Charred wood remaining after a wildfire as a reservoir of macro- and micronutrients in a Mediterranean pine forest

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Abstract. Large amounts of logs and coarse woody debris remain in the ecosystem after wildfires. However, the relevance of the nutrient reservoir contained in the remaining post-fire woody debris for the ecosystem nutrient reserves is rarely considered. In this paper, we determine the carbon and nutrient concentrations in the partially charred wood after a wildfire along an altitudinal gradient and assess the relative magnitude of the nutrient reservoir in the wood in relation to those existing in the first 10-cm soil layer. Soils were poorly developed and nutrients limiting for the vegetation requirements. Charred woody material still contained a relatively high concentration of nutrients compared to those reported for unburnt pine wood, and in general, this decreased with altitude. Partially charred wood represented a considerable pool of nutrients, due to both the relatively high concentrations and to the great amount of biomass still present after the fire. Potential contributions of the charred wood were particularly relevant for N and micronutrients Na, Mn, Fe, Zn and Cu, as wood contained 2–9 times more nutrients than the soil. Post-fire woody debris constitutes therefore a valuable natural element as a potential source of nutrients, which would be lost from ecosystems in cases where it is removed.

Additional keywords: forest management, Mediterranean mountain, post-fire salvage logging, silvicultural treatments, soil nutrients, wood nutrients, woody debris.

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Introduction

Wildfires represent a strong perturbation to the ecosystem nutrient cycle, leading to an immediate nutrient mobilisation from organic pools (Trabaud 1994; Whelan 1995; Page-Dumroese and Jurgensen 2006). Vegetation, litter and soil organic layers are susceptible to consumption by fire in greater or lesser degrees depending on the temperature reached and their flammability. According to their specific temperatures of volatilisation, their nutrients are either released to the atmosphere as smoke or deposited to the soil as ash (Iglesias *et al.* 1997; Neary *et al.* 1999; Johnson *et al.* 2005). As a consequence, fire causes a net decrease in the total nutrient reserves in the ecosystem.

The deposited ash can increase the soil nutrient availability in the short term (Certini 2005; Augusto *et al.* 2008*a*; Pereira *et al.* 2011). Nonetheless, the consequent nutrient enrichment in soil is ephemeral in most cases (Iglesias *et al.* 1997; Wan *et al.* 2001; Yang *et al.* 2003; Ferreira *et al.* 2005), as the reduction of stability and nutrient retention capacity of the soil exacerbate the loss of nutrients by leaching and erosion (DeBano *et al.* 1998; Thomas *et al.* 1999, 2000; Certini 2005; Fernández *et al.* 2007; Shakesby 2011). The existence of a nutrient reservoir in the ecosystem in the long term is therefore key to ensuring the sustainability of the plant community, especially during the first stages of succession (Jurgensen *et al.* 1997; Augusto *et al.* 2000, 2008*b*; Merino *et al.* 2003, 2005).

Coarse woody debris may have an important role in both biochemical cycling and ecosystem functioning. During growth, trees incorporate and accumulate nutrients from the soil in the proportions needed to constitute biomass, even where soils are

poor (Ingestad 1979; Clarkson and Hanson 1980; Chapin *et al.* 2002). On the other hand, woody material usually represents the largest proportion of biomass in the forest, although this varies according to the characteristics of the stand (tree density, forest species, climate, etc.). Overall, it is estimated that coarse woody tree fractions (stem wood excluding bark and thick branches) represent ~75–90% of the total aboveground biomass of pine forests (Ouro *et al.* 2001; Merino *et al.* 2003, 2005). Moreover, this estimate increases to ~95% of the total tree biomass if stumps and roots are also included (Alriksson and Eriksson 1998; Rademacher 2005), while the rest is accounted for by needles, thin branches, twigs, cones and stem bark. Therefore, although nutrient concentrations in woody tissues are usually lower than in the other tree fractions, they can contain a high proportion of the nutrients (Alriksson and Eriksson 1998; Ouro *et al.* 2001; Merino *et al.* 2003, 2005; Rademacher 2005) and act as an ecosystem sink and reservoir.

The sudden nutrient mobilisation and loss provoked during a wildfire and in the immediate period after is restricted mostly to the leaves and fine fractions of vegetation (Trabaud 1994; Johnson *et al.* 2005). However, most of the nutrients contained in the large woody material (trunks and thick branches) and in the roots will likely remain in the ecosystem (Wei *et al.* 1997; Tinker and Knight 2000; Johnson *et al.* 2005), as the temperatures reached inside the first centimetres of the matrix of coarse woody fractions during the heat wave are not high enough to volatilise its components (Czimczik *et al.* 2002). In fact, even after intense stand-replacing crown fires, charring is usually limited to the bark or the outer superficial wood layer, remaining unburnt through most of the standing tree bole (Stocks *et al.* 2004). The nutrients contained in the post-fire coarse woody debris will be progressively released later during the decay process (Brown *et al.* 1996; Wei *et al.* 1997; Ganjegunte *et al.* 2004; Palviainen *et al.* 2010*a*, 2010*b*; Marañón-Jiménez and Castro 2012), allowing their retention by the soil and their availability for microorganisms and developing vegetation (Jurgensen *et al.* 1997; Grove and Meggs 2003; Brais *et al.* 2005; Marañón-Jiménez and Castro 2012).

Ecosystem nutrient losses associated with wildfires have been estimated in several studies (DeBano and Conrad 1978; Wei *et al.* 1997; Thomas *et al.* 1999, 2000; Brais *et al.* 2000; Wan *et al.* 2001; Yang *et al.* 2003; Johnson *et al.* 2005). In this respect, Wei *et al.* (1997) suggested that the nutrients (N and P) contained in unburnt pine stemwood are comparable to the nutrient losses associated with low severity wildfires. Likewise, the contributions of ash deposited after a wildfire to soil nutrient availability and nutrient cycling in the short term has been noted in a considerable number of studies (Bramryd and Fransman 1995; Certini 2005; Augusto *et al.* 2008*a*; Pereira *et al.* 2011; Johnson *et al.* 2012). However, there is scarce information about the elemental concentrations remaining in charred wood after a wildfire, and what is more, the magnitude of the nutrient pools of charred woody material after a wildfire and their potential role in the ecosystem nutrient reserves has not been assessed to date. The estimation of the nutrient reservoir in the post-fire woody debris is a key first step in assessing ecosystem sustainability towards its regeneration. In a previous study, we assessed the long-term effects of the presence of the decomposing post-fire wood biomass on soil fertility and soil biogeochemical

functioning (Marañón-Jiménez and Castro 2012). In this work, we intend to evaluate the potential biogeochemical relevance, in terms of magnitude, of the nutrient pool in the remaining wood at the starting point, before decomposition and after the short-term effects of ash deposition. We analyse the initial macro- and micronutrient concentrations in charred pine logs 6 months after the wildfire, and the available nutrients in the soil 2 years after the fire. This is done across an altitudinal gradient that varies in climatic conditions and pine species, with the potential to affect soil and wood nutritional status. Nutrient pools in the charred wood are further estimated and compared with the pool of nutrients in the soil to evaluate their relevance. The main objectives of this study are to: (1) determine the nutrient concentrations in the charred wood left after a wildfire along an altitudinal gradient and (2) assess the relative magnitude of the nutrient reservoir in the post-fire wood biomass in relation to the available nutrient stocks in the soil.

Materials and methods

Study area

The study site is located in the Sierra Nevada Natural and National Parks (south-east Spain; UTM: 36°57′9.8949″N, 3°29′36.2381″W), where in September 2005 the Lanjarón wildfire burned ~1300 ha of reforested pine forest between 35 and 45 years old (Fig. 1). Fire severity was qualitatively estimated by the visible effects on the trees and on the different woody fractions and understorey vegetation, and by the colour of deposited ashes just after the wildfire. Fire consumed all the leaves, twigs, litter and understorey vegetation, and charred the bark of the trunks. All the trees in the study area were killed and flames reached and consumed the crown of the trees (~8 m high). The colour of the deposited ash varied between clear grey and white. According to these indicators, the fire was classified as a high-severity crown fire by the Forest Service.

The climate is Mediterranean, with rainfall concentrated in the northern hemisphere 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 1465 m above sea level). Snow falls during winter, usually persisting from November to March above 2000 m above sea level. The mean annual temperature is 12.3 ± 0.4°C at 1652 m above sea level (1994–2008; State Meteorological Agency, Ministry of Environment) and 7.8 ± 0.7°C at 2300 m above sea level (2008–10; data from the meteorological station).

The fire-killed pine stands occupy an altitudinal gradient from ~1300 to 2300 m above sea level (Fig. 1). Across this gradient, we established four study sites of ~3 ha (sites 1 to 4) that were similar in terms of fire severity (high), situation (south-west exposure), bedrock (micaschists), tree density and tree size (Table 1). The dominant pine species at each site varied according to climatic conditions (Table 1). 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 ~45% of the surface at ground level (Castro *et al.* 2011). Post-fire vegetation was composed mainly of grasses and forbs with
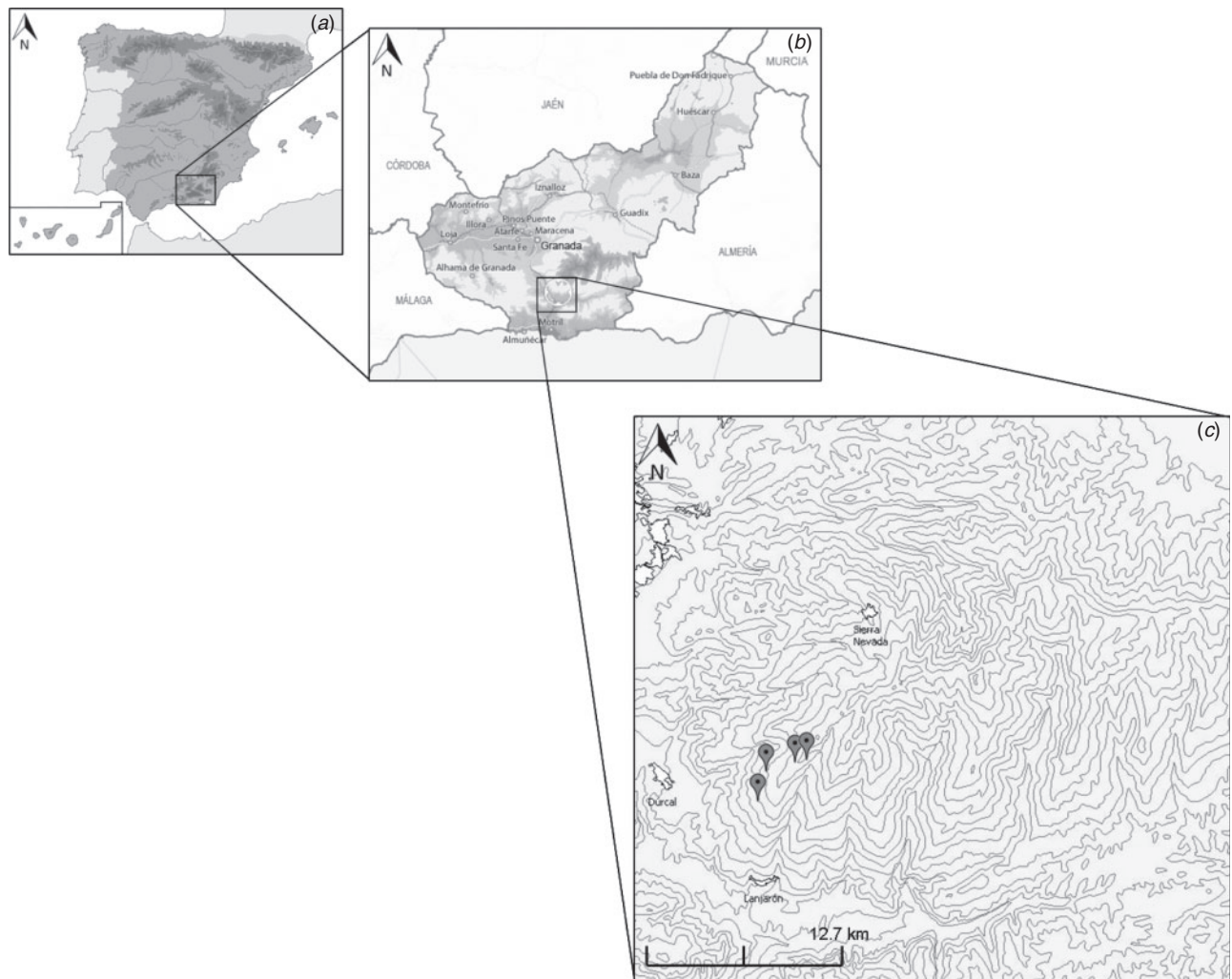
Fig. 1. Location of the study area and relative geographical position of the study sites. (*a*) Iberian peninsula, (*b*) Granada province, (*c*) Sierra Nevada (Spain).

Table 1.   Main pre-fire stand characteristics and dasometric variables of the trees in the study sites

Element	Site			
	1	2	3	4
UTM position	36°57′9.8949″N, 3°29′36.2381″W	36°58′11.9966″N, 3°30′1.7534″W	36°58′6.5527″N, 3°28′49.1254″W	36°58′5.5592″N, 3°28′29.9096″W
Altitude[A] (m above sea level)	1477	1698	2053	2317
Slope	25–30%	25–35%	35%	20%
Pre-fire dominant species	*Pinus pinaster* Ait.	*Pinus nigra* Arnold	*Pinus sylvestris* L.	*Pinus sylvestris* L.
Tree density (individuals ha^{-1})	1477 ± 46	1064 ± 67	1051 ± 42	1058 ± 52
Diameter at 1.30 m (cm)	13.3 ± 0.2	14.5 ± 0.2	10.7 ± 0.2	13.4 ± 0.3
Tree height (m)	6.3 ± 0.1	6.6 ± 0.1	6.2 ± 0.1	6.6 ± 0.2

[A]Altitude in the centre of the delimited area of each site.

a cover of ~70% (Castro *et al.* 2010). Dominant species were *Ulex parviflorus*, *Adenocarpus decorticans*, *Festuca scariosa*, *Dactylis glomerata* and *Euphorbia flavicoma* in site 1; *U. parviflorus*, *A. decorticans*, *F. scariosa*, *Sangisorba minor* and *E. flavicoma* in site 2; *Vaccaria hispanica*, *Sesamoides prostrata*, *Senecio nebrodensis* and *Helianthemum apenninum* in site 3; and *Genista versicolor*, *Festuca* spp. and *S. prostrata* in site 4.

Wood sampling

During tree felling by the Forest Service ∼6 months after the fire (March 2006), discs of 6–8 cm thick were sawed (with a chainsaw) from 50 logs randomly chosen per site and taken to the laboratory. We intentionally delayed wood sampling until this time, so that ash deposited over the charred trunk surfaces had been lost by the effect of wind and rain (see Fig. A1 of the Appendix for information about rain events occurring 9 months after the fire), in order to discard the contribution of nutrients stored in the ashes but lost in the short term. These discs were considered a representative sample of the initial characteristics of the charred wood, because they showed no signs of decomposition. The disc diameter did not differ among sites and was 12.7 ± 0.3 cm of average. The remaining bark was removed and wood discs were oven-dried at 70°C to constant weight to determine the dry weight. 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. The extracted sawdust (<1 mm) from each disc was collected in paper envelopes and stored in a dry place for later chemical analysis.

Wood chemical analyses

The carbon and nitrogen concentrations of sawdust samples were determined using the combustion furnace technique at 850°C (Leco TruSpec autoanalyser, St Joseph, MI, USA), and phosphorus was analysed using the molybdovanadate method (AOAC 1975). Meso- and micronutrients (Ca, Mg, K, Na, Fe, Mn, Zn and Cu) were determined by atomic absorption of the vegetal ash solution (Métodos Oficiales de Análisis de Suelos y Aguas, Ministerio de Agricultura y Pesca 1981) with a Perkin Elmer 5100 spectrometer (Waltham, MA, USA). The sawdust was dried at 105°C by a thermogravimetric analyser (Leco TGA 701), and nutrient concentrations were calculated with respect to the corresponding dry weight.

Soil sampling

In June 2008 (2 years after the wildfire), 12 soil samples were collected from bare areas without woody debris at each site. By that time, we may assume that the immediate post-fire runoff and lixiviation of nutrients in deposited ashes had occurred (Wan *et al.* 2001; Yang *et al.* 2003; Ferreira *et al.* 2005), and thus this sampling allowed us to characterise soil conditions excluding ephemeral effects of ash deposition (see Fig. A1 for information about rain events 2 years after the fire). For each soil sample, three to four soil pits were extracted using a gouge auger (2.5-cm diameter) to 10-cm depth, and homogenised to create a single soil sample. Samples were immediately sieved at 2 mm and stored at 4°C. Within 24 h of soil sampling, two subsamples of 15 and 7.5 g of soil were extracted for 1-h agitation in respective 75-mL volumes of 2 M KCl and 0.5 M NaHCO₃, and filtered through a Whatman GF-D filter. Extracts were frozen at −20°C until analysed (Schinner *et al.* 1995). A 30-g subsample was oven-dried at 105°C for 48 h for gravimetric determination of water content (as the difference between fresh and dry weight) and stored for further analyses. The bulk density was

calculated with the dry weight and volume of the soil fraction <2 mm. 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 (Blake and Hartge 1986).

Soil chemical analyses

From the dried subsample, soil organic matter (SOM) content was determined by incineration at 550°C with a thermobalance (Leco TGA 701, St Joseph, MI, USA) to constant weight (Sparks 1996), whereas total C (C_{tot}) and N (N_{tot}) were determined by combustion at 850°C (Leco TruSpec autoanalyser). 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, 3 and 4), 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 pH meter (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 (Flawil, Sweden). Available inorganic P (P_{inorg}) was determined in $NaHCO_3$ extracts by the Olsen method (Watanabe and Olsen 1965) with a Perkin Elmer 2400 spectrophotometer (Waltham, MA, USA). Meso- and micronutrient concentrations (Ca, Mg, K, Na, Fe, Mn, Zn and Cu) were determined by cation displacement with ammonium acetate and later analysis by atomic absorption with a Perkin Elmer 5100 spectrometer. The cation exchange capacity (CEC) was obtained after saturation of the soil exchange complex with Na^+ cations by adding sodium acetate, and later determination of the displaced Na^+ cations with ammonium acetate by atomic absorption (Burt 2009). The soil texture was determined by the standard pipette method after Robinson-Köhn or Andreasen (Pansu and Gautheyrou 2006). Soil mineralogy was determined by X-ray diffraction (XRD) after milling a soil subsample to powder (Whittig and Allardice 1986) with an X-ray diffractometer (Bruker D8 Advance, Madrid, Spain). All nutrient fractions were calculated with respect to the corresponding dry weight of the soil.

Nutrient pools estimation

The biogeochemical relevance of post-fire wood biomass was assessed by comparing the soil and wood pools of nutrients. In order to estimate the nutrient content of the charred wood, we calculated the dry wood biomass using specific equations developed by Montero *et al.* (2006) and implemented by the INIA in the calculation tool cubiFOR (CeseFor, see http://cubifor.cesefor.com/, accessed 22 December 2011). For each experimental site, the means of dasometric variables (tree density, diameter at breast height and tree height; Table 1) were used in specific equations according to the dominant pine species. The fraction of needles and twigs <2 cm was not considered, because this fraction was consumed during the wildfire. The resultant values of total aboveground biomass per area and the wood nutrient concentrations (Table 2) allowed the estimation of the nutrient content per area of the wood pool for each site.

Table 2.   Nutrient concentrations in the partially charred wood in the four study sites

Values represent means ± standard errors. Different lowercase superscript letters indicate significant differences among means for sites (Tukey *post-hoc* test after one-way ANOVAs). *F*, value of the statistic; *P*, critical probability

Nutrients in wood	Site				*F*	*P*
	1	2	3	4		
C (%)[A]	50.49 ± 0.08	50.60 ± 0.08	50.63 ± 0.07	50.37 ± 0.07	2.46	0.0645
N (%)	0.163 ± 0.004[a]	0.187 ± 0.006[b]	0.189 ± 0.005[b]	50.155 ± 0.005[a]	11.84	≤0.0001
C : N[A]	320.45 ± 8.75[a]	284.77 ± 10.29[b]	278.65 ± 9.29[b]	342.8 ± 12.99[a]	10.03	≤0.0001
N : P[A]	18.90 ± 1.58[a]	20.04 ± 1.33[a,b]	22.54 ± 1.42[b]	28.89 ± 1.60[c]	14.02	≤0.0001
P (ppm)	99.74 ± 5.17[a]	105.42 ± 5.82[a]	91.49 ± 3.55[a]	58.74 ± 2.48[b]	25.95	≤0.0001
Ca (ppm)[A]	622.48 ± 43.54[a]	710.05 ± 48.27[a]	627.32 ± 35.37[a]	438.16 ± 19.61[b]	10.11	≤0.0001
Mg (ppm)	264.56 ± 11.57[a]	264.98 ± 10.12[a]	233.69 ± 9.49[a]	186.98 ± 9.47[b]	13.36	≤0.0001
K (ppm)[B]	575.00 ± 36.75[a]	504.31 ± 27.15[a]	359.33 ± 18.47[b]	203.19 ± 13.51[c]	54.68	≤0.0001
Na (ppm)[B]	69.39 ± 4.58[a]	50.83 ± 2.46[a,b]	40.32 ± 2.56[b,c]	31.03 ± 2.38[c]	19.67	≤0.0001
Fe (ppm)[B]	12.56 ± 2.03[a]	7.82 ± 1.26[a,b]	7.14 ± 1.21[a,b]	4.85 ± 1.02[b]	3.912	0.0097
Mn (ppm)[A]	29.79 ± 2[a]	30.00 ± 1.58[a]	43.39 ± 2.36[b]	67.04 ± 3.25[c]	43.65	≤0.0001
Zn (ppm)[A]	4.63 ± 0.52	4.62 ± 0.49	5.302 ± 0.56	3.870 ± 0.51	0.52	0.6711
Cu (ppm)	1.17 ± 0.07[a]	1.56 ± 0.09[b]	1.35 ± 0.09[a,b]	1.14 ± 0.07[a]	5.67	0.001

[A]Log-transformed data before ANOVA tests.
[B]Square-root-transformed data before ANOVA tests.

Table 3.   Main soil parameters of the study sites

Values represent means ± standard errors. CEC, cationic exchange capacity; SOM, soil organic matter; ρ, bulk density. Different lowercase superscript letters indicate significant differences among means for sites (Tukey *post-hoc* test after one-way ANOVAs, Nemenyi test after Kruskal–Wallis tests for texture and mineralogy). *F/H*, value of the statistic; *P*, critical probability

Soil parameter	Site				*F/H*	*P*
	1	2	3	4		
Soil type[A]	Haplic phaeozems	Haplic phaeozems	Haplic phaeozems	Humic cambisols and haplic phaeozems		
ρ (g cm^{-3})[B]	1.25 ± 0.06	1.34 ± 0.07	1.15 ± 0.06	1.18 ± 0.04	2.15	0.1006
Texture (%)	Sandy loam	Sandy loam	Sandy loam	Sandy loam		
Sand (0.05–2 mm)	59.4 ± 2.4	58.9 ± 3.2	69.0 ± 0.1	69.1 ± 0.7	8.44	0.0378
Coarse loam (0.02–0.05 mm)	10.6 ± 0.8[a,b]	11.9 ± 0.7[a]	9.7 ± 0.4[a,b]	7.3 ± 0.2[b]	8.44	0.0378
Fine loam (0.002–0.02 mm)	15.2 ± 0.7	16.7 ± 1.3	12.5 ± 0.4	13.6 ± 0.5	8.95	0.0300
Clay (<0.002 mm)	14.8 ± 0.9[a]	12.5 ± 1.5[a,b]	8.8 ± 0.3[b]	10.0 ± 0.3[a,b]	8.74	0.0329
Mineralogy (%)						
Quartz	17 ± 3	20 ± 3	17 ± 2	19 ± 2	1.31	0.7273
Clorite (Clinoclore)	4 ± 0.2	3 ± 1	16 ± 3	19 ± 2	8.43	0.0378
Muscovite	51 ± 2	43 ± 4	44 ± 2	50 ± 1	4.53	0.2089
Paragonite	15 ± 1[a,b]	18 ± 2[a]	12 ± 2[a,b]	7 ± 1[b]	9.15	0.0273
Feldespat (Albite)	13 ± 2[a,b]	15 ± 2[a]	10 ± 1[a,b]	5 ± 0.5[b]	8.08	0.0444
pH[C]	7.27 ± 0.04[a]	7.28 ± 0.05[a]	6.71 ± 0.08[b]	5.58 ± 0.10[c]	83.66	≤0.0001
SOM (%)[B]	3.34 ± 0.19[a]	3.32 ± 0.18[a]	3.57 ± 0.18[a]	6.04 ± 0.17[b]	48.79	≤0.0001
CEC (cmol$_+$ kg^{-1})	5.59 ± 0.26[a]	5.31 ± 0.31[a]	4.63 ± 0.31[a]	8.19 ± 0.27[b]	29.71	≤0.0001

[A]Soil types according to the soil map: Lanjarón 1 : 100 000. LUCDEME Project (Delgado Calvo-Flores *et al.* 1993).
[B]log-transformed data before ANOVA tests.
[C]Exponential-transformed data before ANOVA tests.

The nutrient content in the upper-10-cm soil layer was calculated using the bulk density for each site (Table 3) and the nutrient concentrations in the soil (Table 4). The N in the soil pool was referred to the extractable inorganic fraction (NH_4^+ + NO_3^-), because it is broadly accepted that this is the most relevant direct N source for plant nutrition in most of the cases (Killham 1994), whereas direct evidence that organic N contributes significantly to plant N nutrition is still lacking (Näsholm *et al.* 2009).

Data analysis

The differences in nutrient concentrations in wood and soil were analysed with one-way analysis of variances (ANOVAs), with site as the independent factor. The comparison of mean nutrient concentrations between sites was further analysed with Tukey HSD post-hoc tests. Differences in textures and mineralogy between sites were similarly analysed using a non-parametric Kruskal–Wallis test, and, in cases of significant differences, Nemenyi post-hoc tests of multiple comparisons of means

Table 4.   Soil nutrient concentrations in the four study sites

Values represent means ± standard errors. V, percentage of saturation of bases ; C_{tot} and N_{tot}, soil C and N referred to total concentrations. Different lowercase superscript letters indicate significant differences among means for sites (Tukey *post-hoc* test after one-ways ANOVAs). *F*, value of the statistic; *P*, critical probability; $cmol_+ kg^{-1}$, centimoles of positive charges per kilogram of soil

Element	Site				*F*	*P*
	1	2	3	4		
C_{tot} (%)[C]	1.05 ± 0.11^a	1.17 ± 0.10^a	1.30 ± 0.13^a	2.98 ± 0.09^b	44.63	≤0.0001
N_{tot} (%)[C]	0.06 ± 0.01^a	0.07 ± 0.01^a	0.09 ± 0.01^b	0.20 ± 0.01^c	73.49	≤0.0001
C : N[C]	16.36 ± 0.72^a	17.42 ± 0.68^a	13.32 ± 0.68^b	$14.65 \pm 0.68^{a,b}$	6.77	0.0004
NH_4^+ (ppm)[A]	2.52 ± 0.80	3.10 ± 0.82	3.66 ± 0.85	2.62 ± 0.88	0.39	0.7591
NO_3^- (ppm)[A]	0.81 ± 0.24	1.17 ± 0.35	1.47 ± 0.28	2.14 ± 0.44	2.69	0.0521
$N_{inorg} : N_{tot}$ (%)	0.63 ± 0.18	0.80 ± 0.25	0.54 ± 0.12	0.23 ± 0.06	2.12	0.1054
P_{inog} (ppm)[A][C]	$4.96 \pm 1,25^{a,b}$	1.87 ± 0.15^c	$2.64 \pm 0.38^{b,c}$	5.40 ± 0.59^a	10.12	≤0.0001
Ca ($cmol_+ kg^{-1}$)[B]	3.24 ± 0.24^a	3.14 ± 0.23^a	1.70 ± 0.23^b	$2.40 \pm 0.23^{a,b}$	9.13	≤0.0001
Mg ($cmol_+ kg^{-1}$)[B,D]	1.31 ± 0.07^a	1.04 ± 0.06^a	0.65 ± 0.06^b	0.72 ± 0.06^b	20.97	≤0.0001
K ($cmol_+ kg^{-1}$)[B]	0.019 ± 0.002	0.022 ± 0.001	0.018 ± 0.001	0.023 ± 0.001	2.05	0.1141
Na ($cmol_+ kg^{-1}$)[B]	0.0021 ± 0.0007	0.0022 ± 0.0007	0.0012 ± 0.0007	0.0017 ± 0.0007	0.49	0.6900
V (%)	81.81 ± 5.40^a	82.60 ± 5.12^a	55.62 ± 5.12^b	38.89 ± 5.12^b	16.93	≤0.0001
Fe (ppm)[B]	0.060 ± 0.029	0.089 ± 0.034	0.091 ± 0.034	0.025 ± 0.015	1.18	0.3227
Mn (ppm)[B,D]	0.37 ± 0.08^a	0.36 ± 0.05^a	$0.65 \pm 0.09^{a,b}$	0.95 ± 0.17^b	6.25	0.0008
Zn (ppm)[B]	0.026 ± 0.010	0.025 ± 0.008	0.032 ± 0.009	0.009 ± 0.005	1.46	0.2321
Cu (ppm)[B]	0.015 ± 0.007	0.017 ± 0.008	0.014 ± 0.007	0.005 ± 0.005	0.55	0.6484

[A]Extractable concentrations.
[B]Exchangeable concentrations.
[C]log-transformed data before ANOVA tests.
[D]Square-root-transformed data before ANOVA tests.

among sites were performed (Zar 2010). Additionally, correlations between all nutrients were explored separately for the wood and for the soil using Pearson product-moment correlations. The correlation between the mean concentration per site of each nutrient in the soil and in the wood was also explored by the same method. A principal component analysis (PCA) was also performed for nutrients in wood and soil. For this, a correlation matrix with standardisation of variables was used. Further, differences between experimental sites according to the first component scores obtained in the PCA were tested with a one-way ANOVA and Tukey HSD post-hoc tests (Jolliffe 2002; Quinn and Keough 2009).

Data were log- or square-root-transformed when required before the implementation of parametric statistical analyses (ANOVA's, Pearson's correlations and PCA) to improve normality and homoscedasticity (Quinn and Keough 2009). Statistical analyses and models were made with JMP 7.0 software (SAS Institute). In the results that follow, mean values are followed by ±1 s.e.

Results

Wood nutrient concentrations

All nutrient concentrations in wood differed between sites, except Zn and C (Table 2). N was more concentrated in sites 2 and 3, so that the C : N ratio in the wood was lower in these sites (Table 2). The concentrations of P, Ca and Mg were lowest in site 4. The patterns of K, Na and Fe were similar, becoming also lower as altitude increased (Table 2). However, the Mn concentration showed the opposite trend, increasing at higher

elevations (Table 2). Cu was lowest in sites 1 and 4, and highest in site 2 (Table 2).

Strong correlations were found between the N, P and the majority-components of the wood; Ca, Mg and K being positive in all cases (Table A1). These were especially important between K and each of P, Na and Mg ($r = 0.75, 0.59$ and 0.54, $P < 0.0001$ in all cases) and between P and Na ($r = 0.51$, $P < 0.0001$, Table A1). High positive correlations were also found between Mg and each of Ca, Na and P ($r > 0.36$, $P < 0.0001$), and between Fe and each of Cu and Zn ($r > 0.33$, $P < 0.0001$). Additionally, Mn was inversely correlated with K ($r = -0.39, P < 0.0001$, Table A1).

The study sites showed some gradual differences according to the principal components of the wood composition. The first and second principal components obtained in the PCA explained respectively 29.6 and 16.1% of the total variance (Fig. 2a, b). K, P and Mg contributed more to the first component and Zn, C and N to the second (Fig. 2a). According to the first component, site 4 had the lowest scores, and thus, the lowest concentrations of K, P, Mg and highest of Mn. This site was followed by site 3 and then sites 1 and 2, with the latter two not showing any significant difference (one-way ANOVA; $P < 0.0001$; Fig. 2a, b).

Soil parameters and nutrient concentrations

Experimental sites had lower pH values with increasing altitude, whereas SOM and CEC were the highest at the most elevated site (Table 3). Soil nutrient concentrations differed significantly between experimental sites in the case of C_{tot}, N_{tot}, P_{inorg}, Ca, Mg and Mn (Table 4). C_{tot} and N_{tot} showed the same pattern as SOM, being highest at the most elevated site, with the same
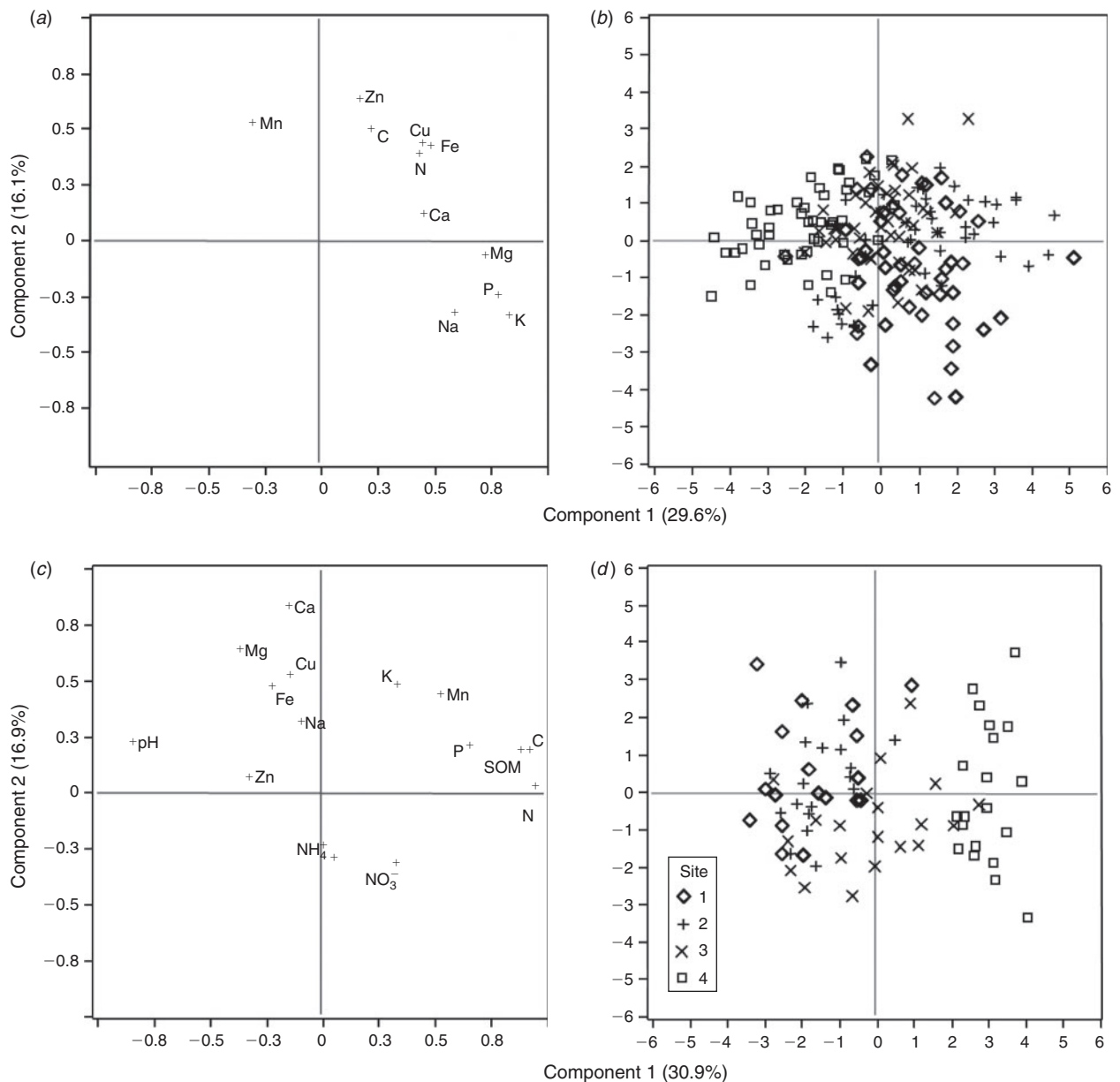
Fig. 2. Principal component analysis (PCA) of wood nutrient concentrations (*a* and *b*), and soil nutrient concentrations (*c* and *d*) in the four different study sites. For an easier visualisation, only the two first principal components are represented. The percentage of contribution to the total variability is between parentheses. (*a*) and (*c*) show the relative contribution of each individual variable to the first two principal components; (*b*) and (*d*) show the value assigned to each wood sample according to these two components. Data were previously log- or square-root-transformed when required to improve normality and homoscedasticity (see footnotes in Tables 3, 4).

tendency for NO_3^- (Tables 3, 4). The C : N ratio in soil was highest in sites 1 and 2 and lowest in site 3 (Table 4). Most of the N in the soil was organic and only ∼0.54% was inorganic. The P_{inorg} was lowest in site 2 and highest in site 4 (Table 4). The exchangeable Ca and Mg showed similar patterns between experimental sites, being higher in sites 1 and 2 (Table 4). Despite the absence of significant differences, Fe, Cu and Zn tended to be lowest at the most elevated site. Mn showed the opposite pattern, increasing with the elevation (Table 4).

The pH, SOM, CEC, C_{tot} and N_{tot}, P_{inorg} and Mn were strongly correlated (Table A2). For the pH, these correlations

were negative ($r < -0.35$, $P < 0.001$ in all cases, Table A2). Ca and Mg were also highly correlated with pH, but positively so ($r > 0.40$, $P < 0.001$ in both cases, Table A2). Also meaningful were the correlations between NO_3^- and NH_4^+ ($r = 0.75$, $P < 0.0001$), Fe and Cu ($r = 0.59$, $P < 0.0001$), and between K and each of C_{tot} and P_{inorg} ($r > 0.39$, $P < 0.001$ in both cases, Table A2).

Some of the study sites could be even more clearly differentiated by their soil nutrients and edaphic parameters than by the wood nutrients, according to the principal components obtained in the PCA (Fig. 2*c*, *d*). The first and second principal

components explained 30.9 and 16.9% of the total variance (Fig. 2*c, d*). The concentrations of N, C, SOM and pH contributed more to the first component, whereas Ca and Mg were the variables that contributed more to the second component (Fig. 2*c*). According to the first component, site 4 had the highest scores, and therefore, the highest concentrations of N, C, SOM and lowest pH. It was followed by site 3, and then sites 1 and 2, without significant differences between these latter two ($P < 0.0001$; one-way ANOVA; Fig. 2*c, d*).

The correlation between the concentration in soil and in wood was significant in the case of both Mn ($r = 0.99$, $P = 0.0078$) and Zn ($r = 0.92$, $P = 0.0787$).

Discussion

The results of this study highlight the potential of post-fire wood biomass as a nutrient source for natural forest regeneration. Two years after the wildfire, soils in the study area showed low nutrient availability, although they varied among study sites likely due to differences of mineralogy and microclimate. On the other hand, the relative potential contributions of the wood pool were high, due to the low soil nutrient availability, the concentrations of these elements still present in the wood after the fire, and the high biomass of charred wood remaining. Moreover, the relative importance of the post-fire wood biomass as a reservoir of nutrients for the ecosystem was quite consistent across study sites, regardless of the differences in soil and wood nutrient concentrations, soil characteristics and wood biomass remaining after the wildfire.

Soil nutrient concentrations

Overall, soil nutrient concentrations in this study were lower than those reported for other soils in the area (Sánchez-Marañón *et al.* 1996) and in other Mediterranean pine forests (De Marco *et al.* 2005; Fierro *et al.* 2007; Blanco *et al.* 2008; Yildiz *et al.* 2010). This may be due to several reasons such as nutrient losses associated with organic layer combustion by the wildfire (DeBano and Conrad 1978; Raison 1979; Certini 2005) and the recurrent history of degradative land use in the area (Padilla *et al.* 2010). The pre-fire existence of a pine forest with a litter input of high C : N ratio and difficult mineralisation could also have contributed to soil acidification and low nutrient availability (van Wesemael 1993; Moro and Domingo 2000; Oyonarte *et al.* 2008), particularly in the case of the inorganic forms of N for plant assimilation. The low pool of nutrients found in the soil is likely insufficient to meet the annual requirements of a mature coniferous forest for available inorganic N ($\sim$40 kg ha^{-1} year^{-1}), K ($\sim$25 kg ha^{-1} year^{-1}), Zn ($\sim$0.14 kg ha^{-1} year^{-1}), Fe ($\sim$0.18 kg ha^{-1} year^{-1}), and to a lesser degree, of P ($\sim$4 kg ha^{-1} year^{-1}) and Mn ($\sim$0.85 kg ha^{-1} year^{-1}). However, despite their low concentrations in this siliceous soil, Ca and Mg were not limiting (Cole and Rapp 1981; Miller 1986; Johnson and Lindberg 1992; Helmisaari 1995; Merino *et al.* 2005).

Among sites, available or exchangeable soil nutrients were driven by differences in pH and SOM, as a result of the different lithology and microclimate, and to a lesser degree by weathering of the parent material and soil development. As altitude increases, temperatures are lower and the lithology becomes more acidic. These factors explain the lower pH found at highest altitudes and the highest SOM, provided the slower mineralisation and prevalence of humification processes (Bohn *et al.* 1993; Silver 1998). The higher SOM determined, in turn, a higher CEC and total C and N at the highest site. Furthermore, the $N_{inorg} : N_{total}$ ratio was also consistent with the greater predominance of humification. The contrasting effects of the decrease in pH and the highest CEC at the most elevated site explains the decreasing pattern of the base saturation with altitude (Porta *et al.* 2003). Similarly, CEC and pH also modulate the pattern of available inorganic P. Phosphorous becomes insoluble at medium–high pH, leading to precipitation mainly with Ca, Mg and Fe. Consequently, P concentrations were highest at the most elevated site due to the highest solubility of phosphates at acid pH and the higher retention capacity of the soil (Porta *et al.* 2003). By contrast, acidity increases the Mn solubility and availability (Godo and Reisenauer 1980), and reinforces the retention of NO_3^- anions by the protonated surfaces of colloids (Ashman and Puri 2002). In addition, the tendency toward lower Cu, Fe and Zn availability at the highest site is likely due to lesser release from a not very weathered parent material. The young nature of these soils is in fact evidenced by the greater presence of easily weatherable clorite minerals at this site (Troeh and Thompson 2005).

Wood nutrient concentrations

The essential nutrients found in charred stemwood are within the range of the concentrations reported in other studies for unburnt pine wood for most of the nutrients analysed. Nonetheless, the mean concentrations of N in pine wood found in this study (0.17%, all sites pooled) exceed the range of values reported in the literature for the same species (0.05–0.15%; Alriksson and Eriksson 1998; Augusto *et al.* 2000, 2008*b*; Merino *et al.* 2005; Palviainen *et al.* 2010*a*). The P concentrations here averaged 89.2 ppm, within the range of values (45–180 ppm) reported in other studies. Similarly, Ca, Mg and K averaged here 605.47 ppm, 238.35 ppm and 413.36 ppm, compared with the ranges of 500–1100 ppm, 100–300 ppm and 250–1000 ppm found for the same elements in the literature (Alriksson and Eriksson 1998; Augusto *et al.* 2000, 2008*b*; Merino *et al.* 2005; Palviainen *et al.* 2010*b*). Nutrient concentrations present in the large wood fractions are therefore still relatively high in comparison with unburnt wood, likely due to the fact that the effects of fire are usually limited to the bark and small fractions of the tree, even in intense stand-replacing fires (Wei *et al.* 1997; Stocks *et al.* 2004).

However, the concentrations of Fe, Mn, Zn, Cu and Na were very low compared with those found in unburnt wood (Harju *et al.* 1997; Alriksson and Eriksson 1998; Saarela *et al.* 2002; Merino *et al.* 2005). This is likely due to their limited availability in soil (see above). This is also supported by the similar patterns across sites of Mn, Zn and Cu both in the wood and in the soil, and by the correlations found between the concentrations in wood and soil in the case of Mn and Zn. The same thing occurred between the N in wood and NH_4^+ in soil, suggesting a limitation of a source of available N in the soil. Thus, nutrients in wood tended to reflect their availability in the soil, being therefore lower at the most elevated sites, although
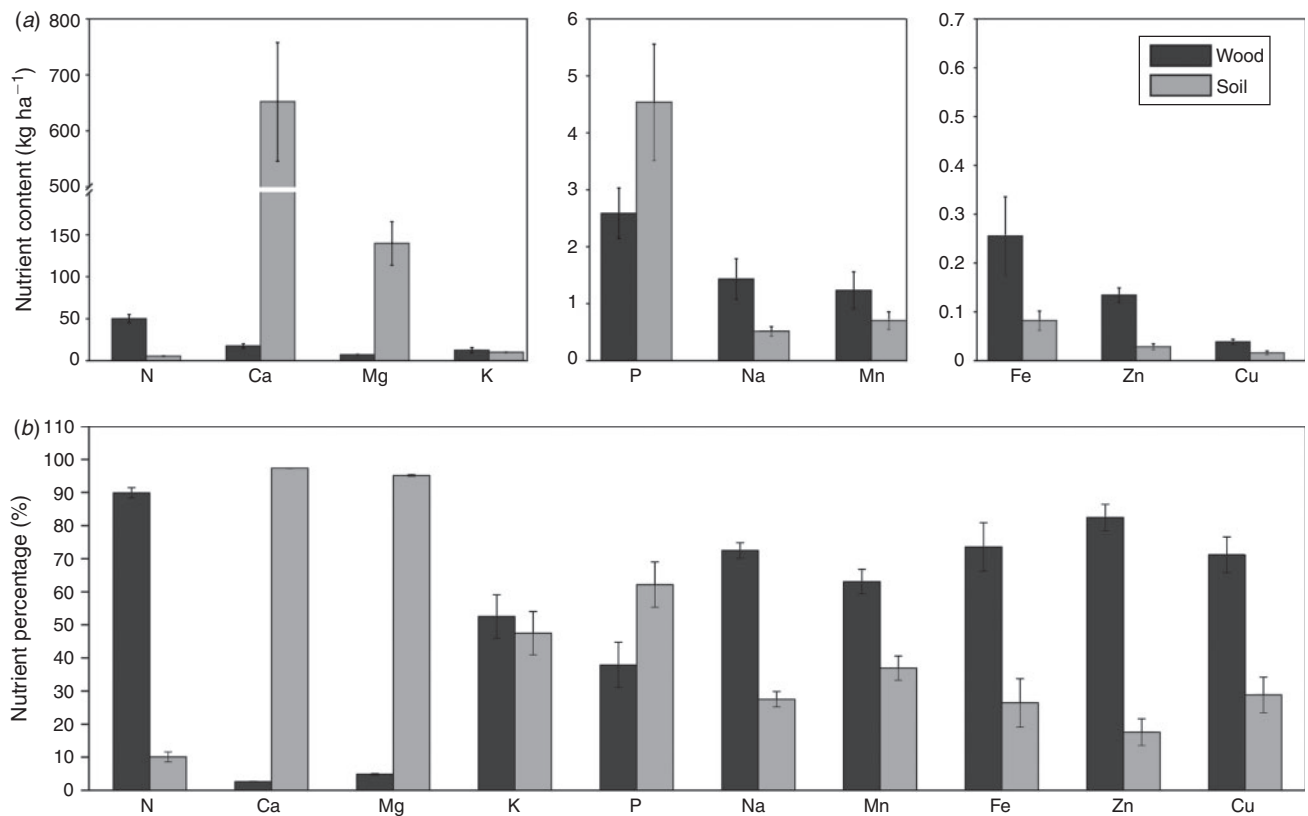
Fig. 3. Nutrient reservoir in the charred wood and soil pools: (*a*) nutrient content in the aboveground wood biomass left after the wildfire and in the upper-10-cm soil layer; (*b*) nutrient percentage relative to the total content in the wood and soil pools. Nitrogen in the soil pool is referred to the extractable inorganic fraction ($NH_4^+ + NO_3^-$). Needles and branches <2 cm were excluded due to their total combustion during the fire. Values of nutrient content are the mean of the four experimental sites, standard errors are represented above each bar. Note in (*a*) the different scale of each graph and the breaks in Ca for better visualisation.

others factors like the differences in composition among the dominant pine species could be also influential (Alriksson and Eriksson 1998; Augusto *et al.* 2000, 2008*b*; Baumann *et al.* 2006).

Relative magnitude of the nutrient reservoir in post-fire woody debris

During a high-severity wildfire, nutrients contained in fine nutrient-rich vegetal fractions, such as leaves and twigs, are mostly volatilised (Trabaud 1994; Johnson *et al.* 2005). However, our results show that a relatively high nutrient concentration was still present in charred wood and that large amounts of biomass remained after the wildfire. Fig. 3 shows the nutrient reservoir contained in soil and aboveground charred wood biomass and the ratio between these two components. The magnitude of the nutrient pools in the post-fire remaining wood was highly relevant from a biochemical perspective. As an example, the estimated N and P reservoirs represented by charred wood remaining (49.9 kg ha^{-1} and 2.6 kg ha^{-1}, Fig. 3) would be comparable to their respective inputs through atmospheric deposition for this area over 8 and 13 years (6.3 kg ha^{-1} year^{-1} of N and 0.2 kg ha^{-1} year^{-1} of P; Morales-Baquero *et al.* 2006). Similarly, the N in the wood pool would be equivalent to the estimated N input by fixation of ~1800

A. decorticans shrubs per ha in a similar Mediterranean ecosystem over at least 50 years (1 kg ha^{-1} year^{-1} of N; Moro *et al.* 1996). Moreover, the magnitude of the nutrient reservoir in the post-fire wood pool is likely even greater than that estimated, as the nutrient concentrations of branches (11% of the total aboveground biomass) are usually higher than those of stemwood (Alriksson and Eriksson 1998; Montero *et al.* 1999). In addition, this does not take into account the nutrient reservoir in belowground biomass (estimated as 34% of the total biomass for this study site) or the nutrient contributions by deposited ashes.

The relative contribution of the wood in relation to the soil pool was especially high in the case of N, Na, Mn, Fe, Zn and Cu, reaching wood : soil ratios up to 9 for N and from 2 to 5 in the case of the micronutrients (Fig. 3). The partially charred wood will therefore be especially suitable, helping to satisfy the requirements of these nutrients that were found insufficient in the soil. Moreover, the important contribution of micronutrients in charred wood biomass represents a sign of their suitable potential as a nutrient reservoir. Trees incorporate and concentrate these micronutrients in their biomass although they were very limited in the soil (Ingestad 1979; Clarkson and Hanson 1980; Chapin *et al.* 2002). As a result, a much greater total amount of these nutrients was contained in wood than in the first 10 cm of soil. In addition, overall the relative contributions of

charred wood remained quite constant among study sites and were independent of the different microclimate, mineralogy, pre-fire dominant species and wood biomass inventory. Nonetheless, we are aware of possible underestimation of soil nutrients because it is referred to the upper 10-cm soil layer. However, limiting nutrients for plants are mostly concentrated in the upper mineral layers (Jobbágy and Jackson 2001), so the relative contributions of each pool are not expected to vary substantially.

In summary, the results of this study show that the remains of partially charred wood biomass act as an important nutrient reservoir, which will provide a source of nutrients in the long term (Marañón-Jiménez and Castro 2012) and help to mitigate the nutrient losses associated with wildfire and post-fire management.

Management implications

Prior forest conditions (tree density, tree diameter and age class, degree of management, nutritional status, etc.), fire severity and post-fire intervention will strongly influence the magnitudes of nutrient pools in the charred wood after a wildfire. In spite of that, the appropriate management of charred woody material remains controversial (McIver and Starr 2001; Beschta *et al.* 2004; Lindenmayer *et al.* 2004, 2008; Donato *et al.* 2006). The results of this study can assist to implement post-fire measures designed to ensure the regeneration and natural sustainability of the ecosystem. Salvage logging (felling and removing charred trunks, often combined with the elimination of the remaining woody debris; McIver and Starr 2001; Beschta *et al.* 2004) is a widely applied management practice in forest ecosystems all over the world. This results in the removal of the nutrient pool contained in aboveground woody debris that could otherwise be reincorporated into the ecosystem biogeochemical cycle. Moreover, post-fire salvage logging represents in these cases an additional perturbation beyond the wildfire that usually exceeds the resilience and adaptation capacity of the ecosystem (Paine *et al.* 1998; Lindenmayer *et al.* 2008). The elimination of the potential nutrient incomes can hinder soil biogeochemical functioning (Marañón-Jiménez and Castro 2012), microbial mineralisation (Marañón-Jiménez *et al.* 2011) and vegetation productivity (Castro *et al.* 2011), thus retarding the capacity of such ecosystems to restore their carbon sink capacity (Serrano-Ortiz *et al.* 2011). For this reason, the biochemical effects of salvage logging also should be added to the considerations to be evaluated during decision making regarding the most suitable post-fire forest management strategy.

Conclusions

The partially charred wood remaining after a forest fire still contains great amounts of nutrients, and therefore represents a valuable reservoir as well as a potential source for the regenerating ecosystem in the longer term. In this study, the magnitude of these stocks was especially prominent in the case of N and the micronutrients Na, Mn, Fe, Zn and Cu, where stocks in the burnt wood were higher than those existing in the upper-10-cm soil layer. Moreover, the relevance of wood as a potential nutrient source coincided with those nutrients that were deficient to satisfy the requirements of a mature forest. Therefore,

the suitability of the remaining woody debris after fires for the nutrient capital of the ecosystem should be considered for post-fire management of burnt areas.

Supplementary material

The photographs of the general appearance of the study area 9 months after the wildfire are available in the Supplementary material, which is available from the journal online (see http://www.publish.csiro.au/?act=view_file&file_id=WF12030_AC.pdf).

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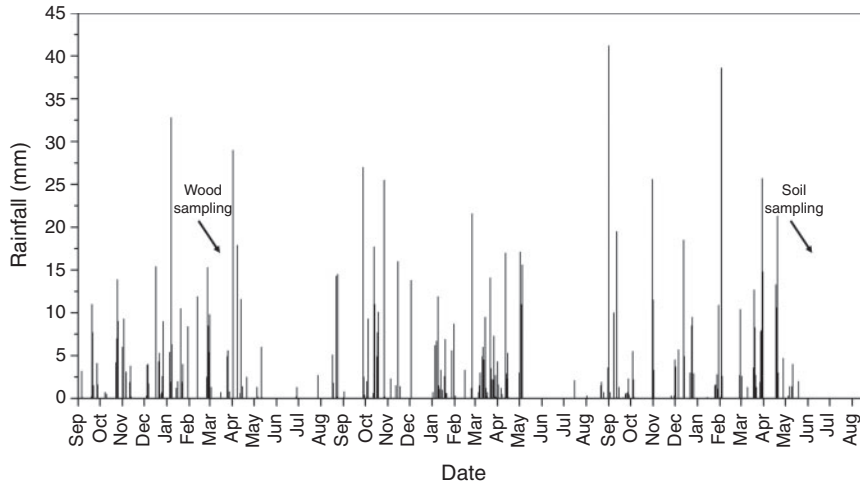
Appendix

Fig. A1. Rain events occurred 9 months after the fire. The graph shows the rainfall pattern between the fire and the collection date of wood samples (6 months after the wildfire) and soil samples (2 years after the wildfire). Data from a meteorological station beside the lowest site.

Table A1.   Pearson product-moment correlation coefficients between each pair of wood nutrients

Values indicate the coefficients of each correlation. Data from all sites are pooled. Critical probabilities of the correlations (P) are indicated: *, $0.01 < P \le 0.05$; **, $0.001 < P \le 0.01$; ***, $P \le 0.001$

Variable	C^A	N	P^B	Ca^A	Mg	K^B	Na^B	Fe^B	Mn^A	Zn^A	Cu
C^A	1										
N	0.26***	1									
P^B	−0.07	0.29***	1								
Ca^A	0.15*	0.25***	0.28***	1							
Mg	0.11	0.27***	0.43***	0.41***	1						
K^B	0.02	0.26***	0.75***	0.22**	0.54***	1					
Na^B	−0.01	0.08	0.51***	−0.06	0.36***	0.59***	1				
Fe^B	0.22**	0.06	0.19**	0.17*	0.28***	0.26***	0.24***	1			
Mn^A	−0.01	0.13	−0.23**	−0.25***	−0.23**	−0.39***	−0.13	0.04	1		
Zn^A	0.13	0.22**	0.03	0.01	0.02	0.02	−0.04	0.33***	0.18*	1	
Cu	0.24**	0.22**	0.33***	0.20**	0.23**	0.18*	0.13	0.36***	0.06	0.18*	1

[A]log-transformed data before ANOVA tests.
[B]Square-root-transformed data before ANOVA tests.

Table A2.   Pearson product-moment correlations coefficients between each pair of soil variables

Values indicate the coefficients of each correlation. Data of all sites are pooled. Critical probabilities of the correlations (P) are indicated: *, $0.01 < P \leq 0.05$; **, $0.001 < P \leq 0.01$; ***, $P \leq 0.001$

Variable	pH^A	SOM^B	CEC	C_{tot}^B	N_{tot}^B	NH_4^+	NO_3^-	P_{inorg}^B	Ca	Mg^C	K	Na	Fe	Mn^C	Zn	Cu
pH^A	1															
SOM^B	−0.67***	1														
CEC	−0.46***	0.81***	1													
C_{tot}^B	−0.70***	0.94***	0.78***	1												
N_{tot}^B	−0.78***	0.90***	0.69***	0.93***	1											
NH_4^+	0.05	0.03	−0.01	0.01	−0.02	1										
NO_3^-	−0.23*	0.33**	0.23*	0.29**	0.27*	0.75***	1									
P_{inorg}^B	−0.35**	0.55***	0.60***	0.62***	0.55***	−0.05	0.13	1								
Ca	0.41***	0.11	0.19	0.05	−0.13	−0.09	−0.08	0.06	1							
Mg^C	0.57***	−0.09	0.10	−0.18	−0.33**	0.02	−0.09	−0.01	0.78***	1						
K	−0.05	0.31**	0.25*	0.39***	0.34**	−0.02	0.01	0.40***	0.35**	0.25*	1					
Na	0.12	−0.04	−0.04	−0.10	−0.07	−0.09	−0.18	−0.10	0.24*	0.19	0.18	1				
Fe	0.20	−0.09	−0.13	−0.07	−0.15	0.03	−0.03	−0.11	0.30**	0.14	−0.10	0.04	1			
Mn^C	−0.37***	0.45***	0.35**	0.51***	0.46***	−0.11	−0.10	0.44***	0.11	−0.10	0.34**	0.10	0.18	1		
Zn	0.14	−0.25*	−0.14	−0.23*	−0.23*	−0.22*	−0.20	−0.15	−0.01	−0.03	−0.11	−0.12	0.24*	0.05	1	
Cu	0.11	0.01	0.06	0.04	−0.07	−0.20	−0.17	0.01	0.26*	0.21	−0.01	−0.10	0.59***	0.29*	0.35**	1

[A]Exponential-transformed data before ANOVA tests.
[B]log-transformed data before ANOVA tests.
[C]Square-root-transformed data before ANOVA tests.