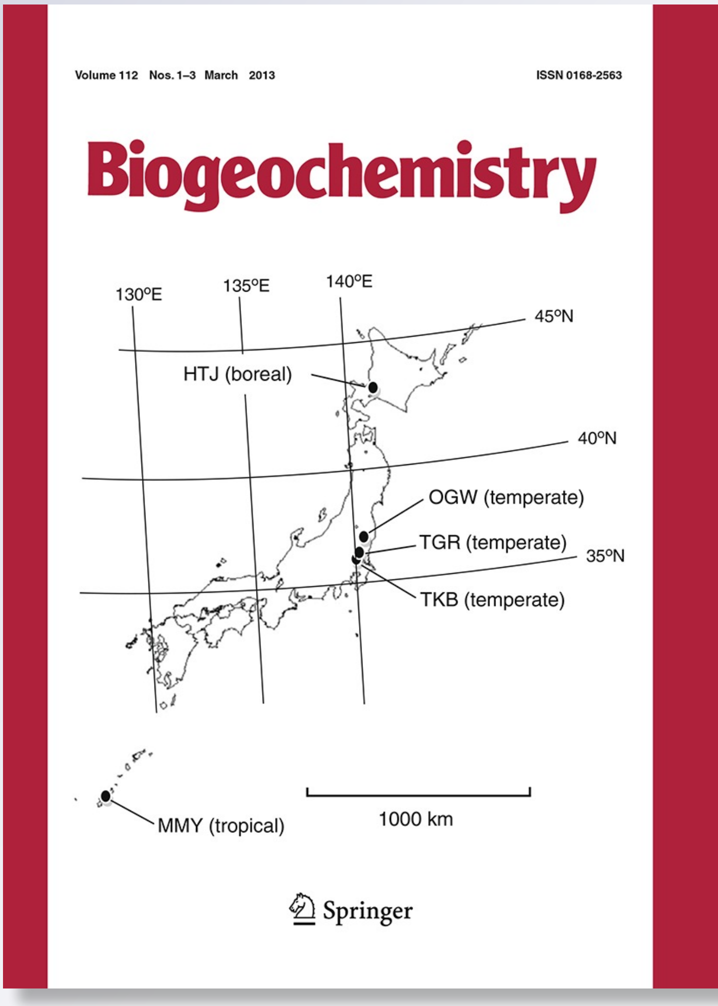
Effect of decomposing post-fire coarse woody debris on soil fertility and nutrient availability in a Mediterranean ecosystem

Sara Marañón-Jiménez & Jorge Castro

Biogeochemistry
An International Journal

ISSN 0168-2563
Volume 112
Combined 1-3

Biogeochemistry (2013) 112:519-535
DOI 10.1007/s10533-012-9744-x



Springer

Your article is protected by copyright and all rights are held exclusively by Springer Science+Business Media B.V.. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.

Author's personal copy

Biogeochemistry (2013) 112:519–535
DOI 10.1007/s10533-012-9744-x

Effect of decomposing post-fire coarse woody debris on soil fertility and nutrient availability in a Mediterranean ecosystem

Sara Marañón-Jiménez · Jorge Castro

Received: 21 July 2011 / Accepted: 15 May 2012 / Published online: 4 June 2012
© Springer Science+Business Media B.V. 2012

Abstract Post-fire coarse woody debris can represent a valuable nutrient reservoir for a regenerating ecosystem, helping to prevent soil fertility losses after a wildfire. However, there is scarce information on its effect on soil nutrient cycling and availability. We established three study sites along an altitudinal gradient in a burnt pine forest (SE Spain). At each site we determined: (1) decomposition rates and nutrient dynamics in charred logs left on the ground, 2 and 4 years after the fire, and (2) available nutrients in the soil and in the microbial fraction below charred logs and in bare soil areas. Despite the relatively slow decay rates in this Mediterranean climate (ca. 10 % of dry weight lost after 4 years), N and P were progressively released by logs, accounting for ca. 40 and 65 % of the initial content respectively after 4 years. This implies that the total aboveground biomass of the burnt forest released around 20 kg ha^{-1} of N and 2 kg ha^{-1} of P during this period. The presence of post fire coarse woody debris consistently increased soil organic matter by around 18 %, total C and N by 42 and 26 %, respectively, dissolved organic C and N by 47 %, available inorganic P by 68 %, and microbial biomass and nitrogen by some 36 and 48 %, respectively. By contrast, soil bulk density decreased by ca. 18 % under logs compared to bare areas. Thus, the fire-killed wood was useful in the recovery of soil fertility and nutrient availability. Leaving the post-fire woody debris on site can enhance the biogeochemical sustainability, microbiological processes and soil ecological functioning. The detrimental effect of post-fire salvage logging on soil fertility should be therefore considered when making management decisions.

Keywords Carbon sequestration · Salvage logging · Silvicultural treatments · Wildfire · Wood decay · Wood nutrient release

Electronic supplementary material The online version of this article (doi:10.1007/s10533-012-9744-x) contains supplementary material, which is available to authorized users.

S. Marañón-Jiménez (✉) · J. Castro
Grupo de Ecología Terrestre, Departamento de Ecología, Facultad de Ciencias, Universidad de Granada, 18071 Granada, Spain
e-mail: smaranon@ugr.es

S. Marañón-Jiménez · J. Castro
Centro Andaluz del Medio Ambiente (CEAMA), Av. del Mediterráneo s/n, 18006 Granada, Spain

Introduction

Wildfires constitute a radical perturbation for the nutrient cycle of an ecosystem, leading to an immediate nutrient mobilization from organic pools (Page-Dumroese and Jurgensen 2006; Trabaud 1994; Whelan 1995). Vegetation, litter, and the soil organic layer are consumed to greater or lesser degrees by fire, and their nutrients are either released to the atmosphere in smoke or deposited on the soil as ash (DeBano and

Author's personal copy

Conrad 1978; Iglesias et al. 1997; Johnson et al. 2005; Neary et al. 1999; Raison 1979; Yang et al. 2003). Consequently, increases in soil nutrients can appear over the short term (Gray and Dighton 2009; Johnson and Curtis 2001; Marcos et al. 2009). Nonetheless, nutrient enrichment is most often ephemeral, and does not usually persist more than several months after the fire (Certini 2005; Iglesias et al. 1997; Wan et al. 2001; Yang et al. 2003), as deposited nutrients can be lost by leaching and erosion (DeBano and Conrad 1978; Fernandez et al. 2007; Shakesby 2011; Thomas et al. 1999). In addition, the loss of soil organic matter and disruption of organic cements in severe wildfires contribute to nutrient impoverishment by minimizing soil exchangeable capacity and stability (Certini 2005; DeBano et al. 1998). Soil nutrient availability is, however, crucial for the recovery of vegetation after a wildfire. Furthermore, the existence of a nutrient reservoir in the ecosystem is key to ensure the sustainability of the plant community, especially during the first stages of succession (Augusto et al. 2000, 2008; Jurgensen et al. 1997; Merino et al. 2005, 2003).

Dead wood progressively releases nutrients through decomposition (Brown et al. 1996; Ganjegunte et al. 2004; Palviainen et al. 2010a, b; Wei et al. 1997) at rates that depend on climatic conditions, species, and substrate (Harmon et al. 1986; Zhou et al. 2007). The nutrients released could be retained by the soil, becoming available for microorganisms and developing vegetation (Brais et al. 2005; Grove 2003; Jurgensen et al. 1997). The effect of decomposing wood on soil would also vary according to soil properties and nutrient status (Klinka et al. 1995; Thiffault et al. 2006). In particular, nutrient storage and contributions of dead wood are especially important in Mediterranean pine forests, which are frequently located on poor soils and with great nutrient demands (Costa-Tenorio et al. 1998; Sardans et al. 2005). Coarse woody debris has also been considered an important structural and functional element for many forest ecosystems (Harmon et al. 1986; Lambert et al. 1980; Spies et al. 1988) and has been defined as a "hot spot" that increases spatial heterogeneity (Hafner et al. 2005; Hafner and Groffman 2005) and wildlife diversity (Castro et al. 2010a; Hutto 2006; Lindenmayer and Noss 2006). Woody material also has been reported to encourage microbial diversity and the abundance of ectomycorrhizal fungi, which are used as primary indicators of a healthy forest soil (Graham et al. 1994). Moreover, the organic substrates and nutrients contained in wood promote the activity of decomposer microorganisms (Marañón-Jiménez et al. 2011), with the consequent enhancement of the nutrient cycling. In addition, logs and other woody debris can mitigate erosion (Fox 2011; Kim et al. 2008; Shakesby et al. 1996; Thomas et al. 2000), which is the main cause of nutrient loss in rain events following intense wildfires (Fernandez et al. 2007; Thomas et al. 1999).

Since dead wood and coarse woody debris have been demonstrated to represent an important nutrient pool in living forests (e.g., Alriksson and Eriksson 1998; Clark et al. 2002; Ganjegunte et al. 2004; Idol et al. 2001; Merino et al. 2003), different degrees of forest management (e.g., clear cutting, logging, etc.) can strongly affect the ecosystem nutrient budget (Augusto et al. 2000, 2008; Johnson et al. 2005; Merino et al. 2005). Nutrient losses associated with wildfires depend mainly on the type of vegetation and fire intensity (Brais et al. 2000; Neary et al. 1999; Page-Dumroese and Jurgensen 2006). Wildfires usually remove the nutrient rich crown material and understory, as well as the organic layer from the forest floor, but most of the large woody material remains in the ecosystem (Johnson et al. 2005; Tinker and Knight 2000; Wei et al. 1997). Thus, a great amount of dead biomass can persist in the standing fire-killed trees even after an intense wildfire, and can represent a potential nutrient reservoir for the regeneration of the ecosystem (Harmon et al. 1986; Page-Dumroese and Jurgensen 2006; Zhou et al. 2007). In fact, charred logs after a forest fire may still have a high nutrient concentration (Wei et al. 1997), since charring is usually limited to the bark or the outer superficial wood layer (Stocks et al. 2004). Thus, the nutrient stock in partially charred logs might be comparable to that reported for unburnt dead wood. Despite the potential relevance of this nutrient source as fire-killed wood decay, information regarding the decomposition and nutrient dynamics of coarse woody debris in Mediterranean areas is completely lacking (Rock et al. 2008; but see Brown et al. 1996), and is also very limited in the case of post-fire woody debris (Grove et al. 2009; Shorohova et al. 2008; Wei et al. 1997). Moreover, the effect of partially charred wood on the soil nutrient availability after a wildfire has not been specifically studied.

Author's personal copy

In this study, we seek to analyse the role of post-fire coarse woody debris on the soil nutrient availability and stocks in a Mediterranean pine forest after a wildfire. We investigate nutrient release by wood during decomposition and its effect on soil fertility. This was done across an altitudinal gradient that varies in climatic conditions and pine species, with the potential to affect the decay rates and the nutrient dynamics between fire-killed wood and soil. We hypothesise that the presence of charred wood over the forest floor will increase soil nutrient availability as the wood decomposes. Similarly, we predict that the presence of microorganisms will be also higher in the presence of charred wood. As a result, the post-fire coarse woody debris would enhance soil fertility and nutrient mobilization in the ecosystem. Thus, the main objectives of this study are to: (1) estimate the rate of nutrient release by fire-killed pine wood during the first 4 years of decomposition in a Mediterranean mountain ecosystem across an altitudinal gradient; (2) assess the effect that post-fire coarse woody debris left over the ground exerts on the soil nutrient concentrations and stocks; and (3) determine their effect on the microbial biomass and nutrients, as well as on the distribution of nutrients among the soil and microbial pools. The final goal is to help clarify the potential effect of post-fire coarse woody debris on soil fertility and nutrient cycling.

Materials and methods

Study area and experimental design

The study site is located in the Sierra Nevada Natural and National Parks (SE Spain; UTM: 456070; 4089811), where in September 2005 the Lanjarón wildfire burned ca. 1,300 ha of reforested pine forest between 35 and 45 years old. It was a high-intensity crown fire that consumed all the leaves, twigs and litter and charred the bark of the trunks. No trees survived inside the study area. The climate is Mediterranean, with rainfall concentrated in spring and autumn, alternating with hot, dry summers. Mean annual precipitation is 470 ± 50 mm, with summer precipitation (June, July and August pooled) of 17 ± 4 mm (1988–2008; climatic data from a meteorological station at 1,465 m a.s.l.). Snow falls during winter, usually persisting from November to March above 2,000 m a.s.l. The mean annual temperature is 12.3 ± 0.4 °C at 1,652 m a.s.l. (State Meteorological Agency, period 1994–2008. Ministry of Environment) and 7.8 ± 0.7 °C at 2,300 m a.s.l. (data from meteorological station, period 2008–2010). Current vegetation is composed mainly of grass and forbs with a cover of approximately 70 % (Castro et al. 2010b).

The fire-killed pine stands occupy an altitudinal gradient from ca. 1,300 to 2,000 m a.s.l. Across this gradient, we established 3 study sites of ca. 3 ha each located at 1,477, 1,698, and 2,053 m a.s.l. (sites 1–3, respectively). The sites were homogeneous in terms of fire intensity (high), slope (25–35 %), situation (southwest exposure), bedrock (micaschists) and soil characteristics (Table 1). The dominant pine species at each site changed according to climatic conditions (Table 2). Tree density was determined by counting the number of individuals in 36 squares of 25 × 25 m randomly distributed in each site. Diameter at the breast height (d.b.h.) and the height of the trees were measured in 360 and 150 individuals, respectively, randomly chosen per site (Table 2).

Between January and March 2006 (4–6 months after the wildfire), the Forest Service felled the trees using manually operated chainsaws, the main branches were lopped off, and all wood was left in situ on the ground. Logs and branches diffusely covered approximately 45 % of the surface at ground level (Castro et al. 2011). Afterwards (March 2006), at each site, we randomly established 50 sampling points where we placed logs to monitor wood decomposition and nutrient dynamics. Each sampling point contained 5 logs, cut by a chainsaw to a standardized length of 75 cm and spread over an area ca. 1 × 1 m (thus 250 logs per site; "experimental logs", hereafter). Each experimental log at a sampling point came from a different tree and from a randomized location along the tree trunk. Thus, they constitute a representative sample of the log characteristics in the study sites in terms of diameter and sectional origin along the trunk.

Wood sampling

Initial wood nutrient concentration and stocks

During the tree felling by the Forest Service (March 2006), a disc of 6–8 cm thick was sawed (with a chainsaw) from 50 logs randomly chosen per site and taken to the laboratory. These discs ("initial discs",

Author's personal copy

Table 1 Main soil characteristics of the upper 10 cm soil layer in bare areas without fire-killed wood

Soil parameter	Site		
	1	2	3
Bulk density (g cm^{-3})	1.25 ± 0.06	1.34 ± 0.07	1.15 ± 0.06
Soil texture	Sandy loam	Sandy loam	Sandy loam
Sand (%)	59.4 ± 2.4	58.9 ± 3.2	69.0 ± 0.1
Coarse loam (%)	10.6 ± 0.8	11.9 ± 0.7	9.7 ± 0.4
Fine loam (%)	15.2 ± 0.7	16.7 ± 1.3	12.5 ± 0.4
Clay (%)	14.8 ± 0.9	12.5 ± 1.5	8.8 ± 0.3
CEC ($cmol^+$ kg^{-1} soil)	5.592 ± 0.256	5.313 ± 0.306	4.633 ± 0.313

The bulk density refers to the soil fraction <2 mm. The soil texture was determined by the standard pipette method after Robinson-Köhn or Andreasen (Pansu and Gautheyrou 2006). The cation exchange capacity (CEC) of the soil was determined by saturation with Na^+ cations and their displacement and by atomic absorption (Pansu and Gautheyrou 2006)

Table 2 Pre-fire forest characteristics at the experimental sites

Forest parameter	Site		
	1	2	3
Pre-fire dominant specie	*Pinus pinaster* Aiton	*Pinus nigra* Arnold	*Pinus sylvestris* Linneo
Tree density (ind. ha^{-1})	1,480 ± 50	1,060 ± 70	1,050 ± 40
Diameter at 1.30 m (cm)	13.3 ± 0.2	14.5 ± 0.2	10.8 ± 0.2
Tree height (m)	6.3 ± 0.1	6.6 ± 0.1	6.2 ± 0.1
Wood biomass (kg ha^{-1})	55,273	47,715	26,166

Wood biomass per hectare was estimated using the means of the tree dimensional variables (tree density, d.b.h and tree height) in each site and the species specific equations developed by Montero et al. (2006) and implemented by the INIA in the calculation tool cubiFOR (CeseFor, http://cubifor.cesefor.com/)

hereafter) are considered a representative sample of the initial characteristics of the fire-killed wood, since they were collected ca. 6 months (mostly winter) after the fire and showed no signs of decomposition. The remaining bark was removed and initial wood discs were oven dried at 70 °C to constant weight to determine the dry weight. Once they were dried, the disc dimensions were measured and the volume of each initial disc was calculated. The average disc diameter at each site ranged from 12.1 to 13.3 cm ("Appendix" section). A sample of sawdust (<1 mm) was extracted from each initial disc for chemical analysis. Sawdust samples were taken from the whole section of the disc to maintain proportions of hardwood and softwood in the log, the composition being considered representative of the whole. For this, we used an adapted mechanical saw with no lubricant to avoid contamination. All this allowed us to estimate the initial dry weight and nutrient content remaining of subsequent decayed wood discs by means of a regression equation established with the morphometric variables of the initial wood discs ("Appendix" section).

Initial nutrient stocks in wood were estimated from data of nutrient concentration and the aboveground dry biomass per area unit. Wood biomass was estimated using the means of the tree dimensional variables (tree density, d.b.h and tree height) in each site and the species specific equations developed by Montero et al. (2006) and implemented by the INIA in the calculation tool cubiFOR (CeseFor, url: http://cubifor.cesefor.com/). The fraction of needles and twigs <2 cm were not considered, since these fractions were consumed during the wildfire (Table 2; Castro et al. 2010b).

Decomposition and time courses of nutrients in wood

A random subsample of 20 of the initially tagged experimental logs was harvested from each site (one

Author's personal copy

per sampling point) after 2 years (June 2008) and 4 years (June 2010). At these decomposition stages, some charred wood pieces were colonized by different species of insects (mostly termites and Coleoptera; author's personal observation) and woody decay fungi (determined by their fruiting bodies as *Pholiota highlandensis* (Peck) Smith. or *Pholiota carbonaria*). Discs of 6–8 cm thick were taken from the longitudinal middle of each experimental log to standardize the possible effect of the distance to the log ends on decomposition and nutrient concentrations. Repeated sampling of discs from the same logs taken in 2006 was not possible, due to the need to standardize the possible effect of the distance to the log ends. Following the same procedure as with the initial discs in 2006, the remaining bark of the wood discs was removed and their dry weight and volume was determined. The diameter of the sampled discs in 2008 and 2010 fell within the range of initial discs ("Appendix" section). As before, a sample of sawdust (<1 mm) was also taken from each wood disc for chemical analysis.

Soil sampling

We sampled soils associated with the logs sampled in 2008 and 2010. Two soil samples were collected per sampling point: one from soil under the harvested log and another from a nearby area of bare soil (no woody debris) ($n = 20$ sampling points $\times$ 2 positions $\times$ 3 sites $\times$ 2 years = 240 soil samples in total). For each soil sample, 3–4 soil pits were extracted using a gouge auger (2.5 cm diameter) to 10 cm depth, and homogenised to compound a single soil sample. Samples were immediately sieved at 2 mm and stored to 4 °C. Within 24 h of soil sampling, three subsamples of 15, 15, and 7.5 g of soil were extracted for 1 h in agitation with 75 ml of 2 M KCl, 0.5 M K_2SO_4, and 0.5 M $NaHCO_3$, respectively, and filtered through a Whatman GF-D filter. A 30 g subsample was oven dried at 105 °C for 48 h for gravimetric determination of water content by the difference between fresh and dry weight, and stored for further analyses. Another subsample was fumigated with $CHCl_3$ for 24 h in vacuum to release the nutrients from the microbial biomass (fumigation-extraction method; Jenkinson and Powlson 1976), after which the soil was extracted with 0.5 M K_2SO_4 and 0.5 M $NaHCO_3$ and filtered as above. Fumigated and nonfumigated extracts were frozen at −20 °C until analysed (Schinner et al. 1995). In 2010, the bulk density of the upper 10 cm of the soil layer was calculated from the dry weight of the soil fraction <2 mm and the volume occupied by this fraction. For each soil pit, this volume was calculated as the difference between the volume of the gouge auger to a depth of 10 cm and the volume of the water displaced by the fraction >2 mm.

Chemical analyses

Carbon and nitrogen concentrations of the sawdust samples were determined using the combustion furnace technique at 850 °C (Leco TruSpec autoanalyzer, St. Joseph, MI, USA), and phosphorus was analysed using the molybdovanadate method (Association of Official Analytical Chemists (AOAC) 1975) with a Perkin Elmer 2400 spectrophotometer (Waltham, MA, USA). The sawdust was dried at 105 °C by a thermogravimetric analyser (Leco TGA 701), and nutrient concentrations referred to the corresponding dry weight.

From the dried subsample, soil organic matter (SOM) content was determined by incineration at 550 °C with a thermobalance (Leco TGA 701) to constant weight (Sparks 1996), whereas total C (C_{tot}) and N (N_{tot}) were determined by combustion at 850 °C (Leco TruSpec autoanalyzer). Total inorganic C (TIC) was measured by acidification with $HClO_4$ in a coulometer (UIC CM-5014, Joliet, IL, USA). The TIC showed mere trace concentrations for these acidic soils (0.0034 $\pm$ 0.0012 % at site 1 and non detectible at sites 2 and 3), so that C_{tot} can be considered as organic C. The soil pH was determined in 2008 samples by stirring and settling in distilled water with a pHmeter (Crison micropH-2001, Barcelona, Spain), according to the international standard ISO 10390 (1994) (Pansu and Gautheyrou 2006). Ammonium (NH_4^+) and nitrate (NO_3^-) were determined from KCl extracts by the Kjeldahl method (Bremner and Keeney 1965) with a Buchi distillation unit B-324 and a Metrohm SM Titrino 702 titrator. From K_2SO_4 extracts (fumigated and nonfumigated), we determined the dissolved organic C (DOC) and dissolved organic N (DON) with a Shimadzu TOC-V CSH analyser (Kyoto, Japan). Microbial C and N (C_{micro} and N_{micro}, respectively) were determined from the differences in DOC and DON between fumigated and nonfumigated subsamples. Available inorganic P

Author's personal copy

(P_{inorg}) was determined in nonfumigated $NaHCO_3$ extracts by the Olsen method (Watanabe and Olsen 1965). Microbial P (P_{micro}) was measured as the difference in P between the fumigated and nonfumigated extracts. Concentration values in the microbial fraction were corrected for extraction efficiency using K_{ec} values of 0.45, 0.40 and 0.40 for C_{micro}, N_{micro} and P_{micro}, respectively (Sparling and West 1988). For simplicity, we refer to the soil variables SOM, C_{tot}, N_{tot}, NH_4^+ and NO_3^-, P_{inorg}, DON and DOC as "soil fractions" and to the microbial variables C_{micro}, N_{micro} and P_{micro} as "microbial fractions", hereafter. All fractions were referred to the corresponding dry weight of the soil.

Data analysis

The percentage of the initial wood weight remaining in the field following the decay process was calculated using the weight of each wood disc in 2008 and 2010 and the estimation of the initial weight for each disc ("Appendix" section). No relationship was found between diameter and initial wood density. Thus, the initial dry weight of the discs depended only on their volume. Furthermore, the initial disc weight better fit the volume of the disc using a linear regression model with no intercept, so this model was used to estimate the initial dry weight of the wood discs collected in 2008 and 2010 ("Appendix" section). The fragmentation of logs has a delay time of at least 25 years (Harmon et al. 1986) so external changes in log volume (bark fragmentation was not considered in this study) was deemed negligible at these initial stages of decay. Thus, the volume of each disc (V_d) sampled after 2 (2008) and 4 years (2010) was used to estimate the initial dry weight from the regression equations.

Differences in wood weight between sites over time could not be analysed with a repeated measures ANOVA, since wood discs could not be sampled following a repeated sampling procedure for methodological reasons (see experimental design). Thus, the sampling year was considered as an independent factor in the statistical analyses. The diameter of the log (and hence size) may influence the decomposition both directly and indirectly (Grove et al. 2009; Mackensen and Bauhus 2003; Shorohova et al. 2008). In addition, due to the experimental design constraints related to the unfeasibility to get replicated altitudinal sites, differences among sites cannot be unambiguously ascribed to differences related to altitude. Thus, the effect of decomposition time on the percentage of initial wood weight remaining was analysed at each site using an ANCOVA, with year as the independent factor and the diameter of each wood disc as a covariate. The initial sampling year (2006) was not considered in the analyses of the percentage of weight loss, since it was considered to be initially zero. For each wood disc, the estimated proportion of the initial dry weight remaining and nutrient concentration over the study period were used to calculate the nutrient content per kg of the initial wood remaining over time. Similarly as before, changes in nutrient concentrations, C/N ratio and nutrient content over time were analysed for each site with ANCOVAs, with year as the independent factor and the diameter as a covariate. For C content, we used a generalized linear model with normal distribution and logarithmic link function.

The effect of year, site, and position (under logs or in bare areas) on soil nutrient and microbial fractions were analysed with factorial ANOVAs when the transformed data satisfied linearity assumptions. For variables that did not fulfil linearity assumptions, we used generalized linear models (GLMs) with a normal distribution and logarithmic link function (P_{micro}, NH_4^+, NO_3^-, C_{micro}, N_{micro}, C/N_{micro}). Stocks per square meter of soil under logs and in bare areas were calculated for the soil sampling of 2010 from the bulk density of each soil sample and its corresponding nutrient and microbial fractions. Then, the effect of site and position on the soil nutrient pool was similarly analysed with two ways factorial ANOVAs or GLMs.

Data were transformed when required to improve normality and homoscedasticity (Quinn and Keough 2009). Statistical analyses were made with JMP 7.0 software (SAS Institute). Throughout the paper, mean values are followed by ±1SE.

Results

Initial wood nutrients and stocks

Initial wood density varied significantly among sites, being 0.73 ± 0.27 g cm^{-3} at site 1, 0.70 ± 0.32 at site 2, and 0.68 ± 0.40 at site 3 ("Appendix" section). The initial N concentration in wood was also different among sites ($P = 0.0004$, one way ANOVA), being

Author's personal copy

lower at site 1 (0.163 ± 0.004 %) than at sites 2 and 3 (0.187 ± 0.005 and 0.189 ± 0.005 %, respectively). The mean initial P wood concentration was 99.66 ± 2.85 mg kg^{-1} (all sites pooled) and did not differ among sites ($P = 0.2011$, one way ANOVA).

Post-fire wood biomass at the study sites was estimated at 43,052 ± 8,720 kg ha^{-1} (three sites pooled, Table 2; Castro et al. 2010b), of which 66 % approx. was aboveground and 34 % approx. corresponded to belowground biomass. This implies an initial stock of 49.6 ± 7 kg ha^{-1} of N and 2.8 ± 0.5 kg $ha^{-1}$of P.

Decomposition and time courses of nutrients in wood

The estimated percentage of the initial wood weight decreased mostly during the first 2 years of decay (Fig. 1), but not from the second to fourth year of decay ($P > 0.05$ at all study sites, one way ANCOVAs; Fig. 1). The percentage of wood weight lost overall was 9 % after 2 years and 10 % after 4 years (cumulative values, Fig. 1). This pattern did not differ among sites (Fig. 1) and the diameter had a significant effect only on dry weight losses at site 2 ($F = 4.54$, $P = 0.0420$, one way ANCOVA; negative correlation).

The composition of partially charred wood varied over time at all study sites for all elements analysed

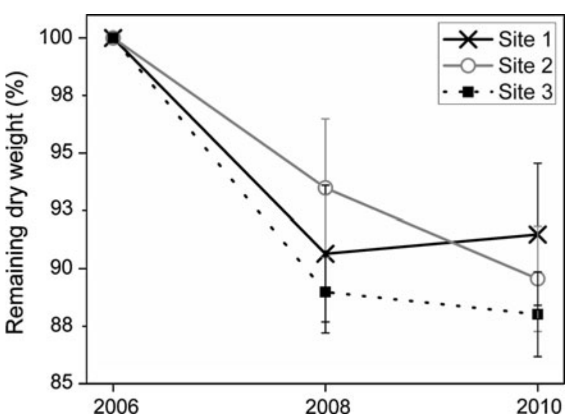


Fig. 1 Time course of the wood dry weight remaining after 4 years of decomposition under field conditions. Dry weight is expressed as a percentage of the initial dry weight of the wood discs. Initial dry weight was estimated with regression equations constructed with the volume and dry weight of initial discs collected in 2006

(Table 3). Overall, the wood N and P concentrations and content decreased as wood decayed (Fig. 2). In the case of N, concentrations changed slightly after the first 2 years of decay, but then sharply fell after 4 years (ca. 35 % of the initial concentration, Fig. 2a). Nonetheless, net N losses were detected even after the first 2 years of decay when expressed as N content per mass unit of the initial wood remaining, reaching ca. 10 and 40 % of the of the initial N content lost after 2 and 4 years, respectively (Fig. 2d). The decrease in the P concentration and content was evident from the beginning of decay, with losses of ca. 40 and 65 % of the initial content after 2 and 4 years, respectively (Fig. 2b, e). By contrast, the C concentration increased sharply after four years, despite an initial decrease during the first 2 years (Fig. 2c). The C content of the remaining wood, however, showed the same pattern as the estimated wood weight remaining, with significant C losses only during the first 2 years (Table 3; Fig. 2f). As a result, the wood C/N ratio increased very slightly or did not vary significantly in the first period but rose sharply afterwards (Table 3; Fig. 3). The diameter of the log also affected the wood N and C contents or concentrations, but had overall a weak effect compared to year (Table 3).

Effect of post-fire coarse woody debris on soil and microbial fractions

Overall, the presence of partially charred wood increased most of the soil and microbial fractions. Soil organic matter (SOM), total C and N (C_{tot} and N_{tot}), dissolved organic C and N (DOC and DON), available inorganic P (P_{inorg}), microbial biomass (C_{micro}), microbial nitrogen (N_{micro}) and the soil C/N ratio (C/N_{soil}) were higher in soil samples under logs than in bare areas (Table 4; Fig. 4). This happened at all sites and either after 2 and 4 years, with no interactions with these factors (Table 4). Exceptions to this were the interactions between position and year emerged in DON and P_{inorg}, although values remained higher under logs in both years (Table 4). The pH was also slightly more basic under logs, although in this case the pattern varied across sites (Table 4; Fig. 4). By contrast, bulk density was lower under logs (Table 4; Fig. 4). However, the presence of wood significantly affected neither the inorganic forms of N (NH_4^+ and NO_3^-), nor microbial P (P_{micro}) nor the C/N ratio in microorganisms (C/N_{micro}) (Table 4).

Author's personal copy

Table 3 Results of the ANCOVA and GLM tests on wood nutrient concentrations and contents

Source	Site	Nutrient concentration				Nutrient content			d.f.
		C	N	P	C/N	C	N	P	
Year	1	**56.28*****	**20.52*****	**22.72*****	**23.77*****	**24.68*****	**38.69*****	**32.05*****	2
	2	**30.30*****	**54.47*****	**41.06*****	**52.80*****	**25.58*****	**77.37*****	**52.07*****	
	3	**35.62*****	**53.46*****	**46.42*****	**51.60*****	**43.32*****	**59.69*****	**52.68*****	
Diameter	1	0.18	1.39	1.36	1.42	**18.43*****	0.96	0.29	1
	2	1.60	**11.43****	1.03	**10.71****	3.42	**4.89***	0.36	
	3	2.63	0.19	0.91	0.04	0.57	0.87	2.71	
Year*Diameter	1	0.68	**5.38****	0.16	**5.53****	**14.13*****	1.33	0.50	2
	2	1.56	1.31	2.61	1.39	5.92	1.49	2.09	
	3	1.18	**3.63***	0.6	**4.00***	1.52	**8.69****	1.33	

Values of the F statistic are presented. F values in bold indicate significant differences ($P \leq 0.05$)

d.f. degrees of freedom

* $0.01 < P \leq 0.05$; ** $0.001 < P \leq 0.01$; ***$P \leq 0.001$

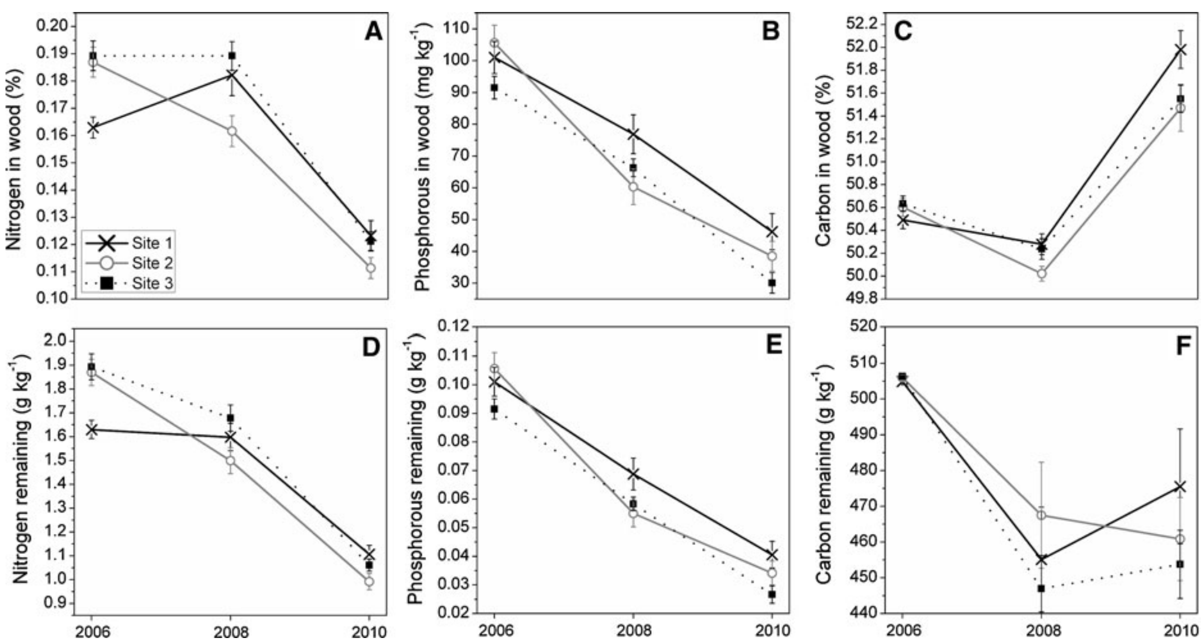


Fig. 2 Time courses of the nutrient and carbon concentrations and contents remaining in the fire-killed wood. **a–c** refer to the nutrient and carbon concentrations; and panels **d**–**f** refer to nutrient and carbon remaining per kg of the initial charred wood. Nutrient and carbon remaining were calculated for each wood disc with the proportion of the initial dry weight remaining and its nutrient concentrations

Nonetheless, when soil and microbial fractions were expressed as content per kg of soil, no significant differences were found between positions under logs and in bare areas for any of these variables ($P > 0.05$, two way ANOVAs or GLMs, Table 5) due to the lower bulk density under logs. Some soil fractions (SOM, C_{tot}, N_{tot}, NH_4^+, DOC and DON), N_{micro} and C/N_{micro} also differed over the years in which they were sampled (Table 4), all being higher in 2010 than in 2008 with the exception of N_{micro} (Fig. 5).

Author's personal copy

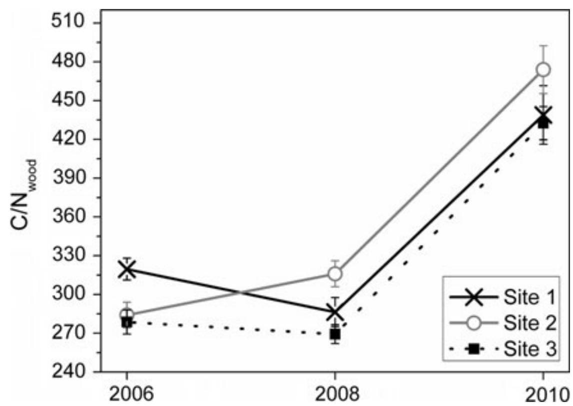


Fig. 3 Time courses of the C/N ratio of fire-killed wood after 4 years of decomposition under field conditions

Discussion

Despite the relatively slow decay rates of pine wood in a Mediterranean climate (ca. 10 % of the initial wood weight was lost after 4 years) nutrients were progressively released from wood over the first 4 years of decay. Most of the soil and microbial fractions were radically affected by the presence of post-fire coarse woody debris scattered over the ground, with consistent increases in areas under partially charred logs. Moreover, these effects became noticeable after 2 years of wood decomposition regardless the site and pine wood species. The presence of logs also altered C and N cycling by modifying the distribution of limiting nutrients between the soil and microorganisms. Altogether, these results constitute clear evidence of the critical biogeochemical role of post-fire coarse woody debris and support the contention that the remaining wood after a wildfire represents an important component of the ecosystem, as it enhances nutrient cycling and ecosystem functioning.

Decomposition and time courses of nutrients in wood

The results show that the partially charred wood still had a high concentration of N (ca. 0.18 %) and P (ca. 100 ppm), with similar or even higher values than the reported for unburnt wood (Alriksson and Eriksson 1998; Augusto et al. 2008; Merino et al. 2005; Palviainen et al. 2010a, b). Fire usually volatilizes nutrients contained in the bark and small fractions of the tree, whereas even in intense stand-replacing fires, the chemical composition of the large wood fractions

Table 4 Results of the ANOVA and GLM tests on soil and microbial fractions

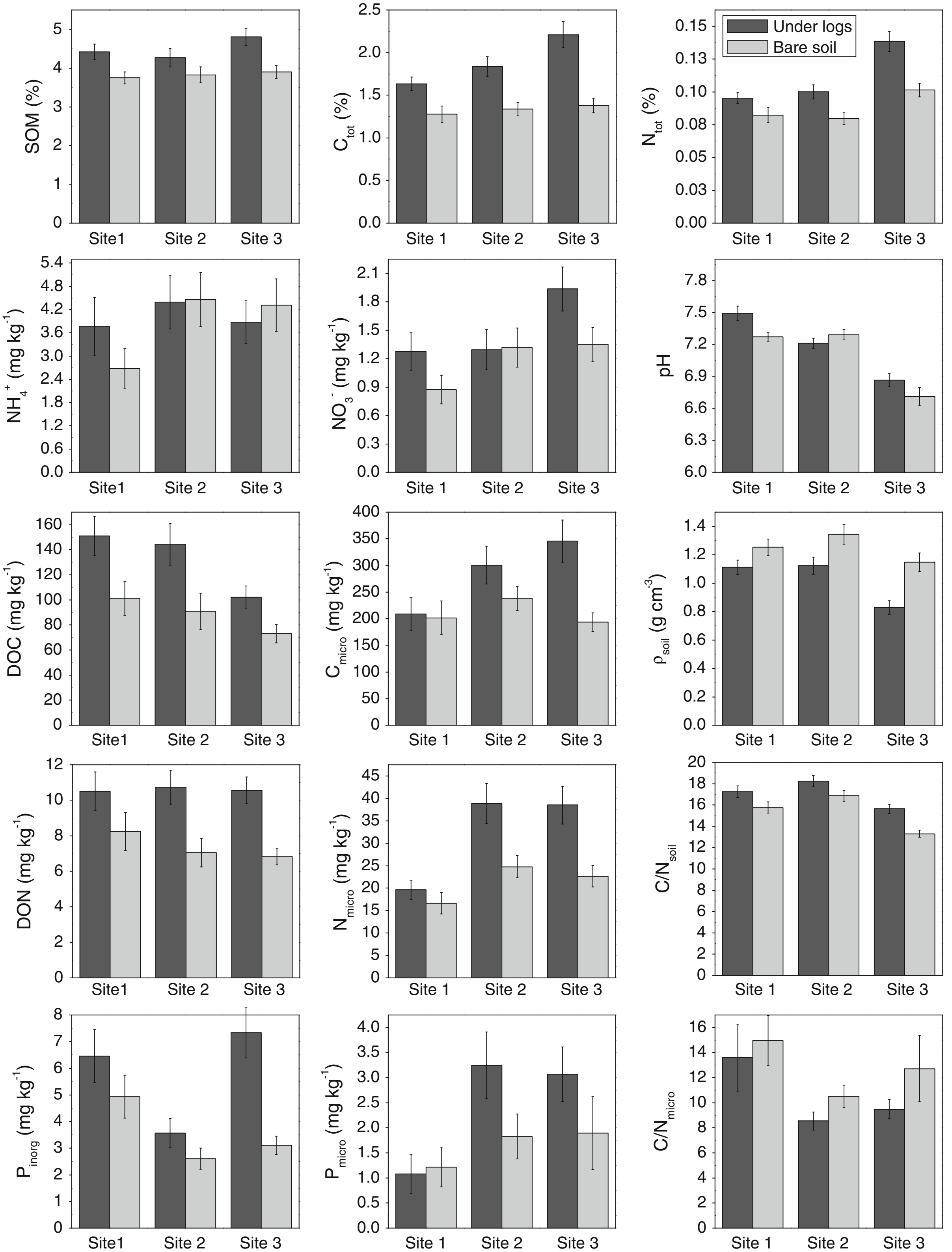
Factor	SOM	C_{tot}	N_{tot}	NH_4^+	NO_3^-	DOC	C_{micro}	DON	N_{micro}	P_{inorg}	P_{micro}	C/N_{soil}	C/N_{micro}	pH	ρ_{soil}	d.f.
Year	22.30***	18.62***	34.33***	5.39*	**0.84**	14.84***	**2.83**	30.94***	3.87*	**0.01**	**2.25**	**1.13**	13.90***			1
Site	**1.91**	3.83*	21.65***	**3.07**	7.29*	4.75**	**5.72**	**0.39**	19.48***	11.68***	6.13*	21.87***	**4.64**	54.09***	10.76***	2
Position	23.25***	50.03***	34.59***	**0.26**	**3.11**	28.99***	8.00**	32.16***	8.02**	24.06***	**0.38**	21.13***	**1.54**	4.06*	23.67***	1
Year*Site	**0.14**	**0.39**	**0.33**	**3.14**	**0.75**	**0.26**	**0.88**	**1.90**	**2.23**	**1.13**	**3.52**	**0.74**	**1.27**			2
Year*Position	**2.94**	**1.16**	**2.24**	**0.22**	**2.47**	**3.83**	**0.65**	3.93*	**0.48**	4.16*	**0.06**	**0.10**	**0.25**			1
Site*Position	**0.51**	**1.08**	**0.45**	**1.42**	**2.26**	**0.28**	**3.42**	**0.20**	**2.07**	**2.64**	**0.74**	**1.09**	**0.33**	3.48*	**1.57**	2
Year*Site*Position	**0.72**	3.49*	4.67*	**0.91**	**0.96**	**1.39**	**3.04**	**1.63**	**4.25**	**0.24**	**0.15**	**0.31**	**0.69**			2

Values of the *F* statistic are presented. The effects of sampling years ("year"), experimental sites ("site"), position in relation to the charred logs (under or in bare areas; "position") and their interactions are shown. *F* values in bold indicate significant differences (P ≤ 0.05). Soil organic matter (SOM), total carbon (C_{tot}), total nitrogen (N_{tot}), ammonium (NH_4^+), nitrate (NO_3^-), dissolved organic carbon (DOC), microbial carbon (C_{micro}), dissolved organic nitrogen (DON), microbial nitrogen (N_{micro}), available inorganic phosphorus (P_{inorg}), microbial phosphorus (P_{micro}), soil C/N ratio (C/N_{soil}), microbial C/N ratio (C/N_{micro}), soil pH (pH), bulk density (ρ_{soil})

d.f. degrees of freedom

* $0.01 < P \leq 0.05$; ** $0.001 < P \leq 0.01$; *** $P \leq 0.001$

Author's personal copy



Author's personal copy

◀ **Fig. 4** Effects of the presence of post-fire coarse woody debris on the soil and microbial fractions, soil pH and bulk density. Bars represent mean soil pH, bulk density, organic matter (SOM), soil fractions (C_{tot}, N_{tot}, C/N_{soil}, NH_4^+, NO_3^-, DOC, DON, and P_{inorg}) and microbial fractions (C_{micro}, N_{micro}, C/N_{micro} and P_{micro}) at the three experimental sites and the two positions: under logs (*black bars*) and bare soil (*grey bars*). Data of different years are pooled, except pH and bulk density, which are available only for 2008 and 2010, respectively. Concentration values in the microbial fractions were corrected for extraction efficiency

remains unaffected (Stocks et al. 2004; Wei et al. 1997). Moreover, there was a strong release of nutrients contained in the fire-killed wood during the first 4 years of decomposition. After this period, the release of N, and particularly of P, from wood was very high, accounting for ca. 40 and 65 % of the initial content, respectively. For P, the decrease was constant over the two sampled periods, whereas slight initial rises in the N concentration were registered at some sites after 2 years, followed by a strong decrease. These patterns were consistent at the three study sites despite certain differences among them. This may be related to an initial nutrient immobilization by micro-organisms colonization of the decomposing wood (Brown et al. 1996; Laiho and Prescott 2004; Ouro et al. 2001), and to the fact that these soils are particularly P limited (mean of 3.54 ± 0.33 mg kg^{-1}), which might explain the relative higher mobilization of this element from wood (Gray and Dighton 2009; Jonasson et al. 1996). Thus, the post-fire coarse woody debris left after a wildfire can still retain a large amount of nutrients, which can be used to preserve and restore the ecosystem nutrient capital. Furthermore, the progressive nutrient release is expected to continue for years as wood decay proceeds, allowing retention by the soil and regenerating vegetation.

By contrast, the release of C, the main wood constituent, occurred fundamentally during the first sampling period, coupled with wood mass losses. Consequently, the C/N wood ratio remained initially constant and sharply increased afterwards. This contrasts with the decrease in the C/N ratio as wood decays reported in most of studies, associated mainly with a progressive N retention by the wood (Clark et al. 2002; Ganjegunte et al. 2004; Harmon et al. 1986; Idol et al. 2001; Yang et al. 2010). Nonetheless, increases in wood C concentration have been reported in some cases at initial stages of decomposition (Garrett et al. 2008; Preston et al. 1998; Sandström

Table 5 Stocks of soil and microbial fractions in positions located under logs and in bare areas for the upper 10 cm of soil

Site	Position	SOM ($kg\ m^{-2}$)	C_{tot} ($kg\ m^{-2}$)	N_{tot} ($g\ m^{-2}$)	NH_4^+ ($g\ m^{-2}$)	NO_3^- ($g\ m^{-2}$)	DOC ($g\ m^{-2}$)	C_{micro} ($g\ m^{-2}$)	DON ($g\ m^{-2}$)	N_{micro} ($g\ m^{-2}$)	P_{inorg} ($g\ m^{-2}$)	P_{micro} ($g\ m^{-2}$)
1	UL	4.855 ± 0.233	1.706 ± 0.078	106.40 ± 7.00	0.498 ± 0.134	0.132 ± 0.028	13.84 ± 1.54	20.37 ± 4.94	0.948 ± 0.085	1.375 ± 0.230	0.469 ± 0.072	0.069 ± 0.059
	BS	5.140 ± 0.277	1.818 ± 0.134	118.94 ± 7.27	0.354 ± 0.077	0.112 ± 0.024	15.24 ± 2.07	32.60 ± 6.20	1.192 ± 0.147	2.149 ± 0.358	0.562 ± 0.098	0.120 ± 0.065
2	UL	5.065 ± 0.406	2.176 ± 0.119	119.91 ± 5.68	0.610 ± 0.111	0.108 ± 0.022	16.62 ± 2.30	34.50 ± 5.07	1.339 ± 0.126	3.833 ± 0.558	0.397 ± 0.077	0.207 ± 0.072
	BS	5.533 ± 0.302	1.958 ± 0.132	120.95 ± 7.21	0.743 ± 0.141	0.193 ± 0.031	13.53 ± 2.40	29.67 ± 3.11	1.162 ± 0.131	2.799 ± 0.381	0.391 ± 0.067	0.168 ± 0.084
3	UL	4.194 ± 0.282	1.995 ± 0.152	126.79 ± 8.48	0.294 ± 0.051	0.140 ± 0.026	8.68 ± 0.91	28.28 ± 3.47	0.966 ± 0.080	2.704 ± 0.256	0.564 ± 0.110	0.266 ± 0.078
	BS	4.403 ± 0.247	1.658 ± 0.149	123.74 ± 10.64	0.561 ± 0.123	0.133 ± 0.024	9.85 ± 1.66	21.45 ± 2.67	0.903 ± 0.090	1.810 ± 0.207	0.386 ± 0.054	0.249 ± 0.180

UL under logs, *BS* bare soil

Values represent means ± standard errors

Author's personal copy

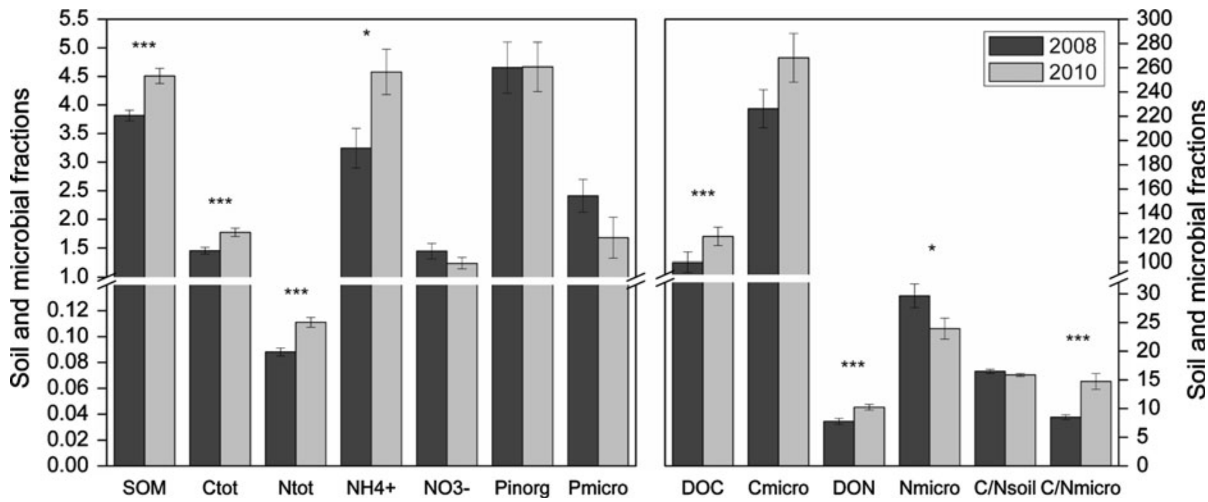


Fig. 5 Differences in soil and microbial fractions between sampling years. Different sites and positions (under logs and bare areas) are pooled. Significant differences among years are indicated: *0.01 < $P \leq 0.05$, **0.001 < $P \leq 0.01$, ***$P \leq 0.001$. Concentration units are % for SOM, C_{tot}, and N_{tot}, and mg kg^{-1} for the rest of fractions. Concentration values in the microbial fractions were corrected for extraction efficiency

et al. 2007; Yang et al. 2010). In our case, the microbial colonization and the associated N retention may be limited by the relatively low moisture retained by wood (Brown et al. 1996; Zhou et al. 2007), provided that the insolation and temperatures are not ameliorated by the forest canopy. As a result, wood becomes more recalcitrant as it decomposes, accentuating the N shortage for the decomposer activity (Ouro et al. 2001; Weedon et al. 2009). In summary, post-fire coarse woody debris played an important role as a reservoir of carbon and as well as a source of nutrients during the initial stages of decomposition, regulating the nutrient availability and preventing sudden losses in the regenerating ecosystem.

Effects of post-fire coarse woody debris on soil and microbial fractions

Overall, most of the soil and microbial fractions were higher and the pH more basic in areas under charred logs. This may be associated either to the nutrient release by partially charred wood (Hafner et al. 2005; Kuehne et al. 2008; Wei et al. 1997) or to the physical protection of soil by logs, as logs and branches can foster a more favourable soil microclimate (Castro et al. 2011; Smaill et al. 2008; Stoddard et al. 2008) and prevent nutrient losses through soil erosion and runoff that would carry away ash deposited after the wildfire (Fox 2011; Kim et al. 2008; Shakesby et al. 1996; Thomas et al. 2000). Thus, post-fire coarse woody debris prompted microbial activity and nutrient cycling, as supported similarly by higher levels of soil respiration in this treatment (Marañón-Jiménez et al. 2011). An exception was found in the inorganic fractions of N (NH_4^+ and NO_3^-), which represent the most available N fractions in the soil. Their fast mobilization between soil, plants, and microorganisms is determined by the convergence of several environmental factors (Killham 1994), making it difficult to detect an effect on them by punctual sampling. Nonetheless, the low values of NH_4^+ under logs coincide with the highest values of microbial biomass and N, suggesting a limitation of available N, both by direct adsorption in SOM and through microbial immobilization (Hafner et al. 2005; Magill and Aber 2000). Probably as a consequence of this N limitation, the microbial P also did not increase significantly under logs and followed a pattern similar to that of the microbial biomass and N. In addition, most of the N and C soil fractions tended to increase between the two sampling years, although proportional, and thus without changes in the soil C/N ratio. This increase could be associated partly with the progressive nutrient release from the wood, although other factors such as interannual differences in the balance between productivity and mineralization, in the phenology of

Author's personal copy

vegetation, or in short-term shifts in the nutrient demands of microorganisms and plants might also determine temporal variations in the soil fractions (Adair and Burke 2010; Hodge et al. 2000; Jandl et al. 2007).

The presence of fire-killed wood also decreased the soil bulk density, likely due to the greater proportion of organic matter. A low bulk density is indicative of soil quality and fertility, facilitating soil aeration and root penetration (Schoenholtz et al. 2000). Lower bulk-density values are also usually associated with higher organic-matter content, porosity and more structured soil (Schoenholtz et al. 2000; Merino and Edeso 1999). On the other hand, this implies that the nutrient stocks of the soil and microbial fractions in the first 10 cm of soil did not differ between positions under logs vs. bare areas. Expressing soil and microbial fractions as stocks per unit area could therefore lead to an underestimation of the overall improvement of soil fertility from the wood. In summary, the presence of wood over the soil generally increased soil nutrients, microbial fractions, and SOM, while decreasing bulk density and affecting the distribution of nutrients between the soil and microorganisms. The resulting improvement in soil fertility could enhance primary productivity and thereby the regeneration of vegetation.

Biogeochemical implications for management and ecosystem processes

There is currently intense debate concerning the appropriate management of fire-killed trees after forest fires (Beschta et al. 2004; Donato et al. 2006; Lindenmayer et al. 2004; McIver and Starr 2001). Post-fire salvage logging (felling and removing charred trunks, often combined with the elimination of the remaining woody debris; Beschta et al. 2004; McIver and Starr 2001) is implemented worldwide (Castro et al. 2010a; Lindenmayer et al. 2004; McIver and Starr 2001; Van Nieuwstadt et al. 2001), but recent studies show that it may impact ecosystem function and regeneration (Castro et al. 2010b, 2011; Donato et al. 2006; Lindenmayer and Noss 2006). The felling and removal of fire-killed trees using ground based yarding techniques may increase soil erosion and compaction, reduce nutrient availability, damage the seedling bank, hamper the regeneration of the plant community, reduce species richness and diversity, and ultimately raise net ecosystem CO_2 emissions (Beschta et al. 2004; Castro et al. 2011; Donato et al. 2006; Lindenmayer and Noss 2006; McIver and Starr 2000, 2001; Serrano-Ortiz et al. 2011). However, the specific role of partially charred wood on the post-fire soil fertility and nutrient mobilization has not been assessed to the date.

The present study shows that the post-fire coarse woody debris has a relevant role for the nutrient cycling and the recovery of the soil fertility. Aboveground wood in the burnt forest represented an initial stock of 49.6 ± 7 kg ha^{-1} of N and 2.8 ± 0.5 kg ha^{-1} of P. A fraction of these stocks were liberated to the system through decomposition, accounting for ca. 20.2 ± 3.5 kg ha^{-1} of N and 1.8 ± 0.3 kg ha^{-1} of P released after only 4 years. These contributions exceed other potential nutrient inputs to the ecosystem, like those due to the atmospheric deposition (ca. 6.3 kg ha^{-1} year^{-1} of N and 0.2 kg ha^{-1} year^{-1} of P; Morales-Baquero et al. 2006), or to the N fixation in leguminous roots as *Adenocarpus decorticans* (ca. 1 kg ha^{-1} year^{-1} of N; Moro et al. 1996), which are present in the study sites. Furthermore, the nutrient release estimations ascend to 30.8 ± 5.9 kg ha^{-1} of N and 2.8 ± 0.6 kg ha^{-1} of P if we also consider the contributions from the below-ground biomass (34 % approx. of the total biomass). Moreover, its effect is long lasting (Smaill et al. 2008), as the nutrient release is slow and progressive. The reduction of the soil bulk density also helps to compensate for the unfavourable effects that soil compaction can have on soil properties (Merino and Edeso 1999). On the contrary, the removal of fire-killed wood, as during salvage logging operations, would translate as a reduction in soil fertility and hence in the regeneration capacity of vegetation (Jurgensen et al. 1997; Lindenmayer et al. 2008; Stoddard et al. 2008). Thus, salvage logging has demonstrated to have detrimental effects on nutrient cycling and ecosystem functioning that should be considered when making management decisions.

Conclusions

The post-fire coarse woody debris after a wildfire still contains a great amount of nutrients that are released through decomposition, augmenting soil fertility and accelerating microbiological processes. Partially charred logs therefore provide a valuable ecosystem service, as they enhance the biogeochemical

Author's personal copy

sustainability, resilience, and functioning, which are key ecological properties for regeneration success.

Acknowledgments We wish to thank Ramón Ruíz Puche for his hard work in the field, Gustavo Román Reche for his assistance in processing the wood samples, and Susana Hitos for her invaluable help and advice in the laboratory analyses. We are especially grateful to Luis Matías for his inspiring suggestions and A. Kowalski for his personal advice. The Environmental Council (Autonomous Government of Andalucía) and the Natural and National Reserves of Sierra Nevada offered support in establishing the treatments. This work was financed by the Projects (SUM2006-00010-00-00) of the National Institute of Researching and Agricultural and Alimentary Technology (INIA), (10/2005) of the Autonomous Organism of National Parks (MMA), GESBOME (P06-RNM-1890) of the Autonomous Government of Andalucía, CSD2008-00040 of *Consolider-Ingenio Montes* of the Spanish Ministry of Education and Science (MICINN), *CARBORED-II* (CGL2010-22193-C04-02), (PTA2009-1782-I) of the Subprogram for Technical Support (MICINN), and by a grant FPU of the Spanish Ministry of Education and Science to S.M.J.

Appendix: Estimation of the initial dry weight of the wood discs to calculate the dry weight lost by the charred wood over time

To estimate the initial dry weight of the discs collected after two (2008) and four (2010) years of decomposition, we used a regression model constructed with the volume and the dry weight of the wood discs initially collected in 2006. Previously, we checked that diameter had no effect on the initial wood density for any of the sites ($P > 0.05$ for all sites), so the diameter did not have to be included as an independent variable in the model. Initial wood density differed among sites (Table 6) despite the absence of differences in the rest of variables, so a regression model was fitted separately for each site. Further, the dry weight of a wood disc must be zero when its volume is zero. For this, the intercept of the regression line was forced to be zero for each regression model. Nonetheless, once the models with intercept were fitted, the H_0 that the intercept was zero was tested in all of them, and the H_0 could not be rejected in most of the cases. The resulting regression equations for each site are:

$W_d = 0.7304172 * V_d$ for site 1;
$W_d = 0.7348488 * V_d$ for site 2;
$W_d = 0.7237018 * V_d$ for site 3;

where W_d and V_d are the dry weight and the volume of the initial wood discs. As the external fragmentation of the log was negligible over the study period, we can assume that the volume of the wood discs (V_d) remained constant during these initial stages of wood decomposition. Thus, the volume of the wood discs of 2008 and 2010 (V_d) was introduced in the constructed regression model to estimate their initial dry weight (W_d).

Table 6 Summary of the variables measured in the wood discs collected in 2006 which were used in the regression models and results of testing the differences between the experimental sites

Variable	Site 1	Site 2	Site 3	F	df	P
Φ_d (cm)				0.28	2	0.7575
Mean	13.3	12.8	12.1			
Range	22.2	18.7	10.8			
W_d (g)				0.03	2	0.9671
Mean	425.01	397.62	344.13			
Range	1390.4	1861.1	1055.8			
V_d^1 (cm^3)				0.09	2	0.9145
Mean	580.7	553.3	497.7			
Range	1895.3	2231.9	1385.7			
ρ_d (g/cm^3)				6.00	2	0.0031
Mean	0.73^a	0.70^{a,b}	0.68^b			
Range	0.27	0.32	0.40			

Different letters indicate significant differences among sites at level $\alpha = 0.05$

F statistic of the contrast of the one-way ANOVAs; *df* degrees of freedom, P critical probability of the contrast, Φ_d diameter of the discs, W_d dry weight of the wood discs, V_d volume of the wood discs; ρ_d density of the wood discs

[1] Assuming a conical shape for each disc, its volume (V_d) in cm^3 was calculated as follows: $V_d = 1/3\pi h(R^2 + Rr + r^2)$ where h is the mean height of the disc in cm; R and r are, respectively, the maximum and minimum mean radii of each disc face in cm

References

Alriksson A, Eriksson HM (1998) Variations in mineral nutrient and C distribution in the soil and vegetation compartments of five temperate tree species in NE Sweden. For Ecol Manage 108(3):261–273

Association of Official Analytical Chemists (AOAC) (1975) Methods of analysis, 12th edn. AOAC, Washington, DC

Augusto L, Ranger J, Ponette Q, Rapp M (2000) Relationships between forest tree species, stand production and stand nutrient amount. Ann For Sci 57(4):313–324

Augusto L, Meredieu C, Bert D, Trichet P, Porte A, Bosc A, Lagane F, Loustau D, Pellerin S, Danjon F, Ranger J, Gelpe J (2008) Improving models of forest nutrient export with equations that predict the nutrient concentration of tree compartments. Ann For Sci 65(8)808–822

Author's personal copy

Beschta RL, Rhodes JJ, Kauffman JB, Griesswell RE, Minshall GW, Karr JR, Perry DA, Hauer ER, Frissell CA (2004) Postfire management on forested public lands of the western United States. Conserv Biol 18(4):957–967

Brais S, David P, Ouimet R (2000) Impacts of wild fire severity and salvage harvesting on the nutrient balance of jack pine and black spruce boreal stands. For Ecol Manage 137(1–3):231–243

Brais S, Sadi R, Bergeron Y, Grenier Y (2005) Coarse woody debris dynamics in a post-fire jack pine chronosequence and its relation with site productivity. For Ecol Manage 220(1–3):216–226

Bremner JM, Keeney DR (1965) Steam distillation methods for determination of ammonium nitrate and nitrite. Anal Chim Acta 32(5):485

Brown S, Mo JM, McPherson JK, Bell DT (1996) Decomposition of woody debris in Western Australian forests. Can J For Res 26(6):954–966

Castro J, Marañón-Jiménez S, Sánchez-Miranda A, Lorite J (2010a) Efecto del manejo de la madera quemada sobre la regeneración forestal post-incendio: desarrollo de técnicas blandas de restauración ecológi*ca*. In: Ramírez L, Asensio B (eds) Proyectos de Investigación en Parques Nacionales: 2006–2009. Organismo Autónomo de Parques Nacionales, Madrid, pp 139–157

Castro J, Moreno-Rueda G, Hodar JA (2010b) Experimental test of postfire management in pine forests: impact of salvage logging *versus* partial cutting and nonintervention on bird-species assemblages. Conserv Biol 24(3):810–819. doi:10.1111/j.1523-1739.2009.01382.x

Castro J, Allen CD, Molina-Morales M, Marañón-Jiménez S, Sánchez-Miranda A, Zamora R (2011) Salvage logging *versus* the use of burnt wood as a nurse object to promote post-fire tree seedling establishment. Restor Ecol 19(4):537–544. doi:10.1111/j.1526-100X.2009.00619.x

Certini G (2005) Effects of fire on properties of forest soils: a review. Oecologia 143(1):1–10

Clark DD, Clark DA, Brown S, Oberbauer SF, Veldkamp E (2002) Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. For Ecol Manage 164:237–248

Costa-Tenorio M, Morla C, Sainz-Ollero H (1998) Los Bosques Ibéricos. Editorial Planeta, Madrid

DeBano LF, Conrad CE (1978) Effect of fire on nutrients in a chaparral ecosystem. Ecology 59(3):489–497

DeBano LF, Neary DG, Ffolliott PF (1998) Fire's effects on ecosystems. John Wiley, New York

Donato DC, Fontaine JB, Campbell JL, Robinson WD, Kauffman JB, Law BE (2006) Post-wildfire logging hinders regeneration and increases fire risk. Science 311(5759): 352. doi:10.1126/science.1122855

Fernandez C, Vega JA, Fonturbel T, Perez-Gorostiaga P, Jimenez E, Madrigal J (2007) Effects of wildfire, salvage logging and slash treatments on soil degradation. Land Degrad Dev 18(6):591–607

Fox DM (2011) Evaluation of the efficiency of some sediment trapping methods after a Mediterranean forest fire. J Environ Manage 92(2):258–265

Ganjegunte GK, Condrona LM, Clinton PW, Davisb MR, Mahieuc N (2004) Decomposition and nutrient release from radiata pine (*Pinus radiata*) coarse woody debris. For Ecol Manage 187:197–211

Garrett LG, Oliver GR, Pearce SH, Davis MR (2008) Decomposition of *Pinus radiata* coarse woody debris in New Zealand. For Ecol Manage 255(11):3839–3845

Graham RT, Harvey AE, Jurgensen MF, Jain TB, Tonn JR, Pagedumroese DS (1994) Managing coarse woody debris in forests of the rocky-mountains. USDA For Serv Intermt Res Stn Res Pap 477:1–13

Gray DM, Dighton J (2009) Nutrient utilization by pine seedlings and soil microbes in oligotrophic Pine Barrens forest soils subjected to prescribed fire treatment. Soil Biol Biochem 41(9):1957–1965

Grove SJ (2003) Coarse woody debris, biodiversity and management: a review with particular reference to Tasmanian wet eucalypt forests. Aust For 66(4):258–272

Grove SJ, Stamm L, Barry C (2009) Log decomposition rates in Tasmanian Eucalyptus obliqua determined using an indirect chronosequence approach. For Ecol Manage 258(4):389–397

Hafner SD, Groffman PM (2005) Soil nitrogen cycling under litter and coarse woody debris in a mixed forest in New York State. Soil Biol Biochem 37(11):2159–2162

Hafner SD, Groffman PM, Mitchell MJ (2005) Leaching of dissolved organic carbon, dissolved organic nitrogen, and other solutes from coarse woody debris and litter in a mixed forest in New York State. Biogeochemistry 74(2):257–282

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. Adv Ecol Res 15:133–302

Hodge A, Robinson D, Fitter A (2000) Are microorganisms more effective than plants at competing for nitrogen? Trends Plant Sci 5(7):304–308

Hutto RL (2006) Toward meaningful snag-management guidelines for postfire salvage logging in North American conifer forests. Conserv Biol 20(4):984–993. doi:10.1111/j.1523-1739.2006.00494.x

Idol TW, Figler RA, Pope PE, Ponder F Jr (2001) Characterization of coarse woody debris across a 100 year chronosecuence of upland oak-hickory forest. For Ecol Manage 149:153–161

Iglesias T, Cala V, Gonzalez J (1997) Mineralogical and chemical modifications in soils affected by a forest fire in the Mediterranean area. Sci Total Environ 204(1):89–96

Jandl R, Lindner M, Vesterdal L, Bauwens B, Baritz R, Hagedorn F, Johnson DW, Minkkinen K, Byrne KA (2007) How strongly can forest management influence soil carbon sequestration? Geoderma 137(3–4):253–268

Jenkinson DS, Powlson DS (1976) Effects of biocidal treatments on metabolism in soil. 5. Method for measuring soil biomass. Soil Biol Biochem 8(3):209–213

Johnson DW, Curtis PS (2001) Effects of forest management on soil C and N storage: meta analysis. For Ecol Manage 140(2–3):227–238

Johnson DW, Murphy JF, Susfalk RB, Caldwell TG, Miller WW, Walker RF, Powers RF (2005) The effects of wildfire, salvage logging, and post-fire N-fixation on the nutrient budgets of a Sierran forest. For Ecol Manage 220: 155–165

Author's personal copy

Jonasson S, Michelsen A, Schmidt IK, Nielsen EV, Callaghan TV (1996) Microbial biomass C, N and P in two arctic soils and responses to addition of NPK fertilizer and sugar: implications for plant nutrient uptake. Oecologia 106(4):507–515

Jurgensen MF, Harvey AE, Graham RT, PageDumroese DS, Tonn JR, Larsen MJ, Jain TB (1997) Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of Inland Northwest forests. For Sci 43(2): 234–251

Killham K (1994) Soil ecology. Cambridge University Press, Cambridge

Kim CG, Shin K, Joo KY, Lee KS, Shin SS, Choung Y (2008) Effects of soil conservation measures in a partially vegetated area after forest fires. Sci Total Environ 399(1–3): 158–164

Klinka K, Lavkulich LM, Wang Q, Feller MC (1995) Influence of decaying wood on chemical properties of forest floors and surface mineral soils: a pilot study. Ann For Sci 52(6):523–533

Kuehne C, Donath C, Muller-Using SI, Bartsch N (2008) Nutrient fluxes via leaching from coarse woody debris in a *Fagus sylvatica* forest in the Solling Mountains, Germany. Can J For Res 38(9):2405–2413

Laiho R, Prescott CE (2004) Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Can J For Res 34(4):763–777

Lambert RL, Lang GE, Reiners WA (1980) Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology 61(6):1460–1473

Lindenmayer DB, Noss RF (2006) Salvage logging, ecosystem processes, and biodiversity conservation. Conserv Biol 20(4):949–958. doi:10.1111/j.1523-1739.2006.00497.x

Lindenmayer DB, Foster DR, Franklin JF, Hunter ML, Noss RF, Schmiegelow FA, Perry D (2004) Salvage harvesting policies after natural disturbance. Science 303(5662):1303

Lindenmayer DB, Burton PJ, Franklin JF (2008) Salvage logging and its ecological consequences. Island Press, Washington

Mackensen J, Bauhus J (2003) Density loss and respiration rates in coarse woody debris of *Pinus radiata*, *Eucalyptus regnans* and *Eucalyptus maculata*. Soil Biol Biochem 35(1):177–186

Magill AH, Aber JD (2000) Dissolved organic carbon and nitrogen relationships in forest litter as affected by nitrogen deposition. Soil Biol Biochem 32(5):603–613

Marañón-Jiménez S, Castro J, Kowalski AS, Serrano-Ortiz P, Reverter BR, Sánchez-Cañete EP, Zamora R (2011) Post-fire soil respiration in relation to burnt wood management in a Mediterranean mountain ecosystem. For Ecol Manage 261(8):1436–1447

Marcos E, Villalon C, Calvo L, Luis-Calabuig E (2009) Short-term effects of experimental burning on soil nutrients in the Cantabrian heathlands. Ecol Eng 35(5):820–828

McIver JD, Starr L (2000) Environmental effects of postfire logging: literature review and annotated bibliography. PNW-GTR-486. USDA Forest Service, Pacific Northwest Research Station, Portland

McIver JD, Starr L (2001) A literature review on the environmental effects of postfire logging. Western Journal of Applied Forestry 16:159–168

Merino A, Edeso JM (1999) Soil fertility rehabilitation in young *Pinus radiata* D. Don. plantations from northern Spain after intensive site preparation. For Ecol Manage 116(1–3): 83–91

Merino A, Rey C, Brañas J, Soalleiro RR (2003) Biomasa arbórea y acumulación de nutrientes en plantaciones de Pinus radiata D. Don en Galicia. Investigación agraria: Sistemas y Recursos Forestales 12 (2):85-98

Merino A, Balboa MA, Soalleiro RR, Gonzalez JGA (2005) Nutrient exports under different harvesting regimes in fast-growing forest plantations in southern Europe. For Ecol Manage 207(3):325–339

Morales-Baquero R, Pulido-Villena E, Reche I (2006) Atmospheric inputs of phosphorus and nitrogen to the southwest Mediterranean region: biogeochemical responses of high mountain lakes. Limnol Oceanogr 51:830–837

Moro MJ, Domingo F, Escarre A (1996) Organic matter and nitrogen cycles in a pine afforested catchment with a shrub layer of *Adenocarpus decorticans* and *Cistus laurifolius* in south-eastern Spain. Ann Bot 78:675–685

Neary DG, Klopatek CC, DeBano LF, Ffolliott PF (1999) Fire effects on belowground sustainability: a review and synthesis. For Ecol Manage 122(1–2):51–71

Ouro G, Perez-Batallon P, Merino A (2001) Effects of sylvicultural practices on nutrient status in a Pinus radiata plantation: nutrient export by tree removal and nutrient dynamics in decomposing logging residues. Ann For Sci 58(4):411–422

Page-Dumroese DS, Jurgensen MF (2006) Soil carbon and nitrogen pools in mid- to late-successional forest stands of the northwestern United States: potential impact of fire. Can J For Res 36(9):2270–2284

Palviainen M, Finer L, Laiho R, Shorohova E, Kapitsa E, Vanha-Majamaa I (2010a) Carbon and nitrogen release from decomposing Scots pine, Norway spruce and silver birch stumps. For Ecol Manage 259(3):390–398. doi:10.1016/j.foreco.2009.10.034

Palviainen M, Finer L, Laiho R, Shorohova E, Kapitsa E, Vanha-Majamaa I (2010b) Phosphorus and base cation accumulation and release patterns in decomposing Scots pine, Norway spruce and silver birch stumps. For Ecol Manage 260(9):1478–1489

Pansu M, Gautheyrou J (2006) Handbook of soil analysis. Mineralogical, organic and inorganic methods. Springer, Montpellier

Preston CM, Trofymow JA, Niu J, Fyfe CA (1998) PMAS-NMR spectroscopy and chemical analysis of coarse woody debris in coastal forests of Vancouver Island. For Ecol Manage 111(1):51–68

Quinn GP, Keough MJ (2009) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

Raison RJ (1979) Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations—review. Plant Soil 51(1):73–108

Rock J, Badeck FW, Harmon ME (2008) Estimating decomposition rate constants for European tree species from literature sources. Eur J Forest Res 127:301–313

Sandström F, Petersson H, Kruys N, Stahl G (2007) Biomass conversion factors (density and carbon concentration) by decay classes for dead wood of *Pinus sylvestris*, *Picea abies* and *Betula* spp. in boreal forests of Sweden. For Ecol Manage 243(1):19–27

Author's personal copy

Sardans J, Peñuelas J, Rodá F (2005) Changes in nutrient use efficiency, status and retranslocation in young post-fire regeneration *Pinus halepensis* in response to sudden N and P input, irrigation and removal of competing vegetation. Trees 19:233–250

Schinner F, Öhlinger R, Kandeler E, Margesin R (1995) Methods in soil biology. Springer, Berlin

Schoenholtz SH, Miegroet HV, Burger JA (2000) A review of chemical and physical properties as indicators of forest soil quality: challenges and opportunities. For Ecol Manage 138(1–3):335–356

Serrano-Ortiz P, Marañón-Jiménez S, Reverter BR, Sánchez-Cañete EP, Castro J, Zamora R, Kowalski AS (2011) Post-fire salvage logging reduces carbon sequestration in Mediterranean coniferous forest. For Ecol Manage 262: 2287–2296

Shakesby RA (2011) Post-wildfire soil erosion in the Mediterranean: review and future research directions. Earth Sci Rev 105(3–4):71–100

Shakesby RA, Boakes DJ, CdOA Coelho, Gonçalves AJB, Walsh RPD (1996) Limiting the soil degradational impacts of wildfire in pine and eucalyptus forests in Portugal: a comparison of alternative post-fire management practices. Appl Geogr 16(4):337–355

Shorohova E, Kapitsa E, Vanha-Majamaa I (2008) Decomposition of stumps in a chronosequence after clear-felling vs. clear-felling with prescribed burning in a southern boreal forest in Finland. For Ecol Manage 255(10):3606–3612

Smaill SJ, Clinton PW, Greenfield LG (2008) Postharvest organic matter removal effects on FH layer and mineral soil characteristics in four New Zealand Pinus radiata plantations. For Ecol Manage 256(4):558–563

Sparks DL (1996) Methods of soil analysis. Part 3. Chemical methods. Soil Science Society of America and American Society of Agronomy, Madison

Sparling GP, West AW (1988) Modifications to the fumigation-extraction technique to permit simultaneous extraction and estimation of soil microbial-C and microbial-N. Commun Soil Sci Plant Anal 19:327–344

Spies TA, Franklin JF, Thomas TB (1988) Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69(6):1689–1702

Stocks BJ, Alexander ME, Wotton BM, Stefner CN, Flannigan MD, Taylor SW, Lavoie N, Mason JA, Hartley GR, Maffey ME, Dalrymple GN, Blake TW, Cruz MG, Lanoville RA (2004) Crown fire behaviour in a northern jack pine-black spruce forest. Can J For Res 34(8):1548–1560

Stoddard MT, Huffman DW, Alcoze TM, Fule PZ (2008) Effects of slash on herbaceous communities in pinyon-juniper woodlands of northern Arizona. Rangel Ecol Manag 61(5):485–495

Thiffault E, Pare D, Belanger N, Munson A, Marquis F (2006) Harvesting intensity at clear-felling in the boreal forest: impact on soil and foliar nutrient status. Soil Sci Soc Am J 70(2):691–701

Thomas AD, Walsh RPD, Shakesby RA (1999) Nutrient losses in eroded sediment after fire in eucalyptus and pine forests in the wet Mediterranean environment of northern Portugal. Catena 36(4):283–302

Thomas AD, Walsh RPD, Shakesby RA (2000) Post-fire forestry management and nutrient losses in *Eucalyptus* and pine plantations, northern Portugal. Land Degrad Dev 11(3):257–271

Tinker DB, Knight DH (2000) Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. Ecosystems 3(5):472–483

Trabaud L (1994) The effect of fire on nutrient losses and cycling in a *Quercus coccifera* garrigue (southern France). Oecologia 99:379–386

Van Nieuwstadt MGL, Sheil D, Kartawinata K (2001) The ecological consequences of logging in the burned forests of East Kalimantan, Indonesia. Conserv Biol 15(4):1183–1186

Wan SQ, Hui DF, Luo YQ (2001) Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecol Appl 11(5):1349–1365

Watanabe S, Olsen RS (1965) Test of an ascorbic acid method for determining phosphorus in water and NaHCO3 extracts from soil. Soil Sci Soc Am J 29:677–678

Weedon JT, Cornwell WK, Cornelissen JHC, Zanne AE, Wirth C, Coomes DA (2009) Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? Ecol Lett 12(1):45–56

Wei X, Kimmins JP, Peel K, Steen O (1997) Mass and nutrients in woody debris in harvested and wildfire-killed lodgepole pine forests in the central interior of British Columbia. Can J For Res 27(2):148–155

Whelan RJ (1995) The ecology of fire. Cambridge studies in Ecology. Cambridge University Press, Cambridge

Yang YS, Guo JF, Chen GS, He ZM, Xie JS (2003) Effect of slash burning on nutrient removal and soil fertility in Chinese fir and evergreen broadleaved forests of mid-subtropical China. Pedosphere 13(1):87–96

Yang FF, Li YL, Zhou GY, Wenigmann KO, Zhang DQ, Wenigmann M, Liu SZ, Zhang QM (2010) Dynamics of coarse woody debris and decomposition rates in an old-growth forest in lower tropical China. For Ecol Manage 259(8):1666–1672

Zhou L, Dai L, Gu H, Zhong L (2007) Review on the decomposition and influence factors of coarse woody debris in forest ecosystem. J For Res 18(1):48–54