and especially for N (*p*<0.001) (available online as Supplementary Data). These observations are probably related to differences in the chemical composition of the forest floor in the three blocks (Table 1). Nonetheless, the vast differences in N release found herein, associated with the block factor, were not accompanied by a significant block x treatment interaction (*p*=0.171). So it can be argued that soil characteristics seem to have very little influence on litter decomposition sensitivity to cuttings. It should be noted that our experimental design allowed us to evaluate the influence of management on microclimate, but not on litter quality. However, this issue was not apparently important for our study, at least in terms of *P. halepensis* needle nutrient composition as we only found an effect of treatments on its Mg concentration in litterfall (Table 4).

3.6. Conclusions

Twelve years after cuttings, the nutrient cycling was modified through reduced nutrient return via litterfall, but the nutrient release through decomposition seems poorly sensitive to management practices. Our results also demonstrate the need to include the shrub layer to obtain an accurate overview of the effects of silvicultural interventions on ecosystem nutrient balances in the long term. In order to optimise nutrient budget management, these observations must be taken into account when making future efforts to analyse and model impacts of harvesting treatments on nutrient cycling in Mediterranean forests.

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Figure captions

Fig 1 Monthly precipitation (a), monthly average soil temperature at the 5 cm depth (b), and monthly average understory air temperature at the 1.5 m height (c). Precipitation was measured in the T100 plot of block II. Soil temperature was measured in all the plots, except the T75 plots of blocks II and III. Understory air temperature (1.5 m high) was measured in the T0, T60 and T100 plots of block I

Fig. 2 Relationship between basal area removed and total litterfall (a) and the monthly dynamics of total litterfall in each silvicultural treatment (b). Black circles represent year 1 and white circles represent year 2 in (a)

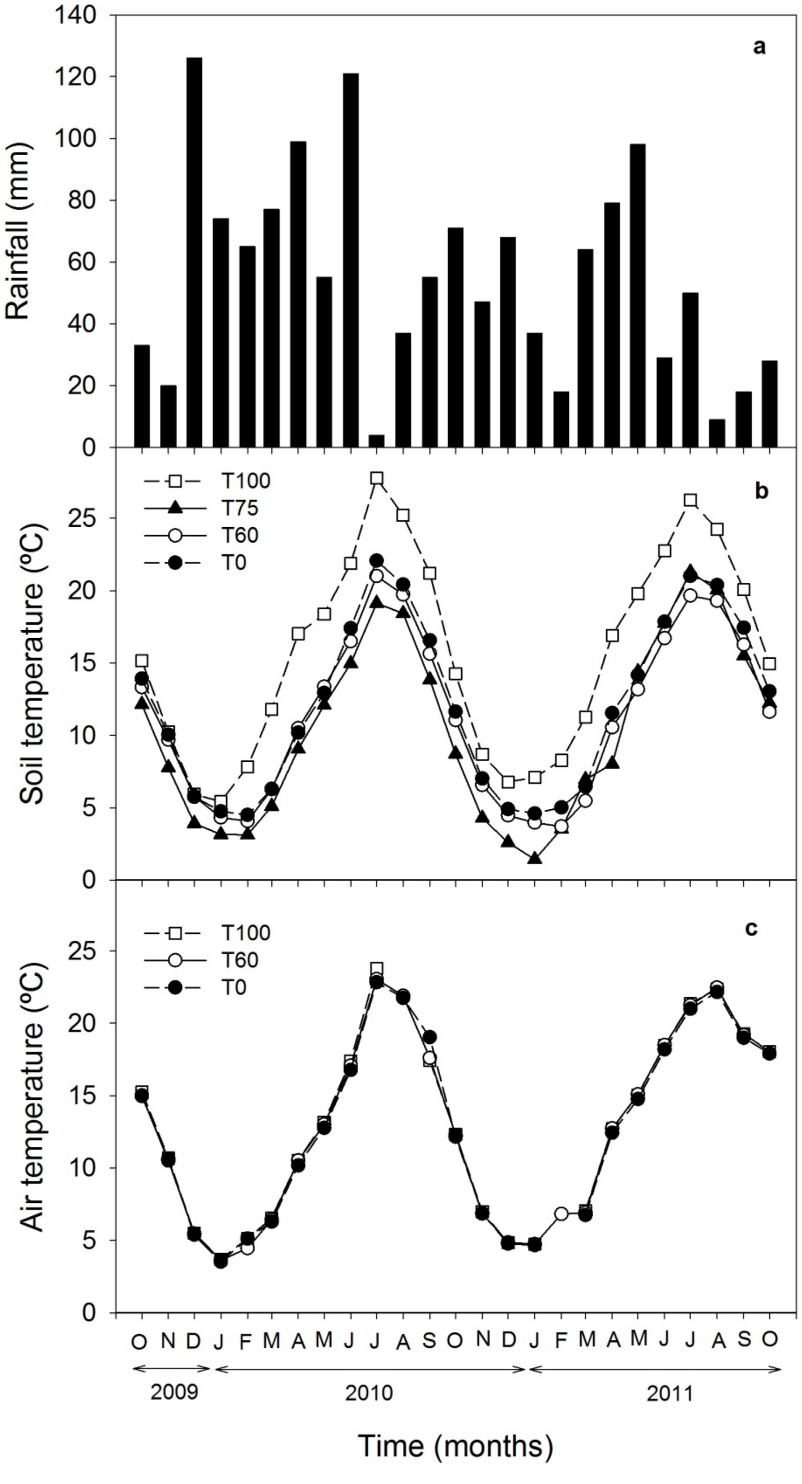
Fig 3 Percent of the leaf mass remaining in the litterbags (a) and field litter moisture on the sampling dates (b) throughout 2 years for each silvicultural treatment. Asterisks indicate significant differences between clearfelling (T100) and the other treatments. Arrows indicate significant differences between untreated (T0) and clearfelling (T100). The mean decay constant (*k*, in year^{-1}) is shown, and different lower case letters indicate significant differences (P=0.049)

Fig 4 Nutrient content dynamics in the decomposed litter for each silvicultural treatment. Asterisks indicate significant differences (P<0.05) between clearfelling (T100) and the other treatments. Error bars represent SD

Fig 5 Nutrients in the decomposing needles released (positive values) or absorbed (negative values) for each silvicultural treatment. Obtained as (Entry et al., 1991): $N_t=C_0 - [(1- W) C_t]$, where N_t is the amount of nutrient released or absorbed at time t (mg g^{-1}), C_0 is the initial nutrient litter concentration (mg g^{-1}), W is weight loss at time t (%) and C_t is the nutrient litter concentration at time t (mg g^{-1}). Asterisks indicate significant differences (P<0.05) between clearfelling (T100) and the other treatments. Error bars represent SD

Supplementary Data Fig 1 Aluminium content dynamics of the decomposed litter for each silvicultural treatment (a) and relationships between aluminium and C (b), K (c) and Ca (d) contents. Asterisks indicate significant differences ($P<0.05$) between clearfelling (T100) and the other treatments in (a). Error bars represent SD

Supplementary Data Fig 2 Nutrients in the decomposing needles released (positive values) or absorbed (negative values) where Block had a significant effect. Obtained as (Entry et al., 1991): $N_t=C_0 - [(1- W) C_t]$, where N_t is the amount of nutrient released or absorbed at time t (mg g^{-1}), C_0 is the initial nutrient litter concentration (mg g^{-1}), W is weight loss at time t (%) and C_t is the nutrient concentration litter at time t (mg g^{-1}). Lower case letters indicate significant differences ($P<0.05$).



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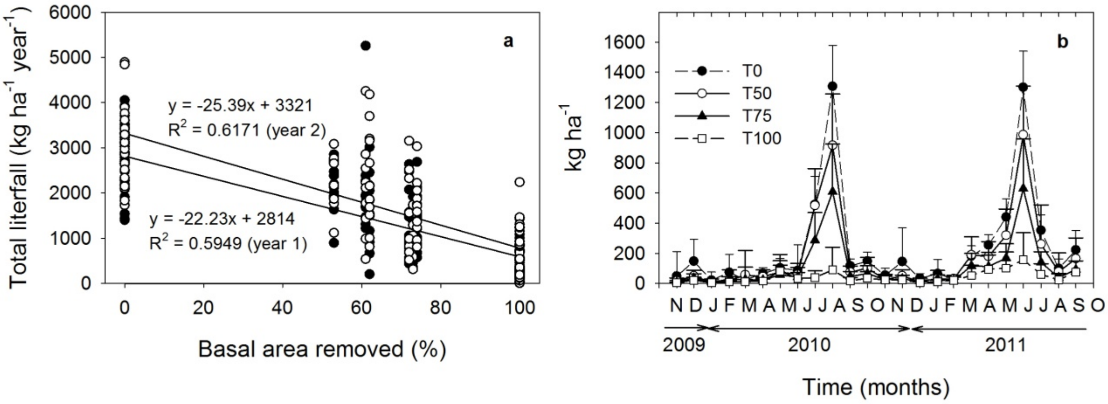

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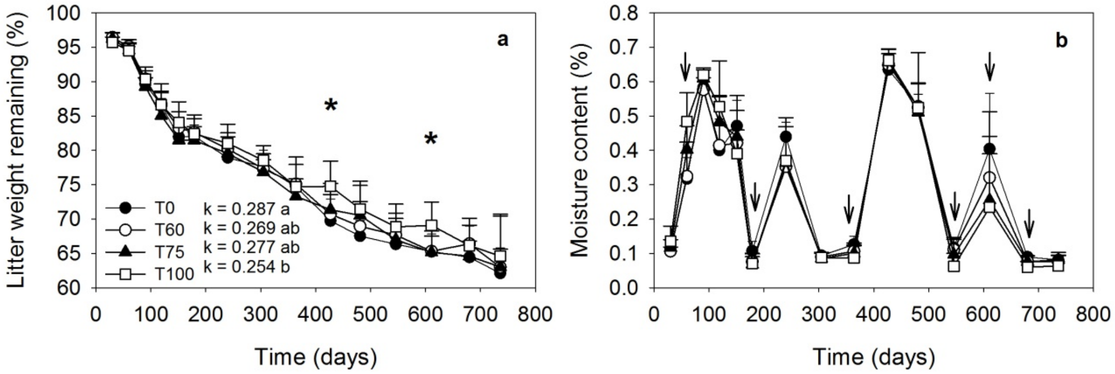

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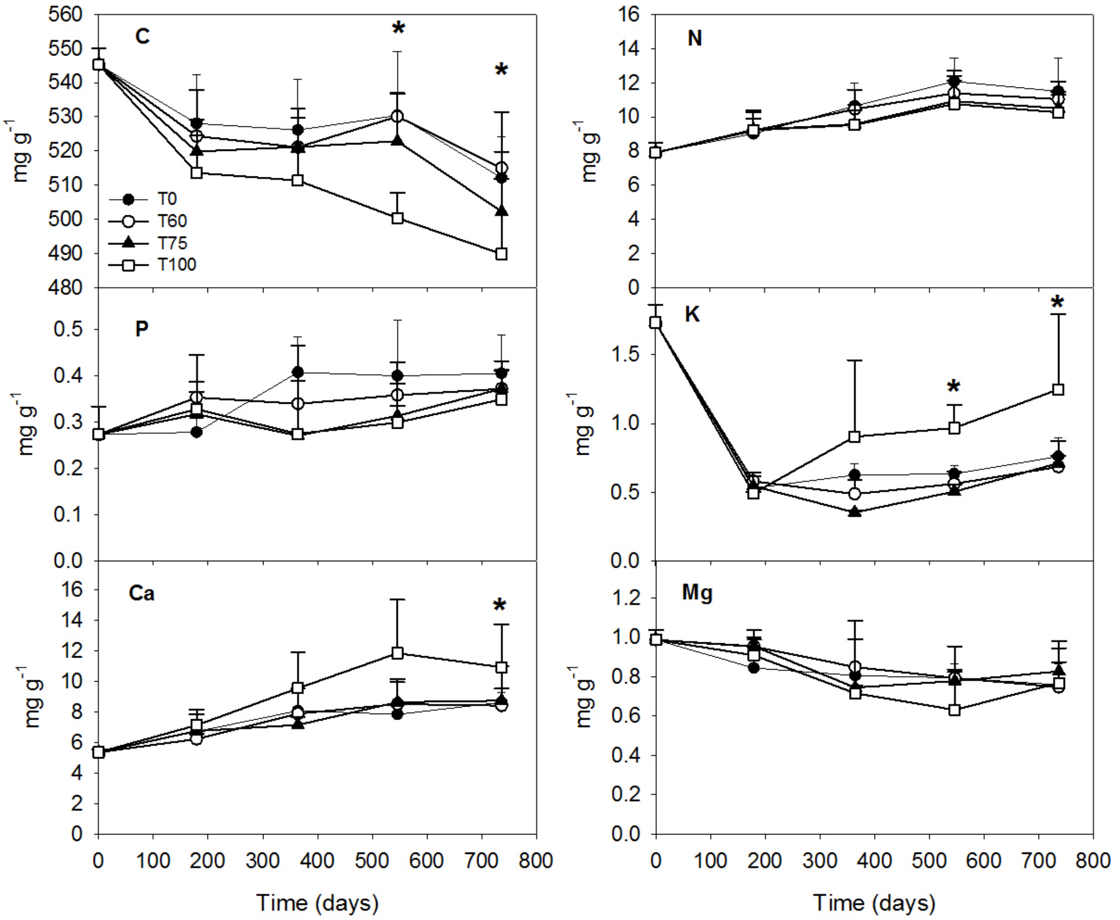

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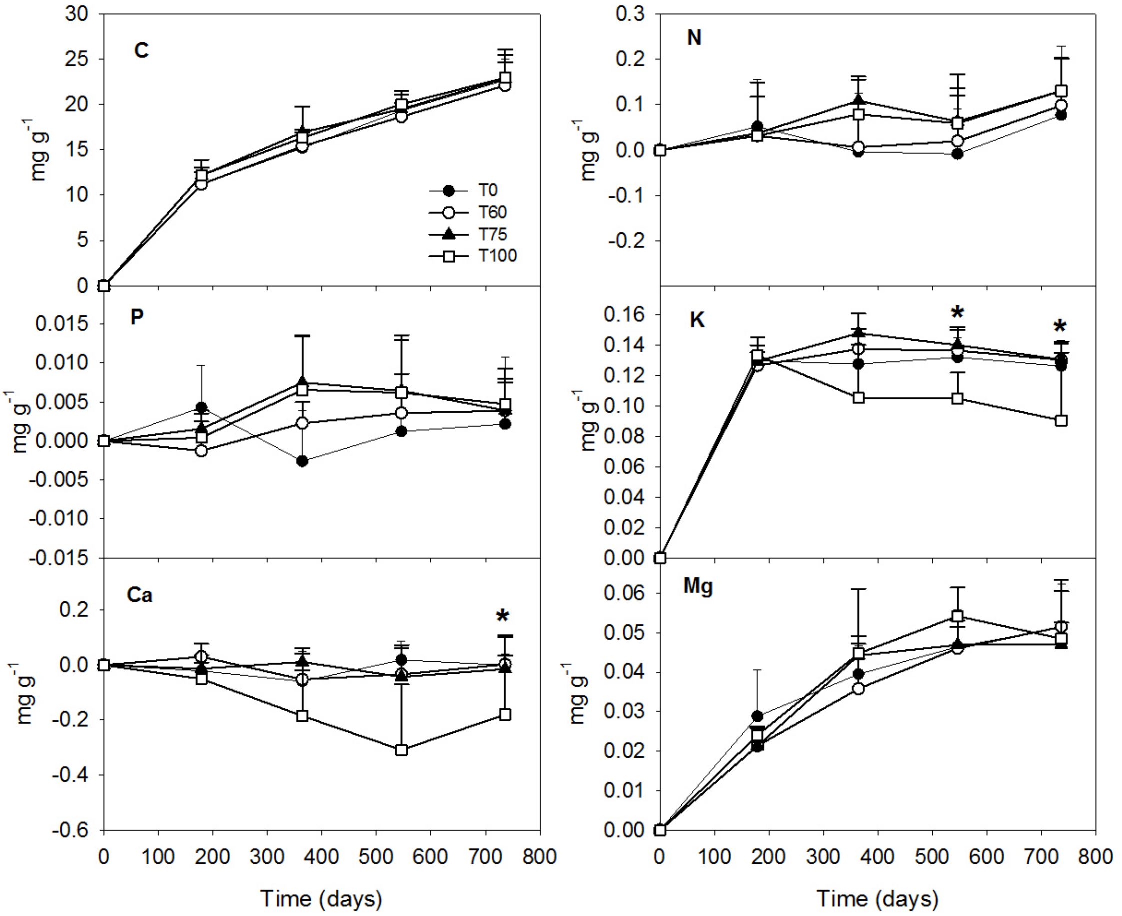

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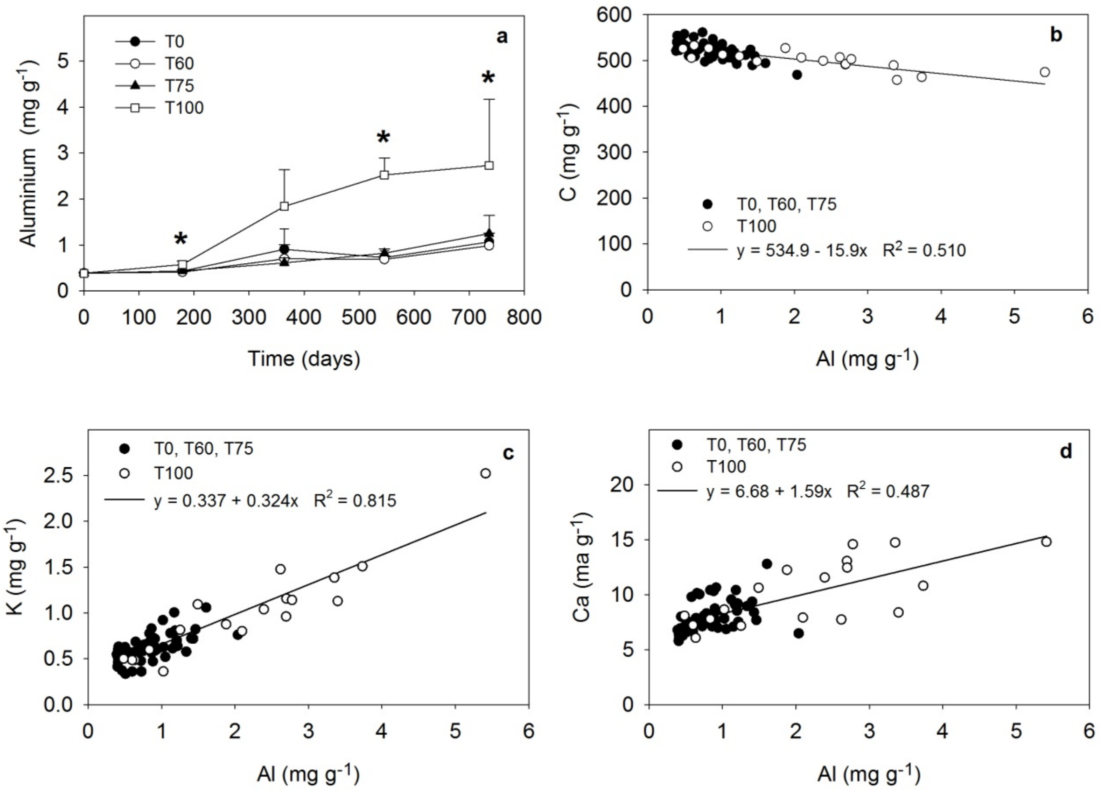

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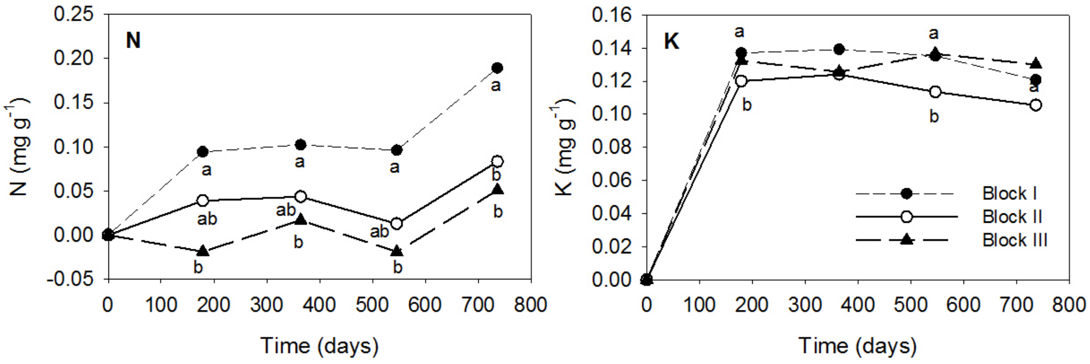

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Table 1. Soil properties in the three study blocks

Block	Location	Depth (cm)[a]	Clay (%)	Silt (%)	Sand (%)	pH	Corg[b] (mg g^{-1})	C[c] (mg g^{-1})	N[c] (mg g^{-1})	P[c] (mg g^{-1})	K[c] (mg g^{-1})	Ca[c] (mg g^{-1})	Mg[c] (mg g^{-1})	C:N
I	Tuéjar Left	0-2*	-	-	-	6.0	367	402.0	16.8	0.44	4.2	18.5	2.29	21.8
		2-6	36.0	39.0	25.0	8.2	60	75.6	3.4	0.22	18.3	36.1	6.01	17.6
		6-10	42.0	39.7	18.3	8.2	41	52.2	2.6	0.23	20.6	30.1	6.45	15.8
II	Tuéjar Right	0-5*	-	-	-	7.8	103	124.0	5.5	0.24	15.3	34.5	5.28	18.7
		5-18	36.0	43.7	20.2	8.3	36	63.1	2.4	0.15	16.0	56.5	5.51	15.0
		18-25	36.0	42.0	22.0	8.3	39	78.1	3.0	0.24	13.2	90.1	4.91	13.0
		25-52	34.0	39.5	26.5	8.4	21	81.0	1.9	0.21	10.5	147.2	4.36	11.0
		>52	28.0	37.7	34.2	8.5	12	94.5	0.9	0.12	6.4	169.5	3.26	13.3
III	Chelva	0-2*	-	-	-	6.4	144	144.0	6.8	0.25	3.6	8.6	1.70	21.2
		2-16	18.0	15.7	66.2	8.0	10	13.7	1.0	0.07	6.3	4.1	2.19	10.0
		16-35	30.0	24.5	45.5	8.5	14	65.9	1.8	0.21	9.3	127.4	3.18	7.7
		>35	18.0	27.2	54.7	8.4	11	111.0	1.2	0.17	2.0	184.6	1.30	9.1

[a] Asterisks indicate organic horizons

[b] Organic carbon

[c] Total content

Table 2. Characterisation of the Shelterwood treatments

Block	Plot	Basal area (m^2 ha^{-1})			Density (stems ha^{-1})		Forest cover (%)
		Pre-treatment	1999[a]	2004[b]	1999[a]	2004[b]	1999[a]
I	T0	27.7	27.3	30.4	1067	833	87.3
	T60	29.5	11.1	15.2	286	286	37.9
	T75	30.4	7.8	12.0	212	207	17.2
II	T0	36.2	37.9	39.4	1167	756	93.7
	T60	29.8	11.6	15.2	331	311	44.7
	T75	26.8	7.4	10.5	188	178	21.4
III	T0	28.9	29.1	32.7	1000	800	85.4
	T60	25.2	11.9	14.8	331	316	34.1
	T75	27.0	7.4	10.0	212	198	19.8

[a] from Galiana et al., (2001)

[b] from González Utrillas et al., (2005)

Table 3. Characterisation of litterfall production in the 2 study years.

		Fraction (kg ha^{-1} year $^{-1}$)						
		Needles	Branches	Bark	Cones	Other organs	Miscellaneous	Total
Year 1	T0	2080 ± 368a	146 ± 226a	151 ± 81a	122 ± 196a	71 ± 47a	84 ± 61a	2653 ± 612a
	T60	1503 ± 558b	30 ± 63b	89 ± 78b	68 ± 174b	42 ± 32b	141 ± 202a	1873 ± 846b
	T75	951 ± 498c	24 ± 73b	51 ± 71c	20 ± 73c	29 ± 22b	151 ± 200ab	1226 ± 666b
	T100	81 ± 206d	1 ± 2c	2 ± 4d	1 ± 2d	2 ± 2c	265 ± 267b	351 ± 332c
Year 2	T0	2218 ± 410a	177 ± 224a	278 ± 119a	75 ± 138a	323 ± 102a	99 ± 84a	3170 ± 687a
	T60	1399 ± 505b	113 ± 287b	188 ± 143b	48 ± 161b	270 ± 137b	222 ± 293ab	2241 ± 871b
	T75	879 ± 454c	15 ± 29b	96 ± 89c	28 ± 64b	170 ± 116c	227 ± 189bc	1416 ± 680c
	T100	140 ± 298d	1 ± 3c	4 ± 7d	0 ± 0c	7 ± 15d	425 ± 393c	576 ± 515d

Mean values ± standard deviation. Lower case letters denote *post hoc* significant differences (p<0.05) for the factor silvicultural treatment. The block factor was not significant in any case.

Table 4. Results of the three-way ANOVA (no replication) with factors silvicultural treatment, block and year on the nutrient concentration of the *needle* and *miscellaneous* litterfall fractions in the summer peaks of production

Factors		Concentration (mg g^{-1})											
		Needle						Miscellaneous					
		C	N	P	K	Ca	Mg	C	N	P	K	Ca	Mg
Treatment	T0	536.6	5.19	0.16	0.95	7.54	**1.03a**	505.4	8.90	0.39	**1.59a**	13.10	**0.96a**
	T60	533.9	5.53	0.18	0.91	7.58	**0.85b**	520.4	7.12	0.27	**3.00ab**	13.77	**1.04ab**
	T75	540.3	5.84	0.18	0.96	6.37	**0.83b**	517.1	8.24	0.35	**2.89ab**	13.17	**0.97a**
	T100	533.8	5.85	0.18	0.99	7.00	**0.83b**	510.4	7.15	0.28	**3.39b**	13.72	**1.34b**
	p	N.S.	N.S.	N.S.	N.S.	N.S.	**0.002**	N.S.	N.S.	N.S.	**0.013**	N.S.	**0.011**
Block	I	535.3	**5.40a**	**0.19a**	**1.09a**	**7.93a**	**0.92ab**	**522.9a**	7.62	0.34	**3.56a**	14.46	1.20
	II	536.8	**5.39a**	**0.17ab**	**0.83b**	**7.15ab**	**0.93a**	**510.1ab**	7.34	0.29	**2.43b**	14.14	1.09
	III	536.5	**6.02b**	**0.16b**	**0.94ab**	**6.28b**	**0.81b**	**507.0b**	8.60	0.33	**2.17b**	11.71	0.94
	p	N.S.	**0.048**	**0.013**	**0.006**	**0.003**	**0.022**	**0.029**	N.S.	N.S.	**0.012**	N.S.	N.S.
Year	1	536.3	5.61	0.18	**0.87**	7.31	**0.93**	513.5	7.71	0.31	**2.32**	13.05	1.06
	2	536.1	5.59	0.16	**1.04**	6.93	**0.84**	513.1	7.99	0.33	**3.12**	13.82	1.09
	p	N.S.	N.S.	N.S.	**0.008**	N.S.	**0.014**	N.S.	N.S.	N.S.	**0.039**	N.S.	N.S.

$p<0.05$ are indicated in bold

Table 5. Total nutrient return via litterfall in the year 2010 for each silvicultural treatment and the associated regression parameters

		C	N	P	K	Ca	Mg
Return[a] (kg ha^{-1})	T0	1376.8 ± 293.3a	15.62 ± 3.54a	0.54 ± 0.14a	2.90 ± 0.72a	24.30 ± 6.25a	2.96 ± 0.64a
	T60	1001.7 ± 410.4b	11.72 ± 5.28b	0.42 ± 0.20ab	2.36 ± 1.50ab	17.93 ± 8.84b	1.96 ± 0.84b
	T75	648.3 ± 347.5b	7.92 ± 4.18b	0.28 ± 0.16b	1.80 ± 1.27bc	11.21 ± 7.20b	1.31 ± 0.73b
	T100	186.3 ± 178.9c	3.09 ± 2.95c	0.11 ± 0.10c	1.34 ± 1.22c	5.61 ± 4.91c	0.54 ± 0.48c
Regr. parameters[b]	a	-11.429	-0.1203	-0.004	-0.0151	-0.1838	-0.0236
	b	1464.5	16.55	0.57	2.98	25.39	3.06
	r^2	0.60	0.52	0.45	0.17	0.47	0.60
	p	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

[a] Mean values (standard deviation). Lower case letters denote *post hoc* significant differences ($p<0.05$) for the factor silvicultural treatment in each nutrient. The block factor was not significant in any case.

[b] The parameters estimated for regression $R=aBA+b$, where R is the total yearly nutrient return (kg ha^{-1}) and BA is the percentage of basal area removed by silvicultural treatments (%).