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Post-fire wood management alters water stress, growth, and performance of pine regeneration in a Mediterranean ecosystem

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ABSTRACT

Extensive research has focused on comparing the impacts of post-fire salvage logging versus those of less aggressive management practices on forest regeneration. However, few studies have addressed the effects of different burnt-wood management options on seedling/sapling performance, or the ecophysiological mechanisms underlying differences among treatments. In this study, we experimentally assess the effects of post-fire management of the burnt wood on the growth and performance of naturally regenerating pine seedlings (*Pinus pinaster*). Three post-fire management treatments varying in degree of intervention were implemented seven months after a high-severity wildfire burned Mediterranean pine forests in the Sierra Nevada, southeast Spain: (a) "No Intervention" (NI, all burnt trees left standing); (b) "Partial Cut plus Lopping" (PCL, felling most of the burnt trees, cutting off branches, and leaving all the biomass on site without mastication); and (c) "Salvage Logging" (SL, felling the burnt trees, piling up the logs and masticating the fine woody debris). Three years after the fire, the growth, foliar nutrient concentrations, and leaf carbon, nitrogen and oxygen isotopic composition ($\delta^{13}C$, $\delta^{18}O$ and $\delta^{15}N$) of naturally regenerating seedlings were measured in all the treatments. Pine seedlings showed greatest vigor and size in the PCL treatment, whereas growth was poorest in SL. The nutrient concentrations were similar among treatments, although greater growth in the two treatments with residual wood present indicated higher plant uptake. Seedlings in the SL treatment showed high leaf $\delta^{13}C$ and $\delta^{18}O$ values indicating severe water stress, in contrast to significantly alleviated water stress indications in the PCL treatment. Seedling growth and physiological performance in NI was intermediate between that of PCL and SL. After six growing seasons, *P. pinaster* saplings in PCL showed greater growth and cone production than SL saplings. In summary, salvage logging has a detrimental effect on the ecophysiological performance and growth of naturally regenerating pine seedlings, compared to alternative post-fire management practices in which burnt logs and branches are left *in situ*. Improved seedling growth and performance is associated with the amelioration of microsite/microclimate conditions by the presence of residual burnt wood, which alleviates seedling drought stress and improves nutrient availability through the decomposition of woody debris.

1. Introduction

Fires severely burn large areas of forests every year in many parts of the world (FAO, 2007). After fire, active management is a common practice in order to restore the vegetation. To this end, it is customary for the local forest service (whether directly or through private contractors) to remove the burnt tree trunks from the site, a process that is referred to as salvage logging (SL) and that often involves the elimination of the remaining woody debris such as branches and snags by chopping, mastication, and fire. (Lindenmayer et al., 2008; McIver and Starr, 2000). Post-fire salvage logging is widely implemented worldwide for multiple reasons (Brown et al., 2003; Castro et al., 2010a; Lindenmayer and Noss, 2006; Lutz and Halpern, 2006; McIver and Starr, 2000). However, SL commonly renders a landscape devoid of most of the woody

Abbreviations: NI, No Intervention; SL, Salvage Logging; PCL, Partial Cut plus Lopping.

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biomass, leading to a simplification of the post-fire habitat structure (Bros et al., 2011; Lindenmayer et al., 2008). Despite being so widely implemented, post-fire salvage logging is currently a controversial issue among restoration ecologists and forest managers (Lindenmayer et al., 2008), as it can adversely affect a large set of ecosystem functions and processes such as plant or animal biodiversity (Beghin et al., 2010; Castro et al., 2010b; Lindenmayer and Noss, 2006; McIver and Starr, 2000), watershed runoff and erosion (Karr et al., 2004; Shakesby et al., 1996), nutrient cycling (Brown et al., 1996; Marañón-Jiménez and Castro, 2013), plant–animal mutualistic interactions (Castro et al., 2012; Cavallero et al., 2013; Rost et al., 2009), or carbon exchange with the atmosphere (Serrano-Ortiz et al., 2011; see Lindenmayer et al., 2008 for a review).

Salvage logging in particular can have major impacts on natural post-fire tree regeneration capacity. The felling and removal of burnt trees using ground-based yarding techniques may increase soil erosion and compaction (Fernandez et al., 2007; McIver and McNeil, 2006), thus precluding seedling emergence and establishment (Castro et al., 2011; Donato et al., 2006). Further, the tree seedling bank and/or resprouts already present (or starting to appear) at time of salvage operations can be damaged, thus reducing seedling density and regeneration capacity (Castro et al., 2011; Fernández et al., 2008; Greene et al., 2006; Martínez-Sánchez et al., 1999). In contrast to these potential negative impacts of salvage logging, the continued presence of residual logs, branches and other coarse woody debris in unsalvaged forests can encourage tree seedling recruitment in several ways. Coarse woody debris reduces solar radiation at the ground level, thereby decreasing soil heating and evaporation, and consequently helping to maintain soil moisture storage (Devine and Harrington, 2007; Martínez-Sánchez et al., 1999). In this way, the remaining burnt wood can act as nurse structures that promote seedling establishment (Castro et al., 2011). In addition, logs and other coarse woody debris represent a potentially important nutrient reservoir that can slowly be incorporated into the mineral soil by decomposition (Ganjegunte et al., 2004; Johnson et al., 2005; Marañón-Jiménez et al., 2013; Marañón-Jiménez and Castro, 2013; Ouro et al., 2001; Zhou et al., 2007), thus becoming available for the regenerating vegetation (Augusto et al., 2000; Stoddard et al., 2008). The presence of burnt wood left on site after a fire might therefore improve plant regeneration both by microclimatic amelioration as well as by improved nutrient supply.

Despite the strong negative effects that post-fire salvage logging may exert on plant regeneration and its other ecological implications, there are few studies addressing the underlying mechanisms that determine tree regeneration success as a function of post-fire management treatment. In this study, we seek to investigate: (1) the effects that residual burnt wood exerts on the growth and reproductive performance of pine seedlings/saplings naturally regenerating after a fire; and (2) the ecophysiological mechanisms underlying differences in plant performance resulting from different post-fire management treatments. In September 2005, the Lanjarón fire burned *ca.* 3500 ha in the Sierra Nevada Natural and National Park (SE Spain). Working in cooperation with the local Forest Service, we established a long-term study plot in an area dominated before the fire by maritime pine (*Pinus pinaster* Aiton), a serotinous pine that often regenerates abundantly after fire (Fernández et al., 2008; Fernandes and Rigolot, 2007). Three replicated treatments were established and they differed in both the amount and spatial structure of burnt wood left on site, ranging in intensity from no intervention to conventional salvage logging (see Castro et al., 2011). We monitored pine performance through the sixth growing season by measuring a combination of variables related to growth and reproduction. Three years after seedling establishment, we also measured leaf macro- and micro-nutrient concentrations, as well as the carbon, nitrogen and oxygen stable isotope ratios (^{13}C, ^{15}N and ^{18}O) of leaf dry matter.

The stable isotope composition of leaves can provide insight into plant water relations in water-limited ecosystems (Moreno-Gutiérrez et al., 2011; Querejeta et al., 2008; Ramírez et al., 2009). The carbon isotope composition of plant tissues ($\delta^{13}C$) provides a useful index for assessing intrinsic water-use efficiency, *i.e.* the ratio of photosynthetic carbon fixation to stomatal conductance (Dawson et al., 2002; Farquhar et al., 1989). Plant water stress can reduce both the photosynthetic rate (A) and stomatal conductance (g_s), although a comparatively sharper decrease of g_s normally boosts water-use efficiency ($WUE_i = A/g_s$) and $\delta^{13}C$ (Dawson et al., 2002; Farquhar et al., 1989). Leaf $\delta^{18}O$ can provide a time-integrated measure of plant stomatal conductance when other sources of variation (mainly differences in source water $\delta^{18}O$) are small (Barbour, 2007; Barbour et al., 2000, 2002; Farquhar et al., 2007; Moreno-Gutiérrez et al., 2011). The relationship between plant $\delta^{18}O$ and g_s is inverse, so that a lower $\delta^{18}O$ value indicates higher stomatal conductance. Since plant $\delta^{18}O$ is related to stomatal conductance but is not affected by photosynthetic rate, it can help separate the independent effects of A and g_s on $\delta^{13}C$ (Barbour, 2007). Therefore, simultaneous measurement of $\delta^{18}O$ and $\delta^{13}C$ in leaf material allows discrimination between biochemical and stomatal limitations to photosynthesis (Barbour et al., 2002; Grams et al., 2007; Keitel et al., 2003; Moreno-Gutiérrez et al., 2011; Querejeta et al., 2008; Scheidegger et al., 2000). Plants growing in fertile, N-rich forest sites tend to show high leaf $\delta^{15}N$ since they take up N that is enriched in ^{15}N. This is so because N losses from the system (by leaching after nitrification, or as gaseous N through denitrification) are depleted in ^{15}N, thus leaving the remaining available N for plants enriched in ^{15}N (Craine et al., 2009; Högberg, 1997; Högberg and Johannisson, 1993). Further, symbiotic ectomycorrhizal fungi are less crucial for plant N uptake in N-rich ecosystems, and the N taken up directly by the plant is comparatively more enriched in ^{15}N (Craine et al., 2009).

We hypothesized that burnt logs and branches left on site after the fire would improve microclimatic conditions for naturally regenerating seedlings through shading and sheltering effects (Hypothesis 1), and would also improve soil fertility in a medium to longer term through nutrient release by wood decomposition (Hypothesis 2). Reduced soil heating and soil moisture evaporation under the shelter of burnt trees and/or coarse woody debris can result in higher soil moisture retention (Castro et al., 2011). This would translate to reduced seedling water stress, which should be reflected in the carbon and oxygen isotopic ratios of their leaves (Hypothesis 3). Altogether, this should lead to poorer growth, vigor and overall performance of pine seedlings growing in salvaged areas compared to those growing in areas with coarse woody debris left on site after the fire (overall Hypothesis).

2. Material and methods

2.1. Study site and species

The study site is located in Sierra Nevada Natural and National Park (SE Spain), where a fire burned 1300 ha of pine forest (3420 ha in total) in September 2005. The site was a *P. pinaster* and *P. nigra* reforestation stand at 1395–1552 m a.s.l. (36° 57′ 9.89″N, 3° 29′ 36.24″ W), with a tree density (measured after the fire) of 1477 ± 46 individuals per ha and a basal trunk diameter of 17.7 ± 0.2 cm (mean ± SE; Castro et al., 2011). The site is located on a SW-oriented hillside (slope: 30.3 ± 5.7%) with micaschist as bedrock. Climate in the area is Mediterranean, with warm, dry summers and mild, rainy winters. Mean annual precipitation at the site is 500 ± 50 mm (1988–2011) and mean annual temperature is 11.8 ± 0.5 °C at 1652 m a.s.l. (State Meteorological Agency, period 1994–2011; Ministry of Environment).

P. pinaster Aiton grows in the western Mediterranean basin and Atlantic areas of the Iberian Peninsula and southern France, from sea level to 1700 m a.s.l. (Franco, 1986). It is a fast-growing species that has been widely used in reforestation planting, thus increasing its distribution area in the Mediterranean basin throughout the 20th century. It produces serotinous cones that protect the seeds from intense heat (Reyes and Casal, 2002). Seeds may still be viable after short heat pulses of above 100 °C (Martínez-Sánchez et al., 1995), and the regeneration of the species after fire relies mostly on the aerial seed bank. Abundant *P. pinaster* seedling regeneration occurred naturally in the area after the fire, with seedling emergence in late February 2006 (*ca.* 6 months after the fire; Castro et al., 2011).

2.2. Experimental design

From 21 April 2006 to 10 May 2006 (*ca.* seven months after the 2005 forest fire), the local Forest Service established a 17.8 ha plot with three randomly distributed replicates of three treatments that differed in their degree of post-fire burnt wood management:

(1) "Non Intervention" (NI), with no post-fire management, leaving all burnt trees standing.
(2) "Partial Cut plus Lopping" (PCL), a treatment where about 90% of burnt trees were cut and felled, with the main branches also lopped off, but leaving all the cut biomass (boles and branches) *in situ* on the ground; after treatment application, felled logs and branches covered 45% of the surface at 0–10 cm from the ground, 61% at 11–50 cm, and 9% at 51–100 cm (Castro et al., 2011).
(3) "Salvage Logging" (SL), where trees were felled and limbed with the use of chainsaws. Woody debris was masticated using a tractor and trunks were manually piled (groups of 10–15). The Forest Service planned to remove the piled trunks with a log forwarder in this SL treatment, but this step was later cancelled due to difficulties in precisely operating machinery within the spatial arrangement of the plots.

The three treatments differed in the degree of intervention (maximum in SL, intermediate in PCL, minimum in NI) and in the habitat structure generated (minimum habitat complexity in SL). The PCL treatment differed from NI in the above-ground habitat structure, including closer contact of burnt wood with the soil in PCL. The size of the resulting nine experimental replicates averaged 2.0 ± 0.2 hectares, with no significant differences in size between treatments (Kruskal–Wallis test, $P > 0.05$). All replicates were homogeneous in terms of orientation (SW), slope (*ca.* 30%) and bedrock (micaschist). The fire was moderate to high in intensity, consuming or totally scorching almost all tree crowns. Burnt trees in the NI treatment felled during the course of the first few post-fire years. The fallen fraction (measured in February of each year) was 0.0% in 2006 and 2007, 13.6 ± 2.7% in 2008, 92.7 ± 0.6% in 2009 and 99.8 ± 0.2% in 2010 (Castro et al., 2012). Accompanying post-fire vegetation was composed mainly of grasses and forbs, with a mean aerial cover in spring 2007 of 41.5 ± 2.4% for NI, 41.6 ± 2.7% for PCL, and 22.8 ± 1.2% for SL (data for non-annual species; Castro et al., 2010a).

2.3. Seedling growth

Seedling growth was monitored twice (2008 and 2012) in each experimental replicate. In September 2008 (after three growing seasons) we conducted a destructive sampling in order to measure seedling biomass as a growth variable. Twelve seedlings per experimental replicate (108 seedlings in total) were randomly selected, cut at ground level and brought to the laboratory. Herbivore damage was not detected in the area (see also Castro et al., 2011), and thus no seedling had to be discarded for this reason. For each seedling, we measured the following growth variables: (i) total height, (ii) leader-shoot elongation during the growing season of 2007 (measuring the length of the leader-shoot section produced in this season), (iii) leader-shoot elongation during the growing season of 2008 (measured in a similar way), (iv) basal trunk diameter, (v) total biomass, (vi) biomass of shoots produced in 2007, (vii) and biomass of shoots produced in 2008. Biomass was measured after oven-drying at 60 °C to constant weight (>48 h).

In January 2012 (after six growing seasons) we measured sapling growth in 20 randomly selected pines per experimental replicate (180 saplings in total). In each pine, we measured total height, leader-shoot elongation during the growing season of 2011, basal trunk diameter, and cone production (no cones were found in the pines at the time of the previous sampling in 2008).

2.4. Seedling nutrient concentrations

Carbon and nutrient concentrations (N, P, Ca, Mg, K, Na, Fe, Mn, Zn, and Cu) were measured in needles from the seedlings harvested in 2008. After drying, two subsamples of needles were taken from the leader-shoot sections corresponding to the elongations of 2007 and 2008 (leader-shoot elongation during the second and third year, respectively). The foliar material was ground with a ball-mill and homogenized. Foliar C and N concentrations were analysed by combustion at 850 °C with a Leco True Spec Autoanalyzer (St. Joseph, MI, USA). Ground samples were ignited to 750 °C and extracts were prepared by dry-ashing dissolution with HCl. From these extracts, P was determined by spectrophotometry with the molybdovanadate method (Association of Official Analytical Chemists (AOAC), 1975), 1975 with a Perkin Elmer 2400 spectrophotometer (Waltham, MA, USA). Concentrations of the other nutrients were measured in needles of the 2008 leader-shoot section only, by atomic absorption with a Perkin Elmer 5100 spectrometer.

2.5. Leaf isotopic analyses

Foliar $\delta^{13}C$, $\delta^{15}N$, and $\delta^{18}O$ were measured in needles from the 2008 leader-shoot section (third growing season after seedling emergence) using a subsample of ground material. Foliar $\delta^{13}C$ and $\delta^{15}N$ were measured in a micromass isotope ratio mass spectrometer GV Instruments Iso Prime (Youngstown, OH, USA) at the Stable Isotope Analysis Laboratory of University of Granada. Six standards were included for their analysis after every 7–8 samples. The repeated analysis of these standards consistently yielded a standard deviation <0.1‰. Foliar $\delta^{18}O$ was measured at the UC Davis Stable Isotope Facility, Davis, California (USA) using a Hekatech HT Oxygen Analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK), following the method described in Kornexl et al. (1999). Leaf samples were converted by pyrolysis in a glassy carbon reactor at 1400 °C to CO and H_2O, and oxygen was analysed as CO. The working standard for O isotopes analysis was microcrystalline cellulose at 30.5‰ versus V-SMOW. The repeated analysis of these standards consistently yielded a standard deviation <0.54‰. The stable isotope composition of plant material is presented in delta notation (δ), relative to a standard:

$$\delta = \left(\frac{R_{samp}}{R_{st}} - 1\right) \times 1000‰$$

where R is the molar ratio of the heavy to light isotopes ($R = {}^{13}C/{}^{12}C$, ${}^{15}N/{}^{14}N$ or ${}^{18}O/{}^{16}O$). R_{samp} refers to the sample and R_{st} to the international standards Vienna-Pee Dee Belemnite, atmospheric N_2 and Vienna Standard Mean Oceanic Water (V-SMOW) for C, N and O, respectively.

2.6. Data analysis

The effect of the treatments on pine seedlings was analysed for all variables using linear mixed models, with treatment as the fixed factor and replicate as a random factor nested within the treatment. Thus, the hierarchical model considered was:

$$Y_{ijk} = \mu + T_i + R(T)_{ji} + \varepsilon_{ijk}$$

where Y_{ijk} is the value of the dependent variable measured in the seedling ijk; μ is the general mean; T_i is the effect of the treatment; $R(T)_{ji}$ is the effect of replicates nested within each treatment, which accounted for the environmental variation within each treatment; and ε_{ijk} is the residual error not accounted for by the rest of factors included in the model. Contrasts were performed by the method of the restricted maximum likelihood (REML).

In the case of variables measured in the leader shoot elongated in both 2007 and 2008 (leader-shoot length, shoot biomass, and C, N, P concentrations) the analysis was performed separately for each year since we were interested in the effect of the treatments rather than in the pattern through time. Furthermore, several processes could be interacting throughout shoot growth (*i.e.* biomass gains in the following years after the shoot elongation, nutrient allocation, etc.), confounding the effects of climatic or environmental factors across years. The relationship between the nutrient concentrations in needles, their isotopic composition and the growth variables were also explored by Pearson product-moment correlations. Differences among treatments in the number of pines that reached maturity after 6 years was analysed using a contingency test, whereas the differences in the number of cones produced per tree were analysed with a Kruskal–Wallis test (pooling data of the three replicates per treatment).

Data were transformed when required to achieve 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.

3. Results

3.1. Growth and leaf nutrient content

Three growing seasons after emergence (September 2008), pine seedlings were significantly taller in the PCL and NI treatments than in SL (Table 1; Fig. 1). Total seedling biomass and basal trunk diameter tended to be higher in the PCL (85.34 ± 6.41 g and 11.87 ± 0.46 mm, respectively) than in NI (66.13 ± 6.23 g and 10.38 ± 0.40 mm, respectively) and SL (74.76 ± 6.57 g and 11.51 ± 0.38 mm, respectively), although these differences were not statistically significant (Table 1). Leader-shoot elongation and biomass production were also higher in the PCL and NI treatments than in SL (Table 1; Fig. 1) in 2008. The same pattern was found for the leader-shoot sections produced in the previous year (2007), although differences between treatments were not statistically significant at this earlier stage (Table 1; Fig. 1).

Six years after the fire (January 2012), pine saplings in the PCL treatment were significantly taller and also showed greater seasonal shoot elongation than those in the SL treatment (Table 1), whereas saplings in the NI treatment showed intermediate growth (Fig. 2). In addition, a higher proportion of saplings had reached the reproductive stage in PCL than in the other treatments (20% in PCL versus 4% in NI and SL; $P = 0.0009$). Cone production was also greater in PCL than in the other treatments ($P = 0.0004$; Fig. 2).

Foliar carbon and nutrient concentrations in the leaf cohorts produced during the second and third growing seasons after seedling establishment were not significantly affected by the treatments (Appendix A).

3.2. C, O and N isotope composition of pine needles

The C and O isotope ratios of pine needles of the 2008 cohort were significantly affected by the post-fire management treatments (Table 1, Fig. 3). Leaf $\delta^{13}C$ was highest in the SL treatment and lowest in the NI treatment, with intermediate values in PCL (Fig. 3). Leaf $\delta^{18}O$ was lower in PCL than in the other two treatments (Fig. 3). Within treatments, we found a strong positive correlation between leaf $\delta^{13}C$ and $\delta^{18}O$ in SL ($r = 0.51$; $P = 0.002$), and a weaker but still significant correlation in NI ($r = 0.32$; $P = 0.065$). By contrast, leaf $\delta^{13}C$ and $\delta^{18}O$ were uncorrelated in the PCL treatment ($r = 0.09$; $P = 0.617$). Leaf $\delta^{13}C$ was positively correlated with foliar N concentration ($r = 0.45$, $P = 0.006$) and with foliar P concentrations ($r = 0.44$; $P = 0.008$) in PCL, but not in the other treatments.

Across treatments, leaf $\delta^{13}C$ was negatively associated with seedling growth variables, including leader-shoot elongation ($r = -0.36$; $P = 0.0002$), total seedling height ($r = -0.29$; $P = 0.003$) and leader-shoot biomass ($r = -0.19$; $P = 0.048$). Leaf $\delta^{18}O$ was negatively associated with seedling growth variables as well, including leader-shoot biomass ($r = -0.33$; $P = 0.001$), total seedling biomass ($r = -0.25$; $P = 0.010$) and basal trunk diameter ($r = -0.21$; $P = 0.033$). Leaf $\delta^{15}N$ was strongly positively associated with foliar N concentration ($r = 0.52$; $P \leqslant 0.0001$), and, to a lesser extent, with foliar P concentration as well ($r = 0.35$; $P = 0.0002$). Leaf $\delta^{15}N$ correlated positively with growth variables such as total seedling height ($r = 0.32$; $P \leqslant 0.001$) and leader-shoot elongation ($r = 0.23$; $P \leqslant 0.017$). Mean leaf $\delta^{15}N$ values were highest in NI (1.03 ± 0.32), intermediate in PCL (0.76 ± 0.28) and the lowest in SL (0.19 ± 0.39), although differences among treatments were not statistically significant due to high within-treatment variability (Table 1).

4. Discussion

The results of this study highlight the key facilitative role that burnt wood can play during post-fire seedling regeneration. After three growing seasons, pine seedlings showed greater growth, vigor, and size in treatments where burnt wood was left on site after the fire. The benefits provided by the presence of burnt wood were clearly corroborated by large differences in sapling growth and reproductive capacity among post-fire management treatments after 6 years. Furthermore, the combined measurement of growth variables, leaf-nutrient concentrations, and isotopic ratios in naturally regenerating seedlings offered valuable insights into the potential ecophysiological mechanisms underlying the effects of different post-fire management treatments on tree regeneration.

4.1. Effect of burnt woody debris on seedling-water relations

Leaf $\delta^{13}C$ and $\delta^{18}O$ data strongly suggest a key role of burnt coarse woody debris in alleviating drought stress during pine seedling establishment. High foliar $\delta^{13}C$ and $\delta^{18}O$ values and a tight positive correlation between $\delta^{13}C$ and $\delta^{18}O$ (indicative of strong stomatal limitation of both photosynthesis and transpiration; Barbour et al., 2002; Grams et al., 2007; Scheidegger et al., 2000) indicate that pine seedlings were severely water stressed in the SL treatment. By contrast, seedlings in the PCL treatment were considerably less water stressed, as indicated by lower foliar $\delta^{13}C$

Table 1
Summary of treatment effects on the growth variables and foliar isotopic composition of the pine seedlings and pine saplings. Pine seedlings were harvested in 2008 (three growing seasons after the wildfire) and pine saplings were measured in 2012 (six growing seasons after the wildfire). The table shows the results of the contrast for the effects of the treatments (fixed factor) and the estimated percentage of the variance attributed to the random components of the model (replicate and residuals). *F*: values of the statistic. df: degrees of freedom of the numerator and denominator, respectively (constructed using the Kenward-Roger's method). *P*: critical probability for the treatment effect.

Sampling year	Variable	Treatment effect			% Variance of the total random components	
		F	df	*P*	Replicate	Residual
2008	Total biomass	0.87	2, 5.99	0.4643	17.74	82.26
	Total height	7.86	2, 6.00	0.0211	7.55	92.45
	Basal trunk diameter	1.00	2, 5.98	0.4211	20.44	79.56
	Leader shoot length 2007	3.37	2, 6.00	0.1046	5.24	94.76
	Leader shoot length 2008	14.80	2, 6.01	0.0047	−1.36	101.36
	Shoot biomass 2007	3.01	2, 6.00	0.1241	−0.80	100.80
	Shoot biomass 2008	8.71	2, 5.88	0.0175	0.29	99.71
	$\delta^{13}C$	10.43	2, 5.95	0.0113	15.84	84.16
	$\delta^{18}O$	7.18	2, 5.86	0.0265	4.13	95.87
	$\delta^{15}N$	0.36	2, 6.01	0.7116	31.63	68.37
2012	Total height	11.07	2, 6.00	0.0097	7.80	92.20
	Basal trunk diameter	2.35	2, 6.00	0.1767	21.77	78.23
	Leader shoot length 2011	6.01	2, 6.00	0.0369	7.98	92.02

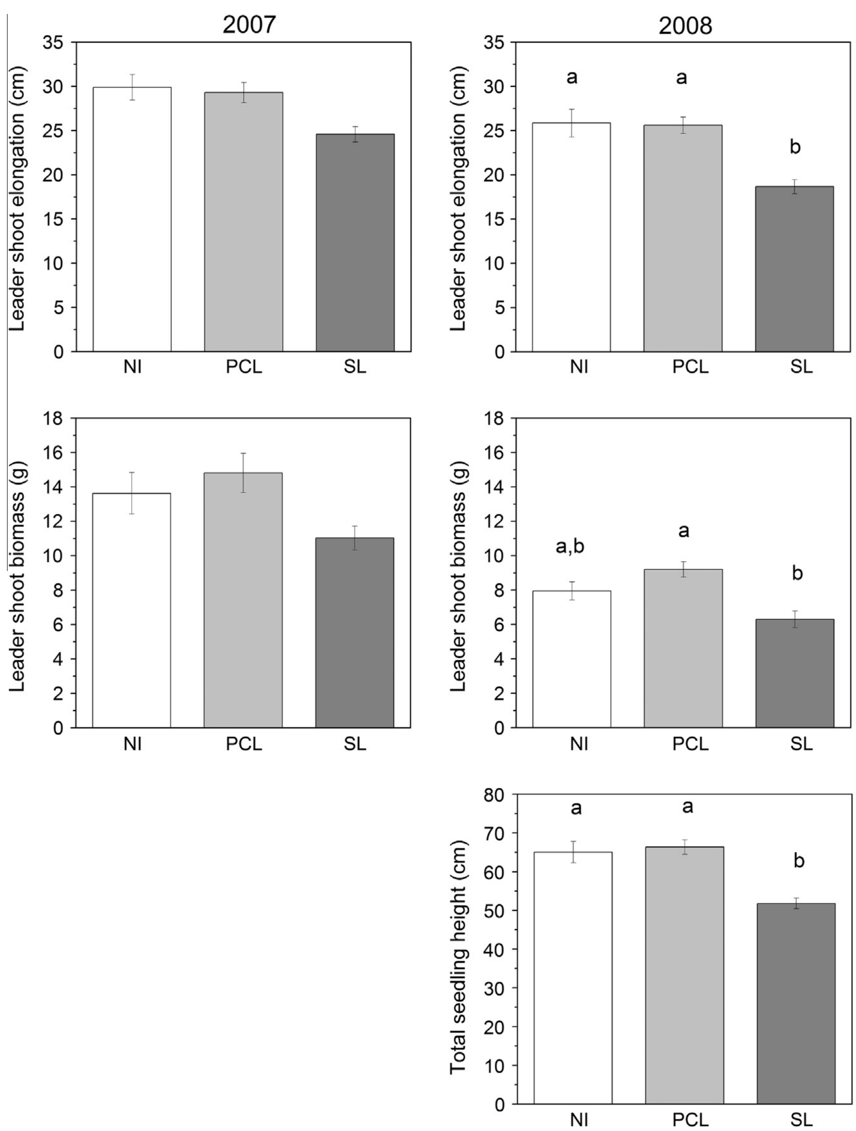

Fig. 1. Growth variables of the pine seedlings. Leader shoot growth during the second (2007) and third (2008) growing season after the wildfire (a–d) and total height in 2008 (three growing seasons after the wildfire) (e) in the different post-fire treatments of burnt wood. NI: non-intervention, PCL: partial cut plus lopping, SL: salvage logging. Different letters above bars indicate significant differences among treatments (Tukey HSD test after mixed ANOVAs).

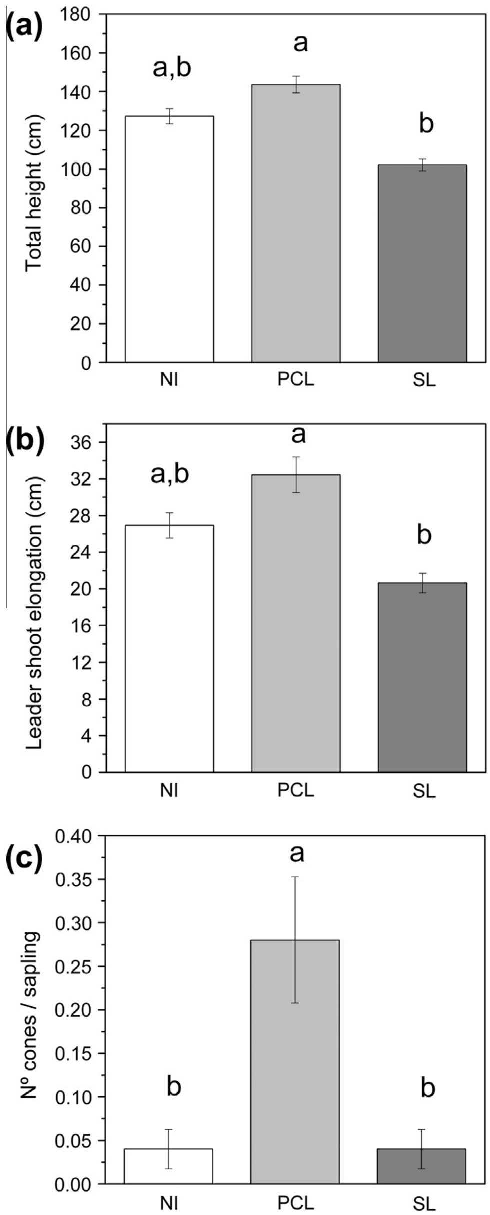

Fig. 2. Growth variables and cone production of the pine saplings. Annual growth (a), cone production (b) and total height (c) of the pines measured in 2012 (six growing seasons after the wildfire) in the different post-fire treatments of burnt wood. Annual growth was measured as the leader-shoot elongation during the previous growing season of 2011. NI: non-intervention, PCL: partial cut plus lopping, SL: salvage logging. Different letters above bars indicate significant differences among treatments (Tukey HSD test after mixed ANOVAs and Kruskal–Wallis test).

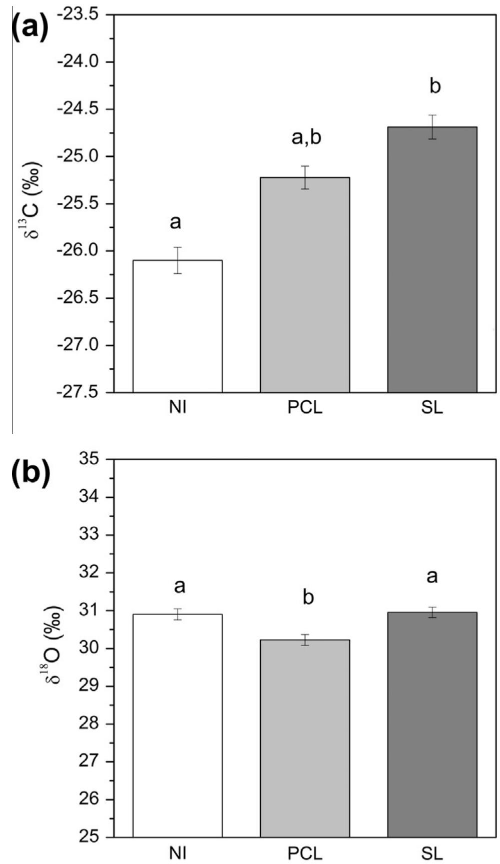

Fig. 3. Leaf isotopic composition of pine seedlings. Carbon (a) and oxygen (b) isotopic composition of pine seedling needles from the part of leader-shoot elongated in 2008 in the different post-fire treatments of burnt wood. NI: non-intervention, PCL: partial cut plus lopping, SL: salvage logging. Different letters above bars indicate significant differences among treatments, $P = 0.003$ and $P = 0.064$ for carbon and oxygen respectively (Tukey HSD test after mixed ANOVAs).

and δ^{18}O values and a lack of correlation between δ^{13}C and δ^{18}O values. Seedlings in the NI treatment showed intermediate results, with only weak correlation between leaf δ^{13}C and δ^{18}O. Closer proximity and contact between burnt woody debris and soil in PCL than in NI may have contributed to more effective microclimate amelioration and soil-moisture retention in the PCL treatment during the first years after the wildfire (Fontaine et al., 2010; Harmon et al., 1986; Maser and Trappe, 1984; Smaill et al., 2008), thus explaining the differences in seedling performance between these two treatments. In a previous paper, we reported that the presence of burnt logs, branches, and in general post-fire coarse woody debris, reduced solar radiation at ground level and soil temperature in the study area (Castro et al., 2011). This in turn reduces soil–water evaporation, and consequently increases soil–water availability for the establishing seedlings, which is especially relevant to warm dry sites with high solar radiation as in the present study (Mediterranean climate and SW aspect). The results of the present study provide insight into the ecophysiological mechanisms underlying the differential seedling responses to various post-fire management practices.

4.2. Effects of burnt woody debris on nutrient acquisition

The biogeochemical role of burnt wood also may have contributed to between-treatment differences in post-fire seedling performance. Burnt logs and woody debris represent a potential source of nutrients that are progressively released to the soil during decomposition (Ganjegunte et al., 2004; Marañón-Jiménez and Castro, 2013; Palviainen et al., 2010a, 2010b). In this sense, the trend towards higher leaf δ^{15}N in the unsalvaged treatment can denote an enhancement of N mineralization and, ultimately, a more active N cycling among soil, plants, and soil microorganisms (Craine et al., 2009) in treatments where burnt wood was left onsite. Moreover, although we found no significant differences in foliar nutrient concentrations among treatments, the larger biomass of seedlings in the unsalvaged treatments implies a higher total nutrient uptake. This suggests that the presence of burnt wood can also enhance the growth of naturally regenerating pine seedlings as a consequence of the improvement of soil fertility and nutrient availability (Marañón-Jiménez et al., 2013; Marañón-Jiménez and Castro, 2013). Notably, the above-mentioned absence of correlation between foliar $\delta^{13}C$ and $\delta^{18}O$ in the PCL treatment was accompanied by a strong positive correlation between $\delta^{13}C$ and foliar N concentration (which was not observed in the rest of the treatments). Then, for seedlings in the PCL treatment, higher $\delta^{13}C$ values point out to increased water-use efficiency as a result of enhanced carboxylative capacity and net photosynthetic rate, rather than reduced stomatal conductance as in the SL treatment (Dawson et al., 2002; Field and Mooney, 1986; Scheidegger et al., 2000).

Nutrient release from wood is, nonetheless, a relatively slow and incremental process that is limited by slow decomposition rates in water-limited ecosystems (Harmon et al., 1986; Marañón-Jiménez and Castro, 2013; Weedon et al., 2009). Thus, seedling growth stimulation by an enhanced nutrient supply from decaying wood is not expected to be substantial during the first years after the fire, but will increase in subsequent years as the decaying wood releases its nutrients. Our results support this hypothesis, as differences in pine growth among treatments (and particularly between PCL and SL) increased over time, ranging from non-significant two years after seedling emergence (leader-shoot elongation in 2007) to sharp differences after three or six years (2008 and 2011 data). The closer contact of wood with soil in PCL relative to NI during these first years in which dead trees were still standing could have contributed to greater seedling growth in PCL as a consequence of higher nutrient release and soil fertility (*e.g.* Marañón-Jiménez and Castro, 2013). Therefore, the results show that tree felling and rearranging post-fire woody debris over the ground surface may shift the positive role of residual wood earlier in time with PCL versus NI, but further study is needed to determine if this difference persists through time. In any case, the positive effects of the presence of burnt coarse woody debris from a biogeochemical perspective may increase over time for a number of years after fire, gaining relevance as wood slowly decomposes.

4.3. Burnt woody debris as nurse objects to facilitate seedling establishment

The results of this study support our working hypotheses, showing that burnt logs and branches left on site after the fire can improve pine seedling establishment and growth by both reducing water stress and increasing nutrient availability. In the context of facilitation theory, these inanimate structures act as nurse objects for pine seedlings (Castro et al., 2011). Facilitation is recognized as an ecological mechanism that improves seedling performance for at least one of the interacting species (Brooker et al., 2008; Callaway, 2007). However, the facilitative interaction must be considered the net result of both positive (*e.g.* amelioration of microclimatic conditions) and negative (*e.g.* above-ground or below-ground competition) forces acting between the counterparts (Callaway, 1998; Callaway and Walker, 1997; Cranston et al., 2012; Holmgren et al., 1997). Numerous studies support the idea that facilitation in water-stressed environments is driven by the amelioration of microclimatic conditions supplied by the canopy of nurse plants, despite a simultaneous negative below-ground effect of the root competition for water and nutrients (Armas and Pugnaire, 2009; Callaway, 1992; Franzese et al., 2009; Gómez-Aparicio et al., 2005; Maestre et al., 2003; Padilla and Pugnaire, 2008; Rey-Benayas, 1998). From this perspective, burnt coarse woody debris is particularly effective as nurse structures, as it provides the multiple benefits of improving microclimatic conditions without competition, while even increasing soil fertility through nutrient release. Previous studies in the same area have reported higher survival of both planted and naturally regenerating seedlings in the presence of burnt logs and branches scattered on the ground (PCL treatment; Castro et al., 2011; Leverkus et al., 2012). Positive effects of burnt coarse woody debris on seedling recruitment and survival have also been reported in other regions (Beghin et al., 2010; Brown et al., 2003; Coop and Schoettle, 2009; Donato et al., 2006; Harmon et al., 1986; Marzano et al., 2013). Moreover, foresters have planted tree seedlings under logs and stumps, snags, logs and rocks (*i.e.,* 'micro-siting') for a long time (Wisconsin Department of Natural Resources, 1990). In summary, burnt wood left on site after a fire, whether logs, branches, or coarse woody debris that might persist after post-fire human management, should be regarded as nurse objects with the potential to foster plant regeneration.

4.4. Management implications

The application of facilitation theory to promote natural forest regeneration or to increase ecological restoration success has advanced significantly in the last decade (Castro et al., 2002, 2006; Gómez-Aparicio et al., 2004; Padilla and Pugnaire, 2006). However, most of this research has focused on the use of live nurse plants that promote the establishment success of a target species (Brooker et al., 2008; Gómez-Aparicio, 2009; Padilla and Pugnaire, 2006), whereas little attention has been paid to inanimate natural nurse structures already present in the area to be restored. Recent studies have demonstrated the positive effects that inanimate objects can have for seedling survival and performance by ameliorating the microclimate and reducing runoff, thereby increasing plant-available water for seedlings (Harrington et al., 2013). Natural inanimate objects offering potential for facilitation include rocks, boulders, terrace risers (Carlucci et al., 2011; Coop and Schoettle, 2009; Peters et al., 2008; Resler et al., 2005; Munguía-Rosas and Sosa, 2008; Smit et al., 2008), piles of cut branches mimicking nurse canopies (Gómez-Aparicio et al., 2005; Padilla and Pugnaire, 2008), or even branches spread on the ground as a result of pruning activity (Castro et al., 2011; Harrington et al., 2013; Hastings et al., 2003; Jacobs and Gatewood, 1999; Stoddard et al., 2008). Moreover, the structural habitats provided by dead logs and branches in disturbed forest areas (whether from fire or other disturbances such as insect outbreaks, droughts, and windstorms) may attract animal seed dispersers, further increasing the positive effects on seedling recruitment (Carlucci et al., 2011; Castro et al., 2010b, 2012; Cavallero et al., 2013; Rost et al., 2009, 2010), and also potentially reducing herbivore damage to the regenerating vegetation (Relva et al., 2009; Ripple and Larsen, 2001). The potential of facilitation by dead tree structures resulting from different disturbances for ecological restoration is very large at the global scale. Fires, insect outbreaks, diseases, windstorms, drought-induced tree mortality, etc. affect large areas of forest globally every year (*e.g.* Allen et al., 2010; Bowman et al., 2009; Frolking et al., 2009), often leaving a substantial aftermath of dead woody structures in post-disturbance ecosystems – land managers could use this residual wood to achieve restoration objectives (Brewer, 2008; Brown et al., 2003; Graham et al., 1994). In this context, the positive effects of microclimatic amelioration by coarse woody debris, plus the benefits provided by nutrient release from wood, have much untapped potential for fostering ecosystem recovery and ecological restoration after severe fires and other forest disturbances.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.07.009.

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