Efecto del Manejo de la Madera Quemada Después de un Incendio sobre el Ciclo del Carbono y Nutrientes en un Ecosistema de Montaña Mediterránea

Sara Marañón Jiménez

Granada, 2011

TESIS DOCTORAL

UNIVERSIDAD DE GRANADA
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EFECTO DEL MANEJO DE LA MADERA QUEMADA DESPUÉS DE UN INCENDIO SOBRE EL CICLO DEL CARBONO Y NUTRIENTES EN UN ECOSISTEMA DE MONTAÑA MEDITERRÁNEA.

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Memoria que la Licenciada Sara Marañón presenta para aspirar al Grado de Doctor por la Universidad de Granada

Esta memoria ha sido realizada bajo la dirección de:
Dr. Jorge Castro Gutiérrez, Dr. Regino Zamora Rodríguez y Dr. Andrew S. Kowalski

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Aspirante al Grado de Doctor

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CERTIFICAN

Que los trabajos de investigación desarrollados en la Memoria de Tesis Doctoral: "Efecto del manejo de la madera quemada después de un incendio sobre el ciclo del carbono y nutrientes en un ecosistema de montaña mediterránea"**, son aptos para ser presentados por la Lda. Sara Marañón Jiménez ante el Tribunal que en su día se designe, para aspirar al Grado de Doctor por la Universidad de Granada.**

Y para que así conste, en cumplimiento de las disposiciones vigentes, extendemos el presente certificado a 2 de septiembre de 2010

Dr. Jorge Castro Gutiérrez **Dr. Regino Zamora Rodríguez**

Dr. Andrew S. Kowalski

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porque llegaste justo cuando más te necesitaba,

y te quedaste!

porque fuiste mi sol, mi luz, mi aliento y mi energía...

Y a mi padre,

a quien debo tantísimo…

“Los que están siempre de vuelta de todo
son los que nunca han ido a ninguna parte”

Antonio Machado.

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AGRADECIMIENTOS

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A ver… ¿por dónde empiezo? Sé que suele ocurrir esto ante una página en blanco, pero en este caso se trata de expresar con palabras todo eso que se apelotona y arremolina en la garganta y pelea por salir cuando echo la vista atrás y recuerdo… y que es tanta esa gratitud… ¡que necesitaría otra tesis para daros las gracias! Gracias por haberme enseñado y ayudado, cada uno a su modo, de la mejor manera en que cada uno supisteis. Por haber estado ahí cuando os necesité, aún sin haberos llamado. Perdón y gracias por haber capeado esas "tormentas", y haber sabido salir ilesos del temporal. Y es ahora que esto llega a su fin…y miro atrás…cuando empiezo a comprender de verdad que tal fin no existe, y que lo realmente importante es ese camino que me habéis ayudado a recorrer, aún a veces sin saberlo. Ese aliento, valentía y ánimos que me habéis prestado cuando se hacía taaaan pedregoso, y esas ganas, esa fé en mí que nunca perdisteis, aún cuando yo sí que lo hiciese, y ese cariño, los abrazos, los consejos y las risas! Porque esta tesis, al igual que yo, está hecha de pequeñas piezas que he ido recogiendo en ese camino, ¡¡y que al fin conseguí encajar!!

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RESUMEN / ABSTRACT

RESUMEN

Tras un incendio forestal, una práctica forestal muy extendida en relación a la madera quemada consiste en su extracción rápida e intensa (saca de la madera). Sin embargo, la retirada de la madera quemada supone una perturbación adicional sobre el ecosistema que puede suponer un impacto negativo y sinérgico sobre su funcionamiento. Por otro lado, la madera quemada puede contener aún una importante cantidad de nutrientes que podrían ser incorporados progresivamente al suelo, favoreciendo así la regeneración natural del ecosistema. En la presente tesis doctoral se pretende analizar el efecto de diferentes grados de manejo de la madera quemada tras un incendio forestal sobre el reciclaje de carbono (C) y nutrientes, así como su implicación sobre la regeneración y el funcionamiento general del ecosistema. Para ello, se establecieron en diversas parcelas a lo largo de un gradiente altitudinal (de *ca.* 1.500 a 2.300 m) tres tratamientos que difieren en su grado de intervención de la madera quemada:

1) *"No Intervención"* (NI), en la que los árboles se dejaron en pie (sin intervención).

2) *"Extracción"* (E), consistente en el corte de todos los árboles, retirada de los troncos, y el triturado de los restos no aprovechables y ramas finas (procedimiento habitual).

3) *"Intervención Intermedia"* (Ii), consistente en el corte, desramado y tronzado en 2-3 trozas del 90% de los árboles, dejando toda la biomasa *in situ* sobre el suelo.

El **Capítulo 1** de esta tesis se dedica a determinar el contenido inicial o capital de nutrientes existente en la madera quemada tras el incendio y a la valoración de su potencial para amortiguar las pérdidas de nutrientes. Esta potencialidad será interpretada en función de la magnitud del reservorio de

nutrientes en la madera en relación con el existente en la capa superior del suelo. En el **Capítulo 2** se evalúa el efecto de la madera quemada sobre la fertilidad del suelo. Para ello se determina la tasa de liberación de nutrientes esenciales mayoritarios que sufre la madera a medida que se descompone. Por otro lado, se analiza el efecto de la presencia de la madera sobre la disponibilidad de nutrientes en el suelo y otros parámetros edáficos. El efecto que ejerce el manejo de la madera quemada sobre el desarrollo de la vegetación a través de la modificación de la fertilidad y del microclima del suelo es objeto de estudio en el **Capítulo 3.** Concretamente, se estudian diversos parámetros fisiológicos y fisiognómicos que permitirán determinar aspectos relacionados con el estrés hídrico, el crecimiento y el estado nutritivo de plántulas de *Pinus pinaster* de regeneración natural tras el incendio. En el **Capítulo 4** se aborda el efecto del manejo de la madera quemada sobre la respiración del suelo. Para ello, se determinará el flujo de CO_2 del suelo existente bajo distintos tratamientos de la madera quemada a diferentes escalas temporales (horaria y estacional), y mediante varias aproximaciones (medidas de campo en condiciones naturales y bajo simulación de eventos lluvia). Por último, en el **Capítulo 5** se pretende determinar el balance del C en el ecosistema resultante de la modulación de las distintas componentes del ciclo del C por el manejo post-incendio de la madera. Con este fin, se comparan los flujos netos de CO_2 a escala de ecosistema de los dos tratamientos más contrapuestos en cuanto al grado de manejo (E, con máxima intensidad de intervención *versus* NI, en ausencia de intervención).

En conjunto, los resultados de esta tesis muestran que la presencia de la madera quemada amortigua las pérdidas de nutrientes que se producen después de un incendio, contribuyendo a la recuperación de la fertilidad, el reciclaje de nutrientes y la dinámica biogeoquímica del ecosistema. Por tanto, la aplicación de técnicas de manejo post-incendio asociadas a la madera quemada de menor intensidad puede mejorar la sostenibilidad y resiliencia ecosistémicas. La mejora en el funcionamiento del ecosistema puede facilitar, por tanto, el proceso de regeneración natural y contribuir, en último término, a la recuperación de la capacidad de secuestro de C.

ABSTRACT

After a wildfire, a widely extended forest practise is the fast and intensive removal of the burnt wood (salvage logging). However, the burnt wood withdrawal represents an additional perturbation for the ecosystem that can have a synergic negative impact on its functioning. On the other hand, the burnt wood can still contain an important amount of nutrients that could be progressively incorporated into the soil and therefore, enhance the natural regeneration of the ecosystem. In this doctoral thesis, we intend to analyze the effect of different degrees of burnt wood management after a wildfire on the carbon (C) and nutrient cycling, as well as the implications for the regeneration and general ecosystem functioning. For this, we established in several sites along an altitudinal gradient (from *ca.* 1500 to 2300 m a.s.l.) three treatments that differed in the intensity of the intervention of the burnt wood:

1) *"Non Intervention"* (NI), in which the burnt trees were left standing (without intervention).

2) *"Salvage Logging"* (SL), consisting of cutting all the burnt trees, removing the trunks and chipping the remaining non profitable fine woody residues (the traditional procedure).

3) *"Cut plus Lopping"* (CL), consisting of felling the 90% of the burnt trees, lopping off the branches and cutting the logs in 2-3 pieces, leaving all the biomass *in situ* over the ground.

Chapter 1 of this thesis is devoted to determine the initial nutrient content or capital existing in the burnt wood after the wildfire, and to the evaluation of its potential to ameliorate nutrient losses. This potential will be assessed according to the relative magnitude of the nutrient reservoir in the burnt wood compared to the existing nutrients in the upper soil layer. In **Chapter 2**, we assess the effect of the

burnt wood on the soil fertility. For this, we determine the release rate of essential macronutrients from the burnt wood as it decomposes. Additionally, we analyse the effect of the presence of burnt wood on the soil nutrient availability and other edaphic parameters. The effect of the burnt wood management on the vegetation performance through the alteration of the soil fertility and microclimate is tackled in **Chapter 3**. Concretely, several physiognomic and physiological variables are measured in naturally regenerating seedlings of *Pinus pinaster* after the wildfire, in order to determine aspects related to their water stress, growth and nutritional status. In **Chapter 4,** we investigate the effect of the burnt wood management on soil respiration. For this, the soil CO_2 flux will be determined in the different treatments at different temporal scales (hourly and seasonal), and by means of different approaches (field measurements, both under natural conditions and under simulated rain events). Finally, **Chapter 5** is aimed to determine the ecosystem C balance as a result of the modulation of several components of the C cycle by the post-fire burnt wood management. With this objective, the net CO_2 fluxes of the two most extreme treatments according to the degree of management are compared at the ecosystem level (SL, subjected to the highest intensity of intervention *versus* NI, in absence of intervention).

Overall, the results of this thesis show that the presence of burnt wood ameliorates post-fire nutrient losses, contributing to the recovery of fertility, nutrient cycling and the biochemical dynamic of the ecosystem. Therefore, the implementation of less intensive post-fire management techniques regarding the burnt wood can improve ecosystem sustainability and resilience. Improved ecosystem functioning can enhance, as a result, the process of natural regeneration and ultimately contribute to the recovery of the C sequestration capacity.

INTRODUCCIÓN GENERAL

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1. LOS INCENDIOS FORESTALES COMO PERTURBACIÓN Y SU PROBLEMÁTICA

El fuego es una de las principales perturbaciones de los ecosistemas terrestres y motor de cambio global, ya que produce una profunda alteración en los patrones de uso del suelo, en los ciclos de nutrientes, así como en el papel del ecosistema como fuente o sumidero de carbono (Lloret *et al.*, 2002; Viedma *et al.*, 2006). En el caso de muchos ecosistemas mediterráneos, el fuego constituye, no obstante, una perturbación natural implícita en su dinámica ecológica (Duguy *et al.*, 2007; Moreno *et al.*, 1998). De este modo, el fuego entendido como proceso natural no conlleva necesariamente la degradación irreversible del ecosistema. Cuando su intensidad, magnitud y frecuencia es baja, el fuego puede contribuir a la movilización y reciclaje de nutrientes y a generar una heterogeneidad de hábitats que fomente la diversidad específica y estructural en el ecosistema (Covington *et al.*, 1997; Kaye y Hart, 1998; Lindenmayer *et al.*, 2008; Selmants *et al.*, 2008; Swanson *et al.*, 2010).

Sin embargo, en las últimas décadas el fuego se ha convertido probablemente en la perturbación más importante en España en términos de magnitud e intensidad, presentando además una elevada frecuencia (Moreno *et al.*, 1998). Esto ha venido condicionado fundamentalmente por factores humanos: plantaciones monoespecíficas de alta densidad en abandono o ausencia de manejo, cambios de usos y aprovechamientos forestales, conflictos económicos y sociales, etc. (Cerdá y Mataix-Solera *et al.*, 2009; Conard *et al.*, 2002). Más aún, algunos escenarios de cambio climático predicen un incremento de las temperaturas y veranos más secos en el área Mediterránea así como en otros muchos ecosistemas del mundo (Giorgi y Lionello, 2008; IPCC, 2007). Esto causaría una desecación más prolongada, un incremento en la inflamabilidad de los restos forestales y, por consiguiente, un mayor riesgo de incendios (Duguy *et al.*, 2007; FAO, 2007). De hecho, esta tendencia se ha constatado en las últimas décadas para algunas regiones (Mouillot *et al.*, 2002; Piñol *et al.*, 1998). Como muestra de ello, sólo en España se producen unos 20.000 incendios forestales al año, quemando en promedio una superficie de 118.000 hectáreas. Bajo la tendencia actual, se calcula que toda la superficie forestal de España se habrá visto afectada por incendios en los próximos dos siglos (datos obtenidos del Ministerio de Medio Ambiente, Medio Rural y Marino, Cerdá y Mataix-Solera *et al.*, 2009).

Los incendios forestales reiterativos y de gran intensidad repercuten negativamente sobre procesos y funciones claves del ecosistema, como la capacidad de secuestro de carbono, y sobre la disponibilidad y el reciclaje de nutrientes (Bond-Lamberty *et al.*, 2004; Certini, 2005; Rutigliano *et al.*, 2002; Trabaud, 1994; Wan *et al.*, 2001). Durante un incendio de alta intensidad se produce la combustión de gran cantidad de materia orgánica y de la biomasa existente, lo que se traduce en una liberación repentina de gran cantidad de carbono y nutrientes en forma de gases a la atmósfera (Trabaud, 1994). El fuego provoca además, la reducción o incluso la eliminación de la capacidad de retención de carbono por parte de la vegetación. Esto supone la transformación del balance de carbono en el ecosistema, que pasa de ser de sumidero a fuente neta de carbono (Amiro, 2001, Amiro *et al.*, 2003, 2006; Mkhabela *et al.*, 2009).

Parte de los nutrientes liberados por el fuego serán depositados en el suelo con las cenizas (Neary *et al.*, 1999, Raison, 1979; Yang *et al.*, 2003). Sin embargo, el fuego también puede alterar las propiedades físicas y químicas de los suelos, pudiendo sufrir estos una pérdida o transformación de la materia orgánica que contienen en sustancias hidrofóbicas y recalcitrantes (Certini, 2005; DeBano *et al.*, 1998; Gonzalez-Pérez *et al.*, 2004). Esto, junto con la disrupción de los agregados y cementantes orgánicos del suelo, conlleva la alteración de parámetros como la textura y estructura, el aumento de la densidad aparente y la disminución de la capacidad de intercambio catiónico y de retención de agua (DeBano *et al.*, 1998;

Certini, 2005). Como resultado, los suelos afectados por incendios forestales son mucho menos estables y especialmente susceptibles a la erosión, especialmente en suelos arenosos y zonas de alta pendiente. Por ello, buena parte de los nutrientes depositados con las cenizas pueden perderse por erosión, arrastre y lixiviado durante los primeros eventos de lluvia (DeBano y Conrand, 1978; Fernández *et al.*, 2007; Shakesby, 2011; Thomas *et al.*, 1999). De este modo, el aumento en la disponibilidad de nutrientes en el suelo que se suele producir tras un incendio es a menudo efímero y no persiste más de varios meses (Certini, 2005, Iglesias *et al.*, 1997; Wan *et al.*, 2001, Yang *et al.*, 2003).

Las condiciones microclimáticas del suelo se verán asimismo alteradas tras un incendio. Así, por ejemplo, la oscilación térmica en el suelo se verá ampliada al perderse la protección proporcionada por la cubierta de la vegetación, hojarasca y otros restos vegetales. La incidencia de la radiación también será mayor, lo que se traduce en un mayor calentamiento del suelo durante las horas centrales del día (Castro *et al.*, 2011) y en una mayor desecación (Alauzis *et al.*, 2004; Castro *et al.*, 2011; Certini, 2005; Sullivan *et al.*, 2011). En resumen, los incendios de alta intensidad originan como resultado pérdidas netas en el capital o reservorios de nutrientes y carbono existentes en el ecosistema, y pueden dar lugar a condiciones microclimáticas más desfavorables para el desarrollo de la vegetación y la actividad microbiana. Esto supone la intensificación de los factores ecológicos que típicamente limitan la actividad y desarrollo biológico en ecosistemas mediterráneos (Costa-Tenorio *et al.*, 1998; Sardans *et al.*, 2005).

La fertilidad y disponibilidad de nutrientes en el suelo es, sin embargo, crucial para la regeneración de la vegetación después de un incendio. Durante las primeras etapas de la regeneración, la vegetación depende especialmente de los aportes externos de nutrientes (Imbert *et al.*, 2004; Landsberg y Gower, 1997). De hecho, la viabilidad del ecosistema y el mantenimiento de su estabilidad no sería posible sin la existencia del suficiente reservorio de nutrientes que asegure la productividad de la comunidad vegetal (Augusto *et al.* 2000; Blanco *et al.*, 2005; Imbert *et al.*, 2004; Miller, 1986). El impacto del fuego sobre las condiciones edáficas y la disponibilidad de nutrientes también determina la abundancia y actividad de los microorganismos (De Marco *et al.*, 2005; Dumontet *et al.*, 1996; Fierro *et al.*, 2007; Fioretto *et al.*, 2005; Hernández *et al.*, 1997; Kara y Bolat, 2009; Saa *et al.*, 1993). Estos parámetros microbianos son de gran importancia para la calidad del suelo, ya que intervienen en la mineralización de la materia orgánica y su transformación en formas asimilables para la vegetación y, en definitiva, en el balance del carbono y reciclaje de nutrientes (Staddon *et al.*, 1999).

2. El manejo forestal post-incendio de la madera quemada: pros y contras de la extracción intensiva

Tras un incendio forestal es común que el hombre actúe sobre la masa afectada. Una práctica forestal muy extendida tras los incendios forestales en relación a la madera quemada consiste en una extracción rápida e intensa (saca de la madera), generalmente en cuestión de meses, en la que se cortan los árboles quemados y en algunos casos los parcialmente dañados, se extraen los troncos, y se eliminan las ramas y otros restos mediante astillado o quema (Bautista *et al.*, 2004; Castro *et al.*, 2009, 2010a,b; Martínez-Sánchez *et al.*, 1999). Ésta es, de hecho, la actuación habitual en España, pero es igualmente común en otros países y regiones como Norteamérica, Australia, regiones tropicales, o en el ámbito de la cuenca mediterránea (Bautista *et al.*, 2004; Lindenmayer *et al.*, 2004, 2008; McIver y Starr, 2000; Van Nieuwstadt *et al.*, 2001). Esto origina un paisaje en el que se cambia de una masa en pie con predominio de árboles calcinados a una superficie despejada de la que se ha eliminado la mayor parte de la biomasa.

Las razones para acometer esta actuación son múltiples y dependen de las particularidades de cada región y los objetivos de restauración del área afectada

(Bautista *et al.*, 2004; Lindenmayer *et al.*, 2008; McIver y Starr, 2000). Muchas masas arboladas están sujetas a explotación forestal y constituyen un sector clave para la economía de muchos países. En tales circunstancias, la corta urgente de la madera permite compensar las pérdidas económicas sufridas por el incendio mediante su comercialización (Harrington, 1996; Lindenmayer y Noss, 2006; McIver y Starr, 2000; Purdon *et al.*, 2004). Sin embargo, la extracción de la madera no resulta siempre económicamente beneficiosa, como queda ejemplificado por los bosques del área Mediterránea, donde con frecuencia la retirada de los troncos quemados implica un coste neto dada la baja calidad y valor económico de la madera (Bautista *et al.* 2004). Además, en este caso existe una normativa legal que regula y limita su posible comercialización (para el caso de Sierra Nevada: BOJA nº 155 de 2011, Decreto 238/2011, de 12 de Julio por el que se establece la ordenación y gestión de Sierra Nevada).

La extracción de la madera ofrece ventajas para el manejo posterior de la zona afectada ya que facilita el acceso y las labores de repoblación y reduce el riesgo de accidentes por el colapso de los árboles quemados durante los trabajos de manejo (Bautista *et al.*, 2004; Martínez-Sánchez *et al.*, 1999; McIver y Starr, 2000; Ne´eman *et al.*, 1995; Spanos *et al.*, 2005). No obstante, la necesidad de acceder al área para su futura restauración dependerá también de la capacidad de regeneración natural y los objetivos de manejo del área. Así, por ejemplo, si el objetivo principal se centra en la preservación de la función del ecosistema y su estructura (como ocurre en el lugar donde se realiza este estudio, el cual se localiza en un Parque Nacional y Natural), puede ser aconsejable dejar la madera quemada *in situ* como un componente esencial para la estructura del hábitat y el reciclaje de nutrientes (Brown *et al.*, 2003). Más aún, si lo que se pretende es potenciar los procesos de regeneración natural puede ser incluso deseable reducir el acceso del ganado doméstico o las personas durante cierto tiempo. En cuanto al riesgo de accidentes, éstos deben ser valorados en cada caso teniendo en cuenta el uso social, recreativo o el tránsito en la zona y pueden ser mitigados cortando los árboles en las zonas más frecuentadas.

Otra de las principales razones que se argumentan para retirar la madera quemada es la de eliminar la carga de combustible muerto con objeto de aminorar el riesgo de nuevos incendios. Los restos de madera gruesos pueden ser, no obstante, menos determinantes para el riesgo de incendios y su severidad de lo que se ha asumido tradicionalmente (Passovoy y Fulé, 2006), en particular en paisajes antropizados (Mortiz *et al.*, 2004; Salvador *et al.*, 2005), mientras que otros factores como la topografía, el microclima, o la densidad de población en la zona pueden ser factores de mayor peso. Otros estudios también argumentan que la extracción intensiva puede incrementar en lugar de reducir el riesgo de incendios a corto plazo, ya que puede conllevar una mayor abundancia de restos de madera de fracción fina de fácil ignición (Donato *et al.*, 2006; Odion *et al.*, 2004; Thompson *et al.*, 2007). Por otro lado, los restos gruesos de madera tienen un menor poder de ignición, y dejados sobre el suelo pueden actuar reteniendo la humedad en su interior (Harmon *et al.*, 1986). Bajo estas condiciones, éstos pueden incluso actuar ralentizando y dificultando la progresión del fuego (Andrew *et al.*, 2000; Campbell y Tanton, 1981). De forma indirecta, la alta densidad de árboles con la que se repueblan con frecuencia las zonas previamente sometidas a la extracción intensiva de la madera, se considera una de las principales causas de riesgo de incendios recurrentes (Thompson *et al.*, 2007).

La reducción del riesgo de plagas (en particular de insectos barrenadores) hacia las masas forestales no afectadas por el incendio es otro de los argumentos para la extracción de la madera quemada. Sin embargo, las larvas de insectos barrenadores se alimentan de floema vivo (Jenkins *et al.*, 2008; Martikainen *et al.*, 2006), por lo que el riesgo se centraría en aquellos árboles parcialmente quemados y debilitados o en aquellos casos en los que la madera quemada mantiene aun floema activo (en incendios de baja intensidad). Por ello, la prevención de este riesgo no siempre requiere una actuación extensiva y generalizada sobre toda la biomasa afectada. Por otro lado, la madera representa la única fuente de alimento para gran cantidad de especies de hongos e insectos, los cuales son de gran importancia para la descomposición de la madera, la liberación de los nutrientes contenidos en ella y constituyen una parte fundamental de muchas cadenas tróficas (Grove y Meggs, 2003; Harmon *et al.*, 1986; Hutto, 2006; McCay y Komoroski, 2004; Reynolds *et al.*, 1992; Torgersen y Bull, 1995).

Por último, y a pesar de su carácter eminentemente subjetivo, cabe mencionar los argumentos de índole psicológica, emotiva y estética. Con frecuencia, el impacto visual que provoca un paisaje arrasado por un incendio con los árboles calcinados es mayor que si estos árboles son retirados. Este factor no es trivial, a pesar de lo que en principio pueda parecer, sobre todo en aquellos casos en los que la población se encuentra vinculada al bosque ya sea económicamente mediante su aprovechamiento y su uso recreativo, o simplemente emocionalmente. En este contexto sociocultural, la administración puede incluso verse presionada por la población a intervenir de forma apresurada sobre las zonas afectadas, a menudo sin previa planificación o valoración de costes y beneficios, tanto económicos como ecológicos. No valorar adecuadamente la actuación forestal más apropiada en cada caso concreto puede repercutir de forma negativa y directa sobre los vecinos de la zona. Por ello, son esenciales la educación ambiental y la información sobre las actuaciones a realizar y sus implicaciones. Involucrar a la población en estas decisiones puede suponer incluso la participación activa y la movilización en las tareas de restauración, e incrementar, por otra parte, el grado de concienciación ambiental, lo que resulta primordial para reducir el riesgo de nuevos incendios provocados.

En definitiva, existen razones de diversa índole para la retirada de la madera, pero igualmente existen razones ecológicas (e igualmente selvícolas) para mantener la madera quemada *in situ*. Esto ha llevado en la última década a una intensa y enriquecedora polémica en torno al manejo post-incendio de la madera quemada (*e.g.*: Beschta *et al.*, 2004; Castro *et al.*, 2009, 2010a, 2011; DellaSala *et al.*, 2006; Donato *et al.*, 2006; Lindenmayer *et al.*, 2008; McIver y Starr, 2000), y cada vez son más numerosas las voces que abogan por un manejo que considere caso por caso con objeto de optimizar el potencial de regeneración natural de la masa y minimizar el impacto sobre el área que se pretende restaurar.

3. LA EXTRACCIÓN INTENSIVA DE LA MADERA COMO PERTURBACIÓN Y EL PAPEL DE LA MADERA QUEMADA COMO ELEMENTO ESTRUCTURAL Y FUNCIONAL DEL ECOSISTEMA

La extracción de la madera supone una perturbación adicional a la producida por el fuego, ya que implica un cambio sustancial en el paisaje, un manejo intenso sobre el área afectada y una retirada de nutrientes del sistema. Si bien, como se decía arriba, un incendio forestal es un proceso natural cuya perturbación no tiene necesariamente consecuencias ecológicas negativas o irreversibles (en una frecuencia e intensidad moderada o baja), la reincidencia de varias perturbaciones sobre una misma zona en un corto lapso de tiempo, como es el caso de la extracción intensiva de la madera tras un incendio, puede provocar un impacto sinérgico y magnificado (Lindenmayer *et al.*, 2008; Lindenmayer y Ough, 2006). Este impacto sobre aspectos estructurales y funcionales clave del ecosistema puede exceder el grado de adaptación que muchas especies presentan a las perturbaciones que ocurren de manera natural (Paine *et al.*, 1998), lo que puede mermar la capacidad de regeneración de las comunidades, con el potencial de provocar impactos negativos acumulados sobre los procesos ecosistémicos (Attiwil, 1994; Lindenmayer *et al.*, 2008).

La perturbación asociada a la saca de la madera puede incrementar la escorrentía y erosión del suelo (Bautista *et al.*, 2004; Beschta *et al.*, 2004; Fernández *et al.*, 2007; Lindenmayer y Noss, 2006; McIver y Starr, 2000;

Wondzell, 2001). Por otro lado, la utilización de maquinaria pesada puede incrementar la compactación del suelo, lo cual, unido al arrastre de los troncos que conllevan algunas técnicas de extracción de la madera, lleva a una reducción de la supervivencia de plántulas y rebrotes que a menudo se encuentran emergiendo al comienzo de los trabajos de extracción, afectando negativamente a la regeneración (DellaSala *et al.*, 2006; Donato *et al.*, 2006; Fernández *et al.*, 2007; Greene *et al.*, 2006; Lindenmayer *et al.*, 2004; Lindenmayer y Ough, 2006; Martínez-Sánchez *et al.*, 1999; McIver y Starr, 2000). Los estudios disponibles apuntan, además, a que la retirada de la madera puede tener un efecto negativo muy importante sobre la biodiversidad de la comunidad de plantas (Ne´eman *et al.*, 1997; Stark *et al.*, 2006), hongos e insectos (Grove y Meggs, 2003), otros invertebrados (Bros *et al.*, 2011), vertebrados (Castro *et al.*, 2010b; Harrington, 1996; Hutto, 2006; Lindenmayer y Ough, 2006; McCay y Komoroski, 2004), así como en los ecosistemas acuáticos y de ribera (Beschta *et al.*, 2004; Karr *et al.*, 2004). Dejar los restos de madera quemada puede tener también efectos positivos directos sobre la regeneración forestal. La presencia de ramas y troncos caídos o en pie reduce la radiación incidente, la temperatura del suelo y aumenta la humedad, lo que puede reducir el estrés hídrico y mejora el establecimiento de la vegetación en ecosistemas mediterráneos (Bautista *et al.*, 2004; Castro *et al.*, 2011). Además, los restos de ramas y troncos esparcidos por el suelo pueden suponer una defensa para plántulas y rebrotes contra la herbivoría por ungulados (Castro *et al.*, 2010a; Ripple y Larsen, 2001; ver Harmon *et al.*, 1986; Relva *et al.*, 2009 para efecto similar de restos de ramas y troncos no quemados). Como resultado, en los últimos años se han incrementado las demandas para implementar actuaciones forestales post-incendio de baja intensidad o ausencia de intervención, basadas en la evidencia de que los restos de madera quemada en descomposición son componentes naturales que promueven la recuperación de los ecosistemas (Beschta *et al.*, 2004; DellaSala *et al.*, 2006; Hutto, 2006; Lindenmayer *et al.*, 2004).

4. *Efecto del manejo de la madera quemada sobre los ciclos biogeoquímicos: estado de la cuestión e hipótesis de trabajo*

A pesar de los numerosos estudios emergentes sobre el efecto contraproducente de la saca de la madera para la estructura y funcionamiento del ecosistema, el papel clave sobre los ciclos biogeoquímicos permanece aún poco estudiado. Esta tesis se centra en el efecto que la madera quemada puede tener en el ecosistema tras un incendio sobre los ciclos de carbono (C) y nutrientes, desde el punto de vista biogeoquímico, y sobre la regeneración, desde el punto de vista ecológico.

Durante un incendio forestal se volatilizan grandes cantidades de carbono y nutrientes (Johnson *et al.*, 2005; Neary *et al.*, 1999; Trabaud, 1994; Wei *et al.* 1997), procedentes fundamentalmente de los restos vegetales de menor tamaño (hojas, hojarasca, corteza, ramas finas y parte exterior del tronco y de las ramas). Sin embargo, incluso tras incendios de alta intensidad, frecuentemente solo la corteza y partes externas del tronco se ven sustancialmente afectadas por el fuego, mientras que aproximadamente un 60% de los restos gruesos de madera previamente muerta y casi todos los troncos de los árboles superiores a 3 cm de diámetro permanecen sin ser quemados (Stocks *et al.*, 2004). Esto se explica ya que las temperaturas que se alcanzan a unos pocos centímetros dentro de la matriz de la madera durante la onda de calor no son lo suficientemente elevadas como para producir la volatilización de sus componentes (Czimczik *et al.*, 2002). De este modo, la mayor parte del material leñoso, que constituye un 75-90% de la biomasa aérea total del árbol (Merino *et al.*, 2003, 2005; Ouro *et al.*, 2001), permanece en el ecosistema (Johnson *et al.*, 2005; Tinker y Knight, 2000; Wei *et al.*, 1997) y, a pesar de la ausencia de datos en la literatura sobre las concentraciones de nutrientes en la madera de árboles quemados tras un incendio, cabría esperar por tanto que buena parte de su composición química permaneciese inalterada. La importancia de la madera muerta como reservorio y potencial fuente de nutrientes se ha puesto de manifiesto en diferentes estudios (*e.g.*: Clark *et al.*, 2002; Harmon *et al.*, 1986; Idol *et al.*, 2001; Wilcke *et al.*, 2005; Zimmerman *et al.*, 1995), pero el reservorio de nutrientes existente en la madera quemada tras un incendio no ha sido evaluado hasta la fecha. Por tanto, nuestra hipótesis de partida se basa en que la madera quemada representa un reservorio de nutrientes de gran magnitud para el ecosistema, debido a la gran biomasa que aún persiste tras un incendio y a la relativamente elevada concentración de nutrientes que se prevé que aún contenga.

La madera quemada, en el caso de no ser extraída, irá liberando el carbono y los nutrientes que contiene de forma progresiva a medida que se descompone. Las tasas de descomposición de la madera que yace sobre el suelo han sido ampliamente estudiadas en numerosos ecosistemas, así como la dinámica y liberación de nutrientes a lo largo de este proceso (Brown *et al.*, 1996; Ganjegunte *et al.*, 2004; Laiho y Prescott, 2004; Lambert *et al.*, 1980; Palviainen *et al.*, 2010a, b). No obstante, apenas existe información publicada al respecto para ecosistemas mediterráneos (Rock *et al.* 2008; pero ver Brown *et al.*, 1996), y esta es también muy limitada para el caso de madera quemada (Grove *et al.*, 2009; Shorohova *et al.*, 2008; Wei *et al.*, 1997). Con todo, cabe esperar que la tasa de descomposición de la madera quemada sea mayor en el caso de encontrarse en contacto con el suelo, dada la mayor retención de humedad y accesibilidad a ella de los descomponedores (Mackensen y Bauhus, 2003; Naesset, 1999; Rice *et al.*, 1997). De la misma manera, los árboles quemados que quedan en pie tras un incendio también estarán sometidos a la descomposición más rápida de su base y sus raíces. Una vez que la resistencia de la madera no es suficiente para soportar el peso del árbol muerto, este caerá al suelo (Aakala *et al.*, 2008; Harrington, 1996; Morrison y Raphael, 1993; Passovoy y Fulé, 2006; Vanderwell *et al.*, 2006) y su descomposición se irá produciendo a una tasa comparable a las registradas para madera en contacto con el suelo. A pesar de todo, la información científica relativa a las tasas de caída de árboles muertos o calcinados por un incendio y los factores que las determinan es extremadamente escasa, y ausente para el caso de bosques mediterráneos.

La liberación de nutrientes y materia orgánica por parte de la madera quemada puede contribuir a la fertilidad del suelo y a la mejora de la disponibilidad de nutrientes y de otros parámetros edáficos como el contenido en materia orgánica, la densidad aparente y la presencia y actividad de los microorganismos. Al igual que antes, algunos estudios abordan el papel de los restos gruesos de madera muerta sobre diferentes parámetros de calidad y fertilidad de los suelos en bosques maduros poco perturbados (Brais *et al.*, 2005; Graham *et al.*, 1994; Grove y Meggs, 2003; Hafner *et al.*, 2005; Hafner y Groffman, 2005; Jurgensen *et al.*, 1997; Kuehne *et al.*, 2008), aunque esto no ha sido específicamente estudiado aún para el caso de la madera quemada en suelos afectados por un incendio.

La extracción de la madera supone, sin embargo, una retirada adicional de nutrientes del ecosistema que se añade a la ya producida por el incendio (Brais *et al.*, 2005; Johnson *et al.*, 2005; Lindenmayer y Noss, 2006) con la consiguiente reducción de los potenciales aportes y de la capacidad de restitución de nutrientes al suelo a medida que la madera se descompone. Además, si los troncos y ramas quemados se dejan sobre el terreno, pueden frenar el arrastre y erosión del suelo que se produce sobre todo durante las primeras lluvias tras un incendio, contribuyendo con ello a minimizar la pérdida de nutrientes existentes en el suelo y en las cenizas depositadas (Fox, 2011; Kim *et al.*, 2008; Shakesby *et al.*, 1996; Thomas *et al.*, 2000). A esto se une la mencionada mejora de las condiciones microclimáticas cuando el suelo se encuentra protegido por restos de madera quemada (Castro *et al.*, 2011; ver Smaill *et al.*, 2008; Stoddard *et al.*, 2008 para madera no quemada). Todo esto también puede contribuir a acentuar el efecto cascada sobre la fertilidad del suelo, la actividad de los microorganismos descomponedores, las tasas de reciclaje de nutrientes y, en definitiva, en la disponibilidad de nutrientes para el conjunto de la comunidad (Brown *et al.*, 2003; McIver y Starr, 2000).

La recuperación de las funciones y procesos ecológicas del suelo por la presencia de la madera quemada puede tener importantes consecuencias para la regeneración de la vegetación tras el incendio, ya que la reducción de la sequía y el aporte de nutrientes (factores que con más frecuencia limitan el desarrollo de la vegetación en ecosistemas mediterráneos; Costa-Tenorio *et al.*,1998; Sardans *et al.*, 2005) suelen traducirse en una mayor supervivencia, crecimiento y productividad (Castro *et al.*, 2011; Jiménez *et al.*, 2007; Querejeta *et al.*, 2008; Matías *et al.*, 2011; Mendoza *et al.*, 2009; Siles *et al.*, 2010; Trich*et al.*, 2008). Por tanto, la mayor disponibilidad de nutrientes y mejores condiciones microclimáticas no sólo pueden llevar a un incremento en la capacidad de establecimiento de las plántulas (Castro *et al.*, 2011; Fernández *et al.*, 2008; Greene *et al.*, 2006; Martínez-Sánchez *et al.*, 1999; McIver y Starr, 2000, 2001), sino que también estas podrían desarrollarse mejor y tomar ventaja de las condiciones más favorables proporcionadas por la presencia de la madera quemada en años posteriores. A pesar del potencial efecto del manejo post-incendio de la madera quemada sobre el capacidad de regeneración de la vegetación (ya sea natural o repoblada), existen pocos trabajos que estudien este aspecto bajo condiciones experimentales controladas. Además, la mayor parte de estos estudios experimentales sólo tratan el efecto de los tratamientos más contrapuestos (la extracción intensiva de la madera frente a la ausencia de intervención; Martínez-Sánchez *et al.*, 1999; Pérez y Moreno, 1998; Spanos *et al.*, 2005), a pesar del gran abanico de posibilidades de manejo intermedio existentes.

A raíz del incremento de la fertilidad, la actividad microbiana del suelo también podría verse incrementada, al disponer, como se hipotetiza, de mayor cantidad de nutrientes (Hamman *et al.*, 2008; Mabuhay *et al.*, 2006; Trumbore *et al.*, 1996), sustratos orgánicos (Coleman *et al.*, 2004; Franzluebbers *et al.*, 2001) y humedad en el suelo (Almagro *et al.*, 2009; Carlyle y Bathan, 1988; Davidson *et al.*, 1998; Kirschbaum, 2000; Lloyd y Taylor, 1994) en presencia de madera quemada. Además, la mayor productividad de la vegetación y presencia de raíces contribuirá a un incremento de la actividad metabólica, ya sea a través de su propia respiración o mediante la liberación de exudados orgánicos utilizables por los microorganismos (Craine *et al.*, 1998; Irvine *et al.*, 2007; Janssens *et al.*, 2001; Knapp *et al.*, 1998; Litton *et al.*, 2003; Mkhabela *et al.*, 2009; Yanai *et al.*, 2000). El resultado de esta actividad respiratoria puede ser inferido a través de los flujos de CO_2 del suelo, que serán interpretados como un indicativo más de la calidad del suelo en respuesta al manejo forestal post-incendio de la madera (Staddon *et al.*, 2009; Weber, 1990). Existen numerosos trabajos sobre el efecto del fuego sobre los flujos de CO_2 del suelo (*e.g.*: Dore *et al.*, 2010; Gough *et al.*, 2007; Hamman *et al.*, 2008; Hubbard *et al.*, 2004; Kobziar, 2007; McCarthy and Brown, 2006; O'Neill *et al.*, 2006; Yermakov y Rothstein, 2006). Sin embargo, a pesar de la importancia de conocer el efecto que las diferentes prácticas de manejo forestal post-incendio tienen sobre el balance del carbono, la literatura existente sobre la respiración del suelo en función del manejo de la madera quemada es muy escasa (ver Irvine *et al.*, 2007; Mkhabela *et al.*, 2009) y, en todo caso, el impacto de la extracción intensiva de la madera quemada en los flujos de CO_2 del suelo aún no ha sido abordado.

Por último, el manejo de la madera quemada no sólo puede afectar al reciclaje de nutrientes y a las tasas de actividad biológica, sino que también puede repercutir en el ciclo del carbono de forma decisiva. Como se ha mencionado, las emisiones de carbono del suelo pueden verse alteradas por el tratamiento de la madera aplicado tras el incendio. Además, la descomposición de la madera también contribuye al total de emisiones de CO_2 que se producen en el ecosistema (Jomura *et al.* 2008; Progar *et al.*, 2000). Sin embargo, esto no implica necesariamente que la madera quemada provoque un aumento neto de las emisiones de CO_2 a la atmósfera a escala de ecosistema. De hecho, puesto que la presencia de la madera quemada puede fomentar la capacidad de regeneración y productividad de la vegetación (Castro *et al.*, 2011; Donato *et al.*, 2006; Martínez-Sánchez *et al.*, 1999), la retención de carbono también puede verse incrementada. El balance entre las emisiones (fuentes) y el secuestro (sumideros) de carbono en el ecosistema como resultado del manejo forestal post-incendio tiene implicaciones globales de gran relevancia para las políticas dirigidas a la optimización del secuestro de carbono (Lindenmayer *et al.*, 2008; Stark *et al.*, 2006). A pesar de esto, no existen estudios hasta la fecha que evalúen el efecto del manejo post-incendio de la madera sobre el intercambio neto de carbono a nivel de ecosistema. La determinación del balance de carbono resultante de la extracción de la madera quemada frente a su persistencia cobra en esta tesis una dimensión global, ya que integra desde la perspectiva biogeoquímica los diferentes efectos que el manejo post-incendio de la madera puede tener sobre los diferentes componentes del ecosistema.

5. ÁREA DE ESTUDIO Y DISEÑO EXPERIMENTAL GENERAL

Los estudios que se desarrollan en los sucesivos capítulos de la presente tesis fueron realizados en el Parque Natural y Nacional de Sierra Nevada, en un área afectada por un incendio ocurrido en Septiembre de 2005 (“incendio de Lanjarón”, UTM: 462673, 4094115). Dicho incendio afectó a 3.425 ha en total, de las cuales unas 1.300 ha aproximadamente eran bosques de pinos de reforestación de 35-50 años de edad, de manera que la madera de los árboles quedó carbonizada en los primeros centímetros de su superficie. En esta zona se seleccionaron cuatro parcelas localizadas a diferente altitud (Parcelas 1-4 en adelante, ver cuadro 1). Las especies de pino presentes en cada parcela son diferentes según su distribución altitudinal. El clima de la zona es Mediterráneo, con precipitaciones concentradas en primavera y otoño, alternando con veranos cálidos y secos. La precipitación media anual a 1465 m de altitud es de 470±50 mm, con una precipitación estival (Junio, Julio y Agosto conjuntamente) de 17±4 mm (datos climáticos procedentes de una estación meteorológica cercana a la zona de estudio, periodo 1988-2008). Hay nieve durante los meses más fríos de invierno, a menudo persistente desde Noviembre a Marzo a partir de los 2000 m de altitud. La temperatura media anual es de 12.3±0.4 ºC a 1652 m de altitud, mientras que la media de las temperaturas máximas es de 16.2±0.6 ºC y la media de las mínimas es de 7.6±0.5 ºC (Agencia Estatal de Meteorología, periodo 1994–2008). La temperatura media anual a 2300 m de altitud es de 7.8±0.7 ºC (dato procedente de un sensor instalado en una torre de flujo turbulento en la parcela 4, periodo 2008–10). La vegetación actual está compuesta mayoritariamente por herbáceas y arbustos con una cobertura de un 75% aprox. (Castro *et al.*, 2010a). Todas las parcelas son homogéneas en cuanto a intensidad del fuego (alta intensidad), exposición (suroeste) y roca madre (micaesquistos) (Cuadro 1).

Cuadro 1: *Características principales de las parcelas de estudio.*

PARCELA 1	**Altitud[1]:** 1.477 m **Tipo de suelo[2]:** Phaeozems háplicos, inclusiones de Cambisoles eútricos **Pendiente:** 25-30% **Especie Forestal Dominante:** *Pinus pinaster* **Especies herbáceas y arbustos dominantes:** *Ulex parviflorus*, *Adenocarpus decorticans*, *Festuca scariosa*, *Dactylis glomerata*, *Euphorbia flavicoma* **Densidad de árboles previa al incendio:** 1.480±50 **Diámetro de los árboles a la altura del pecho:** 13,3±0,2 cm **Altura media de los árboles:** 6,3±0,1 m
PARCELA 2	**Altitud[1]:** 1.698 m **Tipo de suelo[2]:** Phaeozems háplicos, inclusiones de Cambisoles eútricos y húmicos **Pendiente:** 25-35% **Especie Forestal Dominante:** *Pinus nigra* **Especies herbáceas y arbustos dominantes:** *Ulex parviflorus*, *Adenocarpus decorticans*, *Festuca scariosa*, *Sangisorba minor*, *Euphorbia flavicoma* **Densidad de árboles previa al incendio:** 1.060±70 **Diámetro de los árboles a la altura del pecho:** 14,5±0,2 cm **Altura media de los árboles:** 6,6±0,1 m
PARCELA 3	**Altitud[1]:** 2.053 m **Tipo de suelo[2]:** Phaeozems háplicos, inclusiones de Cambisoles eútricos y húmicos **Pendiente:** 35% **Especie Forestal Dominante:** *Pinus sylvestris* **Especies herbáceas y arbustos dominantes:** *Vaccaria hispanica*, *Sesamoides prostrata*, *Senecio nebrodensis*, *Helianthemum apenninum* **Densidad de árboles previa al incendio:** 1.050±40 **Diámetro de los árboles a la altura del pecho:** 10,8±0,2 cm **Altura media de los árboles:** 6,2±0,1 m
PARCELA 4	**Altitud[1]:** 2.317 m **Tipo de suelo[2]:** Cambisoles húmicos y Phaeozems háplicos **Pendiente:** 20% **Especie Forestal Dominante:** *Pinus sylvestris* **Especies herbáceas y arbustos dominantes:** *Genista versicolor*, *Festuca* spp., *Sesamoides prostrata* **Densidad de árboles previa al incendio:** 1.060±50 **Diámetro de los árboles a la altura del pecho:** 13,4±0,3 cm **Altura media de los árboles:** 6,6±0,2 m

[1]Altitud medida en el centro de la parcela.[2] Según Mapa de Suelos. Hoja Lanjarón 1:100.000. Proyecto LUCDEME. Ministerio de Agricultura Pesca y Alimentación. (1993)

Entre Enero y Mayo de 2006, (4-8 meses después del incendio), se establecieron tres tratamientos de manejo post-incendio de los árboles quemados, en tres réplicas o subparcelas por cada tratamiento para las parcelas 1, 2 y 3 (3 réplicas x 3 tratamientos = 9 réplicas por parcela). Las réplicas, de al menos 2 ha de extensión cada una, se dispusieron contiguas entre sí, distribuidas de forma aleatoria dentro de cada parcela siguiendo un diseño de bloques (Fig. 1). En el caso de la parcela 4, no se subdividió en réplicas o subparcelas y cada tratamiento fue aplicado a un área de unas 35 ha aprox. (Fig. 1), debido a que en esta parcela fueron instaladas torres para la medida del flujo turbulento de CO_2 mediante la técnica de eddy covarianza, para lo cual se requiere una mayor extensión con objeto de asegurar que los flujos medidos proceden del tratamiento en cuestión ("área fuente") (Baldocchi, 2003; Schmid, 1994, 1997, 2002).

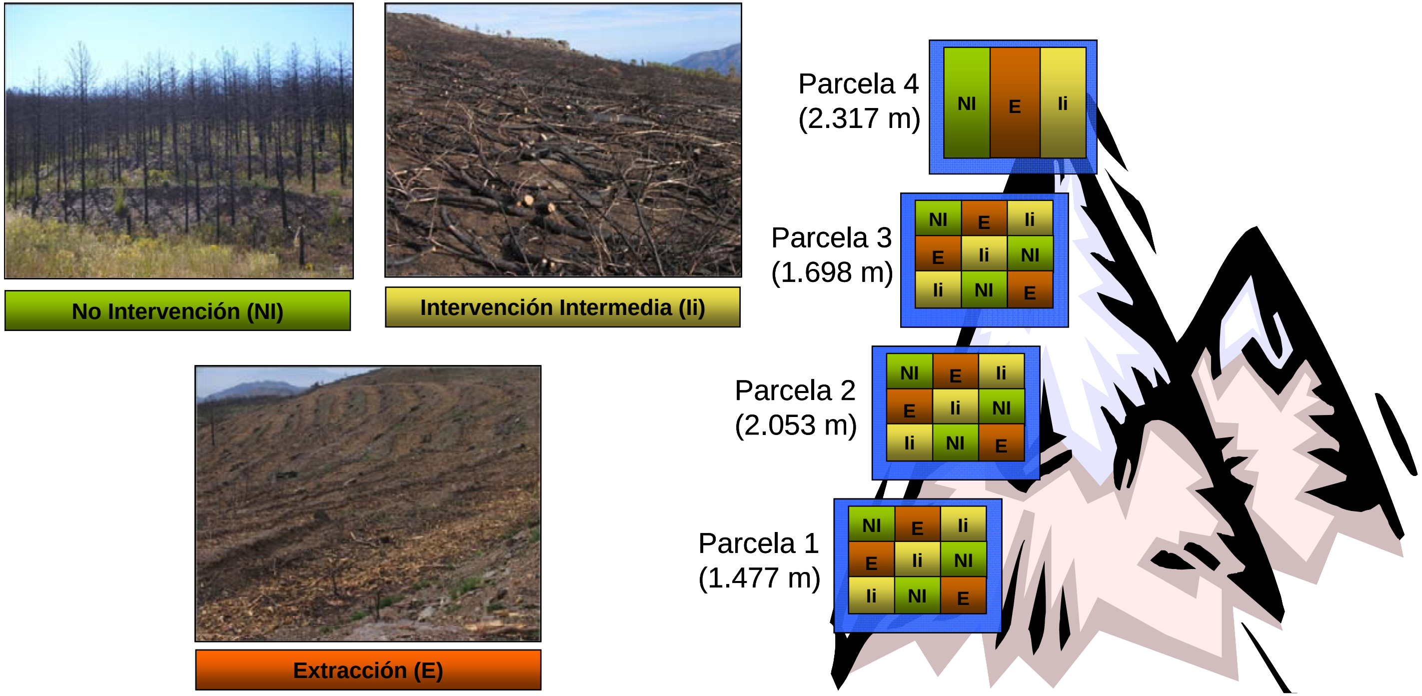

Figura 1: *Esquema del diseño experimental general utilizado en los diferentes estudios de la tesis y fotografías de diferentes tratamientos de la madera quemada aplicados. En el caso de la parcela 4, cada tratamiento fue aplicado a una sola área más extensa que en el resto de las parcelas, debido a que la medida del flujo turbulento de* CO_2 *mediante la técnica de eddy covarianza realizada en esta parcela requiere una mayor extensión de cada tratamiento.*

Los tratamientos de la madera quemada que se aplicaron fueron:

1**)** *"No Intervención"* o *"Non Intervention"* (NI), en el que se dejaron en pie todos los árboles quemados (sin intervención) (Fig. 1). No obstante, los árboles se fueron cayendo de forma natural y progresiva a lo largo de los años, lo cual ha sido monitorizado como parte complementaria a los estudios de los que consta esta tesis. Así, ningún árbol se había caído aún en la zona de estudio tras el invierno de 2006-2007, un 13% de los árboles se cayeron tras el invierno de 2007-2008, un 83% se habían caído tras el invierno de 2008-2009 y un 98% tras el invierno de 2009-2010 (Fig. 2).

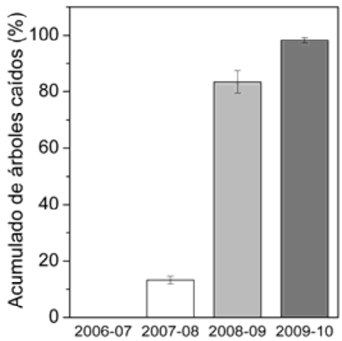

Figura 2: *Porcentaje acumulado de árboles caídos a lo largo del tiempo. Los valores representan el promedio en las parcelas de estudio 1, 2 y 3. Por cada parcela y réplica fueron inicialmente marcados 100 árboles en los tratamientos NI e Ii (1.800 árboles en total), y fueron monitorizados en años sucesivos para determinar la tasa de caída.*

2) *"Intervención Intermedia"* (Ii) ó *"Cut plus Lopping"* (CL), consistente en el corte y desramado de los árboles quemados, y el troceado de los troncos con una sierra mecánica con objeto de facilitar su contacto con el suelo. La biomasa dejada *in situ* con este tratamiento es igual a la del tratamiento "Control", pero con las ramas y restos de madera cubriendo el 45% aprox. de la superficie del suelo (Castro *et al.*, 2011) (Fig. 1).

3) *"Extracción"* (E) ó *"Salvage Logging"* (SL), en el que se talaron los árboles quemados, se desramaron, y el tronco se cortó en 2-3 trozas de unos 3 m que se apilaron en grupos de 10-12 para su posterior retirada con un autocargador. Las ramas finas y otros restos no aprovechables se trituraron con una desbrozadora

de cadenas (Fig. 1). En las parcelas de más difícil acceso, la retirada de los troncos no fue posible, por lo que los troncos se dejaron apilados sobre el terreno. Este tratamiento es el más frecuentemente utilizado por la administración tras los incendios forestales y es, de hecho, el tratamiento que se aplicó al resto del área afectada por el incendio que rodea a cada una de las parcelas experimentales (Castro *et al.*, 2010a).

Los tratamientos se diferencian por tanto en su intensidad de manejo de la madera quemada, siendo por orden: E > Ii > NI.

6. Objetivos y estructura en capítulos

Partiendo de las hipótesis mencionadas, esta tesis se enfocará de manera general en el análisis de los posibles efectos del manejo post-incendio de la madera sobre la dinámica de nutrientes y sus implicaciones sobre la regeneración y balance de C en el ecosistema. Este objetivo general supone el reto de abordar una cuestión de aplicabilidad directa para la gestión forestal recurriendo a diversas disciplinas tradicionalmente disociadas en la ciencia. De este modo, diversos aspectos químicos y edafológicos, fisiológicos, ecológicos y de física atmosférica serán estudiados y considerados de manera aplicada. Para ello, se han utilizado técnicas e instrumentación innovadoras como son el análisis de isótopos estables ^{13}C y ^{15}N, los sistemas de cámaras IRGA portátiles para la medida de flujos de CO_2 del suelo o las torres de flujo turbulento para la medida de flujos netos de CO_2 con la técnica "eddy-covarianza". Finalmente, los resultados obtenidos se interpretan y discuten desde una perspectiva transversal para obtener un panorama global e integrador de la cuestión que se plantea. Con este objeto, la pregunta general será desgranada en diferentes objetivos que serán abordados, según su temática, en forma de capítulos (Fig. 3):

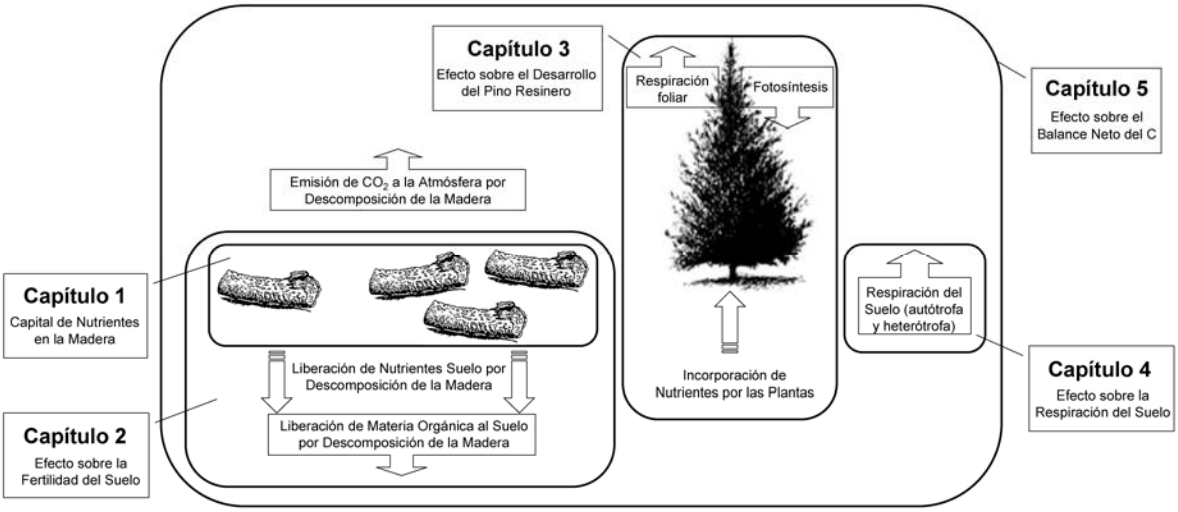

Figura 3: *Esquema conceptual simplificado de los posibles procesos entre los diferentes compartimentos y flujos del ciclo del C y nutrientes en el ecosistema afectados por la presencia de madera quemada tras el incendio. Los flujos de C se indican mediante flechas con llamada, los flujos de nutrientes se indican mediante flechas discontinuas. En cada uno de los capítulos de esta tesis (representados mediante rectángulos redondeados y sus etiquetas) se abordan uno o varios de los procesos considerados, y en el último capítulo se aborda el balance neto del C, lo que permite determinar el efecto global sobre el ecosistema.*

El primer objetivo, abordado en el **Capítulo 1** de esta tesis, será el de determinar el contenido o capital de nutrientes existente en la madera quemada que se deja en el ecosistema tras el incendio. Se valorará la utilidad potencial de la madera quemada como elemento natural para amortiguar las pérdidas de nutrientes. Esta potencialidad será función de la magnitud del reservorio de nutrientes en la madera en relación con el disponible en los primeros centímetros del suelo.

En el **Capítulo 2** se determinará el efecto que tiene la madera quemada sobre la fertilidad del suelo. Para ello se estudiará, por un lado, la tasa de liberación de nutrientes mayoritarios que experimenta la madera a medida que se descompone. Por otro lado, se analiza el efecto de la presencia de la madera sobre la disponibilidad de nutrientes en el suelo y otros parámetros edáficos.

El efecto que ejerce el manejo de la madera quemada sobre el desarrollo de la vegetación a través de la modificación de la fertilidad y del microclima del suelo será objeto de estudio en el **Capítulo 3.** En concreto, se estudiarán diversos parámetros fisiológicos, fisiognómicos y bioquímicos que permitirán determinar aspectos relacionados con el estrés hídrico, el crecimiento y el estado nutritivo de plántulas de *Pinus pinaster* de regeneración natural tras el incendio.

En el **Capítulo 4** se aborda la modificación de las tasas respiratorias de los microorganismos y raíces del suelo en respuesta a la alteración de los parámetros edáficos y, de forma indirecta, de la vegetación. Para ello, se determinará el flujo de CO_2 del suelo existente bajo distintos tratamientos de la madera quemada a diferentes escalas temporales (horaria y estacional) y mediante varias aproximaciones (medidas de campo en condiciones naturales y en condiciones controladas de humedad).

Por último, en el **Capítulo 5** se pretende determinar el balance del C en el ecosistema resultante de la modulación de las distintas componentes del ciclo del C por el manejo post-incendio de la madera. Con este fin, se comparan los flujos netos de CO_2 a escala de ecosistema de los dos tratamientos más contrapuestos en cuanto al grado de manejo (E, con máxima intensidad de intervención *versus* NI, en ausencia de intervención).

Las conclusiones que se extraigan de esta tesis permitirán poner de manifiesto la relevancia que el manejo de la madera quemada puede tener sobre el funcionamiento y dinámica del ecosistema desde el punto de vista biogeoquímico. Más aún, posibilitan vislumbrar las implicaciones a escala global que las estrategias de manejo post-incendio de los bosques mediterráneos pueden tener sobre las emisiones de C. Por todo ello, representan también una llamada de atención sobre la importancia de considerar el aspecto biogeoquímico para asegurar la estabilidad y sostenibilidad de los ecosistemas forestales. Los resultados de esta tesis podrán servir, por tanto, como instrumento de apoyo en la toma de decisiones para la gestión forestal post-incendio.

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CHAPTER 1:

MACRO AND MICRONUTRIENT CONTENT IN BURNT WOOD AFTER A WILDFIRE IN A MEDITERRANEAN PINE FOREST

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ABSTRACT

Even after a high-intensity wildfire, large amounts of logs and coarse woody debris remain in the ecosystem. In this study, we analyze the initial C and nutrient concentrations (N, P, Ca, Mg, K, Na, Fe, Mn, Zn, Cu) in burnt pine logs just after a wildfire in four sites along an altitudinal gradient, and the available nutrients in the upper 10 cm of soil in absence of woody residues two years after the fire. To evaluate its relative relevance, nutrient pools in the burnt wood are compared to those available in the soil. Overall, soil characteristics of the experimental sites were mainly driven by differences in pH and CIC, likely as a result of differences in mineralogy and microclimatic conditions of the sites. Soils were poorly developed and nutrients limiting for the vegetation requirements. Burnt wood still contained a relative high concentration of nutrients compared to those reported for unburnt, dead pine wood, and in general, decreased with altitude. In particular, Cu, Zn and Mn in burnt wood reflected the availability of these micronutrients in soil, as a response of their limitation. Burnt wood represented a considerable pool of nutrients, both due to the relatively high concentrations and to the great amount of biomass still present after the fire. Potential contributions of the burnt wood were particularly relevant for N, K and micronutrients Na, Mn, Fe, Zn, Cu, as they represented approx. a 93%, 62% and 72-87% respectively of the amount of nutrients existing in soil and wood pools. Burnt wood remaining after a wildfire therefore constitutes a valuable natural element as a reservoir and potential source of nutrients, which would be lost from ecosystems in the case of being removed.

Keywords: Forest management, silvicultural treatments, woody debris, wildfire, wood nutrients, soil nutrients, Mediterranean mountain, post-fire salvage logging

1. INTRODUCTION

Wildfires exert a radical perturbation to the ecosystem nutrient cycle, leading to an immediate nutrient mobilization from organic pools (Page-Dumroese and Jurgensen, 2006; Trabaud, 1994; Whelan, 1995). Vegetation, litter and soil organic layers are susceptible to be consumed in greater or lesser degrees by fire, and their nutrients either released to the atmosphere as smoke or deposited to the soil as ash (DeBano and Conrand, 1978; Iglesias *et al.*, 1997; Johnson *et al.*, 2005; Neary *et al.*, 1999; Raison, 1979; Yang *et al.*, 2003). As a consequence, increases in soil nutrients can appear on the short term (Gray and Dighton, 2009; Johnson and Curtis, 2001; Marcos *et al.*, 2009). Nonetheless, the 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 especially in steep areas or sandy soils (DeBano and Conrand, 1978; Fernández *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).

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 (Chapin *et al.*, 2002; Clarkson and Hanson, 1980; Ingestad, 1979). 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 about 75-90% of the total aboveground biomass of a pine forests (Merino *et al.*, 2003, 2005; Ouro *et al.*, 2001). Moreover, this estimation ascends to about 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 the nutrient concentrations in the woody tissues are usually the lowest compared to the rest of the tree fractions, they can contain a high proportion of the nutrients. As an example, the contents of nutrients in the woody fractions are estimated to represent *ca.* 25-60% of N, 50-70% of P, 65-75% of K, Mg and Zn, respectively, 75-80% of Ca, Mn and Cu, and 75-80% of Fe contained in the aboveground pine biomass (Alriksson and Eriksson, 1998; Merino *et al.*, 2003, 2005; Ouro *et al.*, 2001; Rademacher, 2005). Thus, woody tissues can store the largest amounts of nutrients in the tree, thus acting as an ecosystem sink and reservoir.

Wildfires provoke a sudden mobilization and loss of nutrients from the system, although they are restricted mostly to the leaves and fine fractions of vegetation (Johnson *et al.*, 2005; Trabaud, 1994). 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 (Johnson *et al.*, 2005; Tinker and Knight, 2000; Wei *et al.*, 1997), as the temperatures reached inside the first centimeters of the matrix of coarse woody fractions during the heat wave are not high enough to volatilize its components (Czimczik *et al.*, 2002). In fact, charring is usually limited to the bark or the outer superficial wood layer, and even after intense, stand-replacing crown fires, more than approx. 60% of the pre-existing coarse woody debris and almost all standing tree boles greater than 3 cm of diameter remain unburned (Stocks *et al.*, 2004). The nutrients contained in the coarse burnt woody debris will be progressively released later during the decay process (Brown *et al.*, 1996; Ganjegunte *et al.*, 2004; Palviainen *et al.*, 2010a, 2010b; Wei *et al.*, 1997), allowing their retention by the soil and their availability for microorganisms and developing vegetation (Brais *et al.*, 2005; Grove and Meggs, 2003; Jurgensen *et al.*, 1997).

Ecosystem nutrient losses associated with wildfires have been estimated in several studies (Brais *et al.*, 2000; DeBano and Conrad, 1978; Johnson *et al.*, 2005; Wan *et al.*, 2001; Wei *et al.* 1997). In this respect, Wei *et al.* (1997) suggested that the nutrients (N and P) contained in pine unburnt stemwood are comparable to the nutrient losses associated with low severity wildfires. However, to our knowledge, there are no data about elemental concentrations in burnt wood to date, and what is more, the magnitude of the nutrient pools of burnt wood after a wildfire and their potential role in the ecosystem nutrient reserves has not been assessed yet. The estimation of the nutrient reservoir in the burnt wood is however a key first step to assess ecosystem sustainability towards its regeneration. In this work we intend to evaluate the nutrient concentration and reservoir in burnt wood after a stand-replacing fire. We analyze the initial macro and micronutrient concentrations in burnt pine logs just after the wildfire, and the available nutrients in the soil where burnt wood is absent. 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. Nutrients pools in the burnt wood are further estimated and compared to the nutrients in the soil pools to evaluate their relative relevance. The main objectives of this study are to: 1) determine the nutrient concentrations in the burnt wood left after a wildfire along the altitudinal gradient, and 2) assess the relative magnitude of the nutrient reservoir in the burnt wood in relation to the available nutrient stocks in the soil.

2. MATERIAL AND METHODS

2.1. STUDY AREA

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. 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 1465 m a.s.l.). Snow falls during winter, usually persisting from November to March above 2000 m a.s.l. The mean annual temperature is 12.3±0.4ºC at 1652 m a.s.l. (State Meteorological Agency, period 1994-2008. Ministry of Environment) and 7.8±0.7ºC at 2300 m a.s.l. (data from meteorological station, period 2008-10).

The burnt pine stands occupy an altitudinal gradient from *ca.* 1300 to 2300 m a.s.l. Across this gradient, we established 4 study sites of *ca.* 3 ha (sites 1 to 4, respectively) that were similar in terms of fire intensity (high), situation (southwest 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 with the use of 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). Post-fire vegetation was composed mainly of grasses and forbs with a cover of approximately 70% (Castro *et al.*, 2010). Dominant species were *Ulex parviflorus*, *Adenocarpus decorticans*, *Festuca scariosa*, *Dactylis glomerata* and *Euphorbia flavicoma* in site 1; *Ulex parviflorus*, *Adenocarpus* *decorticans*, *Festuca scariosa*, *Sangisorba minor* and *Euphorbia flavicoma* in site 2; *Vaccaria hispanica*, *Sesamoides prostrata*, *Senecio nebrodensis* and *Helianthemum apenninum* in site 3; and *Genista versicolor*, *Festuca* spp., and *Sesamoides prostrata* in site 4.

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	456070; 4089811	455449; 4091728	457244; 4091551	457719; 4091518
Altitude[1] (m a.s.l.)	1477	1698	2053	2317
Slope (%)	25-30%	25-35%	35%	20%
Prefire dominant species:	*Pinus pinaster* Aiton	*Pinus nigra* Arnold	*Pinus sylvestris* Linneo	*Pinus sylvestris* Linneo
Tree density (invividuals 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

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

2.2. SOIL SAMPLING

In June 2008 (2 years after the wildfire), 12 soil samples were collected from bare areas without woody debris at each site, characterizing soil conditions excluding the short term effects of ash deposition, once ash runoff and the lixiviation of its nutrients had occurred. For each soil sample, 3-4 soil pits were extracted using a gouge auger (2.5 cm diameter) to 10 cm depth, and homogenized to compound a single soil sample. Samples were immediately sieved at 2 mm and stored to 4ºC. Within 24 h of soil sampling, two subsamples of 15 and 7.5 g of soil were extracted for 1 h in agitation with 75 mL of 2M KCl and 0.5M $NaHCO_3$, respectively, and filtered through a Whatman GF-D filter. Extracts were frozen at -20ºC until analyzed (Schinner *et al.*, 1995). A 30 g subsample was oven-dried at 105ºC for 48 h for gravimetric determination of water content by the difference between fresh and dry weight, and stored for further analyses. 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.

2.3. SOIL CHEMICAL ANALYSES

From the dried subsample, soil organic matter (SOM) content was determined by incineration at 550ºC 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 850ºC (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±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 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. 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 micronutrients (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. 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 referred to the corresponding dry weight of the soil.

2.4. Wood sampling

During tree felling by the Forest Service (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. These discs are considered a representative sample of the initial characteristics of the burnt wood, since they were collected *ca.* 6 months (mostly winter) after the fire and 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 70ºC 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.

2.5. *WOOD CHEMICAL ANALYSES*

The carbon and nitrogen concentrations of sawdust samples were determined using the combustion furnace technique at 850ºC (Leco TruSpec autoanalyzer), and phosphorus was analysed using the molybdovanadate method [Association of Official Analytical Chemists (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 Plantas, 1981) with a Perkin Elmer 5100 spectrometer. The sawdust was dried at 105ºC by a thermogravimetric analyser (Leco TGA 701), and nutrient concentrations referred to the corresponding dry weight.

2.6. *NUTRIENT POOLS ESTIMATION*

The biogeochemical relevance of the remaining burnt wood was assessed by comparing both the soil and wood pools of nutrients as a result of the wildfire. In order to estimate the nutrient content of the burnt 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, url: http://cubifor.cesefor.com/). For each experimental site, the means of dasometric variables (tree density, d.b.h and tree height; table 1) were introduced to specific equations according to the dominant pine species. The fraction of needles and twigs <2 cm were not considered, since these fractions were consumed during the wildfire. The resultant values of biomass per area allowed the estimation of the nutrient content per area of the wood pool for each site.

The nutrient content in the upper 10 cm soil layer was calculated using the nutrient concentrations in the soil and the bulk density for each site (Table 2). The N in the soil pool was referred to the extractable inorganic fraction ($NH_4^+ + NO_3^-$), since 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).

2.7. Data analysis

The differences in nutrient concentrations in wood and soil were analyzed with one-way analysis of variances (ANOVAs), with site as the independent factor. The comparison of mean nutrient concentrations between sites was further analyzed with Tukey HSD *post-hoc* tests. Differences in textures and mineralogy between sites were similarly analyzed using a non-parametric Kruskal-Wallis test, and, in cases of significant differences, Nemenyi *post-hoc* tests of multiple comparisons of means among sites were performed. Additionally, correlations between all nutrients were explored separately for the wood and for the soil using Pearson 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 standardization 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 to improve normality and homocedasticity (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 ±1SE.

3. RESULTS:

3.1. 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 2). Soil nutrient concentrations differed significantly between experimental sites in the case of C_{tot}, N_{tot}, P_{inorg}, Ca, Mg and Mn (Table 3). C_{tot} and N_{tot} showed the same pattern as SOM, being highest at the most elevated site, with the same tendency for NO_3^- (Tables 2 and 3). The C/N ratio in soil was higher in sites 1 and 2 and lowest in site 3 (Table 3). Most of the N in the soil was organic and only *ca.* 0.54% was inorganic. The extractable P_{inorg} was lower in site 2 and higher in site 4 (Table 3). The exchangeable Ca and Mg had similar patterns between experimental sites, being higher in sites 1 and 2 (Table 3). Despite the absence of significant differences, Fe, Cu and Zn tended to be lowest at the most elevated site. Mn had an opposite pattern, increasing with the elevation (Table 3).

Table 2: *Main soil parameters of the study sites. Values represent means ± standard errors. CEC: cationic exchange capacity; SOM: soil organic matter; ρ: bulk density. Different letters above means indicate significant differences among sites (Tukey post-hoc test or after one-ways ANOVAs or Nemenyi test after Kruskal-Wallis tests). F / H: Value of the statistics, P: Critical probability.*

Soil Parameter	Site 1	Site 2	Site 3	Site 4	F / H	*P*
Soil type[1]	Haplic phaeozems, with eutric cambisols	Haplic phaeozems, with eutric and humic cambisols	Haplic phaeozems, with eutric and humic cambisols	Humic cambisols and haplic phaeozems		
ρ (g cm^{-3})	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	59.4±2.4	58.9±3.2	69.0±0.1	69.1±0.7	8.44	0.0378
Coarse loam	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	15.2±0.7	16.7±1.3	12.5±0.4	13.6±0.5	8.95	0.0300
Clay	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
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
Albite	13±2^{a,b}	15±2^{a}	10±1^{a,b}	5±0.5^{b}	8.08	0.0444
pH	7.270±0.040^{a}	7.282±0.049^{a}	6.713±0.084^{b}	5.581±0.101^{c}	83.66	≤0.0001
SOM (%)	3.339±0.186^{a}	3.317±0.180^{a}	3.573±0.179^{a}	6.037±0.174^{b}	48.79	≤0.0001
CEC ($cmol_+ kg^{-1}$)	5.592±0.256^{a}	5.313±0.306^{a}	4.633±0.313^{a}	8.191±0.272^{b}	29.71	≤0.0001

[1]*Soil types according to the soil map Lanjarón 1:100.000 LUCDEME Project, Ministry of Agriculture, Fisheries and Foods (1993).*

Table 3: *Soil nutrient concentrations in the four study sites. Values represent means±standard errors. V: Percentage of bases saturation; C_{tot} and N_{tot}: soil C and N referred to total concentrations, respectively. Different letters above means indicate significant differences among sites (Tukey post-hoc test after one-ways ANOVAs). F: Value of the statistic, P: Critical probability.*

Soil Variable	Site 1	Site 2	Site 3	Site 4	F	*P*
C_{tot} (%)	1.047±0.115[a]	1.168±0.105[a]	1.304±0.130[a]	2.981±0.088[b]	44.632	≤0.0001
N_{tot} (%)	0.062±0.007[a]	0.068±0.006[a]	0.094±0.006[b]	0.204±0.006[c]	73.488	≤0.0001
C/N	16.36±0.72[a]	17.42±0.68[a]	13.32±0.68[b]	14,65±0.68[a,b]	6.774	0.0004
NH_4^+ (ppm)[1]	2.516±0.801	3.101±0.822	3.664±0.852	2.621±0.880	0.392	0.7591
NO_3^- (ppm)[1]	0.809±0.243	1.170±0.352	1.471±0.279	2.138±0.439	2.695	0.0521
N_{inorg}/N_{tot} (%)	0.626±0.182	0.804±0.249	0.540±0.122	0.233±0.061	2.117	0.1054
P_{inog} (ppm)[1]	4.960±1,253[a,b]	1.874±0.149[c]	2.645±0.383[b,c]	5.396±0.589[a]	10.123	≤0.0001
Ca ($cmol_+$ kg^{-1})[2]	3.238±0.244[a]	3.144±0.231[a]	1.705±0.231[b]	2.399±0.231[a,b]	9.130	≤0.0001
Mg ($cmol_+$ kg^{-1})[2]	1.311±0.067[a]	1.044±0.064[a]	0.653±0.064[b]	0.720±0.064[b]	20.970	≤0.0001
K ($cmol_+$ kg^{-1})[2]	0.0188±0.0016	0.0219±0.0015	0.0184±0.0015	0.0226±0.0015	2.051	0.1141
Na($cmol_+$ kg^{-1})[2]	0.00213±0.00071	0.00217±0.00067	0.00116±0.00067	0.00168±0.00067	0.490	0.6900
V (%)	81.811±5.398[a]	82.596±5.121[a]	55.622±5.121[b]	38.886±5.121[b]	16.932	≤0.0001
Fe (ppm)[2]	0.059±0.029	0.089±0.034	0.091±0.034	0.025±0.015	1.181	0.3227
Mn (ppm)[2]	0.369±0.080[a]	0.356±0.052[a]	0.651±0.088[a,b]	0.953±0.167[b]	6.254	0.0008
Zn (ppm)[2]	0.026±0.010	0.025±0.008	0.032±0.009	0.009±0.005	1.461	0.2321
Cu (ppm)[2]	0.015±0.007	0.017±0.008	0.014±0.007	0.005±0.005	0.552	0.6484

[1]*Extractable concentrations;* [2] *exchangeable concentrations.*

The pH, SOM, CEC, C_{tot} and N_{tot}, P_{inorg} and Mn were strongly correlated (Appendix A). For the pH, these correlations are negative (R^2>0.35, P<0.001 in all cases, Appendix A). Ca, Mg and pH presented also very high correlations, although for these nutrients the relationship with pH was positive (R^2>0.40, P<0.001 in all cases, Appendix A). Also meaningful are the correlations between NO_3^- and NH_4^+ (R^2=0.75, P<0.0001), Fe and Cu (R^2=0.59, P<0.0001), and between K and C_{tot} or P_{inorg} (R^2>0.39, P<0.001 in all cases, Appendix A).

The study sites can be differentiated by their soil nutrients and edaphic parameters according to the principal components obtained in the PCA (Fig.1B and D). The first and second principal components explain a 30.9% and 16.9% of the total variance (Fig. 1A and B). 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. 1A). According to the first component, the site 4 had the highest scores, followed by the site 3, and then sites 1 and 2, without significant differences between these latter two (P<0.0001; one-way ANOVA; Fig. 1B).

3.2. Wood nutrient concentrations

All nutrient concentrations in wood differed between sites, except Zn and C (Table 4). N was more concentrated in sites 2 and 3, so that the ratio C/N in the wood was lower in these sites (Table 4). The concentrations of P, Ca and Mg resulted the lowest in site 4. The patterns of K, Na and Fe were similar, becoming also lower as altitude increased (Table 4). However, the Mn concentration had again the opposite pattern, increasing at higher elevations (Table 4). Cu was lower in sites 1 and 4, and highest in site 2 (Table 4).

Table 4: *Nutrient concentrations in the burnt wood in the four study sites. Values represent means ± standard errors. Different letters above means indicate significant differences among sites (Tukey post-hoc test after one-ways ANOVAs). F: Value of the statistic, P: Critical probability.*

Wood Nutrient	**Site**				F	P
	1	**2**	**3**	**4**		
C (%)	50.49±0.08	50.60±0.08	50.63±0.07	50.37±0.07	2.456	0.0645
N (%)	0.163±0.004[a]	0.187±0.006[b]	0.189±0.005[b]	0.155±0.005[a]	11.841	≤0.0001
C/N	320.45±8.75[a]	284.77±10.29[b]	278.65±9.29[b]	342.8±12.99[a]	10.029	≤0.0001
N/P	18.90±1.58[a]	20.04±1.33[a,b]	22.54±1.42[b]	28.89±1.60[c]	14.019	≤0.0001
P (ppm)	99.74±5.17[a]	105.42±5.82[a]	91.49±3.55[a]	58.74±2.48[b]	25.946	≤0.0001
Ca (ppm)	622.48±43.54[a]	710.05±48.27[a]	627.32±35.37[a]	438.16±19.61[b]	10.114	≤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)	575.00±36.75[a]	504.31±27.15[a]	359.33±18.47[b]	203.19±13.51[c]	54.678	≤0.0001
Na (ppm)	69.39±4.58[a]	50.83±2.46[a,b]	40.32±2.56[b,c]	31.03±2.38[c]	19.672	≤0.0001
Fe (ppm)	12.562±2.035[a]	7.816±1.263[a,b]	7.136±1.212[a,b]	4.853±1.025[b]	3.9120	0.0097
Mn (ppm)	29.79±2[a]	30.00±1.58[a]	43.39±2.36[b]	67.04±3.25[c]	43.646	≤0.0001
Zn (ppm)	4.629±0.519	4.618±0.496	5.302±0.562	3.870±0.515	0.517	0.6711
Cu (ppm)	1.167±0.071[a]	1.556±0.094[b]	1.353±0.086[a,b]	1.145±0.072[a]	5.670	0.001

Strong correlations were found between the N, P and the majority-components of the burnt wood Ca, Mg and K being positive in all cases (Appendix B). These were especially important between K and P, Na or Mg (R^2=0.75, 0.59 and 0.54 respectively, $P<0.0001$ in all cases) and between P and Na (R^2=0.51, $P<0.0001$, Appendix B). High positive correlations were also found between Mg and Ca, Na or P ($R^2>0.36$, $P<0.0001$), and between Fe and Cu or Zn ($R^2>0.33$, $P<0.0001$). Additionally, Mn was inversely correlated to K (R^2=0.39, $P<0.0001$, Appendix B).

The study sites were also different according to the principal components of the wood composition, although in this case the sites can not be distinguished as clearly as according to their soil nutrients. The first and second principal components obtained in the PCA explained the 29.6% and 16.1% of the total variance, respectively (Fig. 1C and D). K, P and Mg contributed more to the first component and Zn, C and N to the second (Fig. 1C). According to the first component, the site 4 had the lowest scores, followed by site 3 and then sites 1 and 2 (one-way ANOVA; P<0.0001; Fig. 1D).

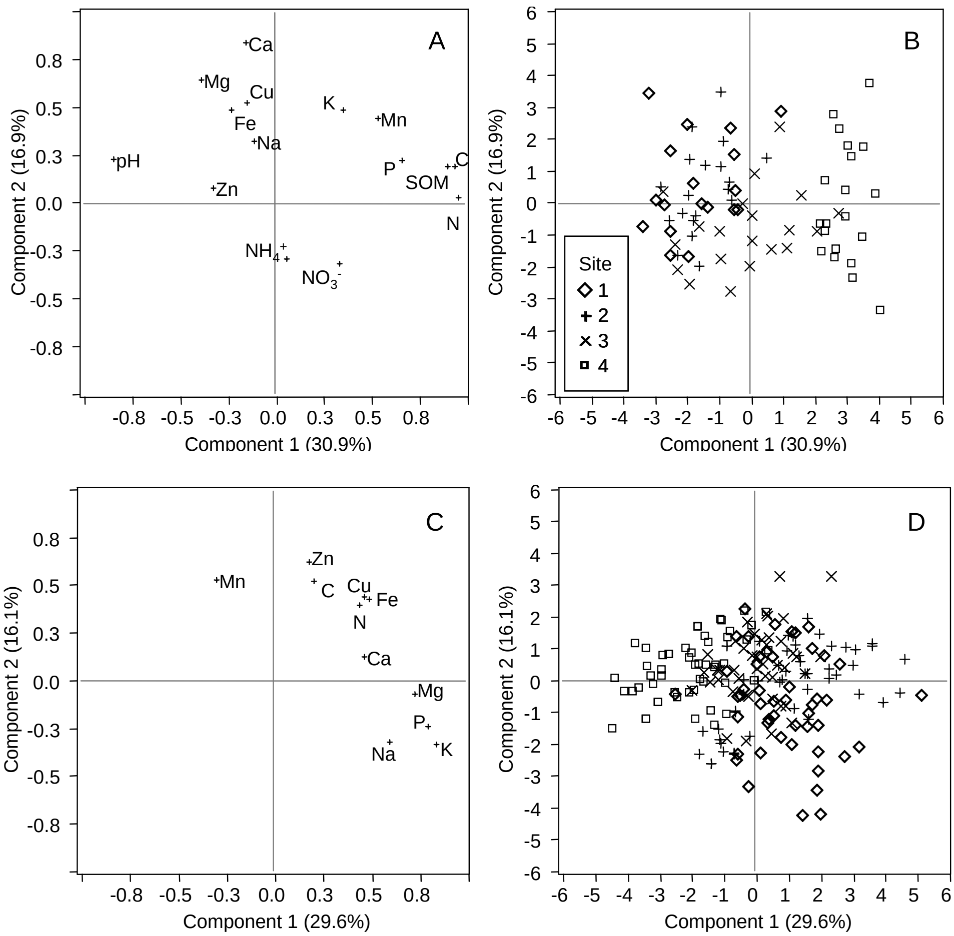

Figure 1: *Principal component analysis (PCA) of soil nutrient concentrations (A and B), and wood nutrient concentrations (C and D) in the four different study sites. For an easier visualization, only the two first principal components are represented. The percentage of contribution to the total variability is between parentheses. A and C refer to the relative contribution of each individual variable to the first two principal components, B and D refer to the value assigned to each wood sample according to these two components.*

In addition, correlations between the concentration of each nutrient obtained in the soil and in the wood were significant in the case of the Mn (R^2=0.98, P=0.0078) and the Zn (R^2=0.77, P=0.0787).

4. DISCUSSION:

The results of this study highlight the potential of burnt wood as a nutrient source for natural forest regeneration. Two years after the wildfire, soils in the study area showed very low nutrient availability, although they varied among the study sites likely due to differences of mineralogy and microclimate. On the other hand, the relative potential contributions of the wood pool were very relevant, 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 burnt wood still present. Moreover, the relative relevance of the burnt wood 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.

4.1. 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 (Blanco *et al.*, 2008; De Marco *et al.*, 2005; Fierro *et al.*, 2007; Yilziz *et al.* 2010). This is likely due to the combination of the young and poorly developed soils, especially at the highest elevations (Sánchez-Marañón *et al.*, 1996); the nutrient losses associated to the organic layer combustion by the wildfire (Certini, 2005; DeBano and Conrand, 1978; Raison, 1979); and the high slopes, which increase ash runoff and erosion (Fernández *et al.*, 2007; Shakesby, 2011; Thomas *et al.*, 1999). It is also worth mentioning the recurrent history of degradative land use (deforestation for agricultural uses, consequent nutrient depletion and vulnerability to soil erosion and further soil perturbation for reforestation; Padilla *et al.*, 2010). The pre-fire existence of a pine forest with a litter input of high C/N ratio and difficult mineralization could also have contributed to soil acidification and low nutrient availability (Moro and Domingo, 2000; Oyonarte *et al.*, 2008; van Wesemael, 1993), particularly in the case of the inorganic forms of N for plant assimilation. The low pool of nutrients found in the soil are insufficient to meet the annual requirements of available inorganic N (*ca.* 40 kg $ha^{-1}year^{-1}$), K (*ca.* 25 kg $ha^{-1}year^{-1}$), Zn (*ca.* 0.14 kg $ha^{-1}year^{-1}$), Fe (*ca.* 0.18 kg $ha^{-1}year^{-1}$), and to a lesser degree, of P (*ca.* 4 kg $ha^{-1}year^{-1}$) and Mn (*ca.* 0.85 kg $ha^{-1}year^{-1}$) of a mature coniferous forest (Cole and Rapp, 1981; Helmisaari, 1995; Johnson and Lindberg, 1992; Merino *et al.*, 2005; Miller, 1986). However, despite their low concentrations in this siliceous soil, Ca and Mg were not limiting.

Among sites, available or changeable soil nutrients were modulated 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 increase, 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 mineralization and prevalence of humification processes (Bohn *et al.*, 1993; Silver, 1998). The higher SOM determined, in turn, a higher CEC, 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 pattern of available P_{inorg} was determined by the CEC and presence of Ca, Mg and Fe in soil, which can form insoluble phosphates and lead to their precipitation (Porta *et al.*, 2003). Similarly, the contrasting effects of the decrease in pH and the highest CEC at the most elevated site explain the decreasing pattern of the base saturation with altitude (Porta *et al.* 2003). By contrast, the acidity increases the Mn solubility and availability (Godo and Reisenauer, 1980), and reinforces the retention of NO_3^- anions by the protoned surfaces of colloids (Ashman and Puri, 2002). In addition, the tendencies of lower Cu, Fe and Zn availability at the highest site are 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 (Thompson and Troeh, 2005).

4.2. Wood nutrient concentrations

The essential nutrients found in burnt stemwood are within the range of the concentrations reported in other studies for unburnt pine wood for most of the nutrients analized. 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%). The P concentrations here averaged 89.2 ppm *versus* the values of 45-180 ppm in other studies. Similarly, Ca, Mg and K averaged here 605.47 ppm, 238.35 ppm and 413.36 ppm, respectively, *versus* 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.*, 2008; Merino *et al.*, 2005; Palviainen *et al.*, 2010a, 2010b). This suggests that nutrient losses suffered by the large wood fractions were not relevant, since the effects of fire are usually limited to the bark and small fractions of the tree, even in intense stand-replacing fires (Stocks *et al.*, 2004; Wei *et al.*, 1997).

However, the concentrations of Fe, Mn, Zn, Cu and Na were very low compared to those found in unburnt wood (Alriksson and Eriksson, 1998; Harju *et al.*, 1997; Merino *et al.*, 2005; Saarela *et al.*, 2002). This could be likely due to their limited availability in soil (see above). This is also supported by the similar patterns of Mn, Zn and Cu both in the burnt wood and in the soil across sites, 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 others factors like the differences in composition among the dominant pine species could be also influencing (Alriksson and Eriksson, 1998; Augusto *et al.*, 2008, 2000; Baumann *et al.* 2006).

4.3. Relative magnitude of the nutrient reservoir in burnt wood

During a high-intensity wildfire, nutrients contained in fine nutrient-rich vegetal fractions, such as leaves and twigs, are mostly volatilized (Johnson *et al.*, 2005; Trabaud, 1994). However, our results show that a relatively high nutrient concentration was still present in burnt wood and that great amounts of biomass remained after the wildfire, both over and underground. Therefore, the magnitude of the nutrient pools in the remaining burnt wood was very relevant from a biochemical perspective. As an example, the N and P reservoirs represented by burnt wood (75.3 kg ha^{-1} and 3.9 kg ha^{-1}, Fig. 2) would be comparable to the inputs of atmospheric deposition for this area during 12 and 20 years, respectively (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 the equivalent to the estimated N input by fixation of *ca.* 1800 *Adenocarpus decorticans* per ha in a similar Mediterranean ecosystem during at least 75 years (1 kg $ha^{-1}year^{-1}$ of N; Moro *et al.*, 1996). Moreover, the magnitude of the nutrient reservoir in wood is likely even greater than that estimated, as the nutrient concentrations of roots (34% of the total biomass) and branches (11%) are usually higher than those of stemwood (Alriksson and Eriksson, 1998, Montero *et al.*, 1999).

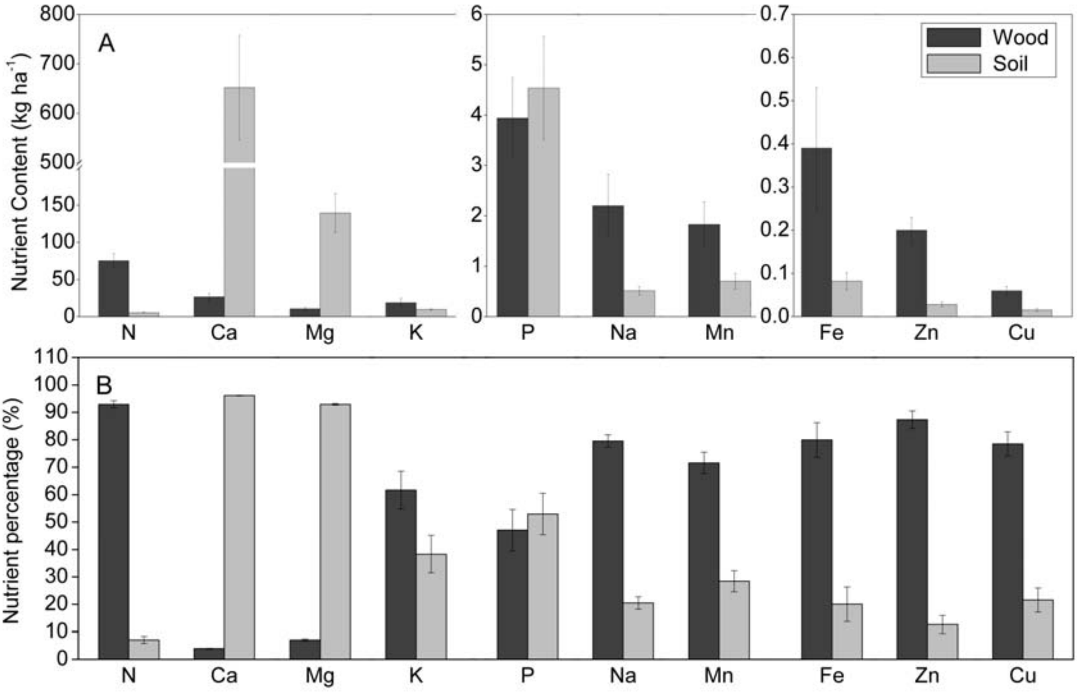

Figure 2: *Nutrient reservoir in the burnt wood and soil pools. A. Nutrient content in the burnt wood left after the wildfire and in the upper 10 cm soil layer. B. Nutrient percentage relative to the total content in the wood and soil pools. Nitrogen in the soil pool is referred to the extractable inorganic fraction (NH_4^+ + NO_3^-). Roots and bark are included in the biomass estimations, but 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 visualization.*

The relative contribution of the burnt wood in relation to the soil pool was especially high in the case of N, K, Na, Mn, Fe, Zn and Cu. The burnt 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 burnt wood 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 (Chapin *et al.*, 2002; Clarkson and Hanson, 1980; Ingestad, 1979). 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 burnt wood remained quite constant among study sites and was independent of the different microclimate, mineralogy, pre-fire dominant species and wood biomass inventory. Nonetheless, we are aware of possible underestimation of the soil nutrients pools, since 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. Summarizing, the results show that the remains of burnt wood biomass act as a relevant nutrient reservoir that help to regulate nutrient availability and ameliorate the nutrient losses associated with the wildfire.

4.4. Management implications

The prior forest conditions (tree density, tree diameter and age class, degree of management, nutritional status, etc.), fire intensity and the post-fire intervention will radically determine the magnitudes of nutrient pools in the burnt wood after a wildfire. In spite of that, the appropriate management of burnt trees after forest fires remains controversial (Beschta *et al.*, 2004; Donato *et al.*, 2006; Lindenmayer *et al.*, 2004, 2008; McIver and Starr, 2001). Results in 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 burnt trunks, often combined with the elimination of the remaining woody debris; Beschta *et al.*, 2004; McIver and Starr, 2001) is a widely applied management practise in forest ecosystems all over the world. However, it implies the retrieval of the nutrient pool contained in burnt wood that could otherwise be reincorporated to the ecosystem biogeochemical cycle. Moreover, post-fire salvage logging represents in these cases an additional perturbation beyond the wildfire, usually exceeding the resilience and adaptation capacity of the ecosystem (Lindenmayer *et al.*, 2008; Paine et al 1998). For this reason, the biochemical impacts of salvage logging should be also added to the considerations to be evaluated during the decision-making regarding the most suitable post-fire forest management strategy.

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APPENDIX A:

Table A1: *Pearson correlations between each pair of soil variables. Values indicate the coefficients of each correlation. Data of all sites are pooled.*

Variable	pH	SOM	CEC	C_{tot}	N_{tot}	NH_4^+	NO_3^-	P_{inorg}	Ca	Mg	K	Na	Fe	Mn	Zn	Cu
pH	1															
SOM	-0.67***	1														
CEC	-0.46***	0.81***	1													
C_{tot}	-0.70***	0.94***	0.78***	1												
N_{tot}	-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}	-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	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	-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

*Critical probabilities of the correlations (P) are indicated: *0.01<P≤0.05, **0.001<P≤0.01, ***P≤0.001.*

APPENDIX B:

Table B1: *Pearson correlations between each pair of wood nutrients. Values indicate the coefficients of each correlation. Data of all sites are pooled.*

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

*Critical probabilities of the correlations (P) are indicated: *0.01<P≤0.05, **0.001<P≤0.01, ***P≤0.001.*

CHAPTER 2:

EFFECT OF DECOMPOSING BURNT WOOD ON SOIL FERTILITY AND NUTRIENT AVAILABILITY IN A MEDITERRANEAN ECOSYSTEM

Sara Marañón-Jiménez and Jorge Castro

Under review

ABSTRACT

Burnt wood can represent a valuable nutrient reservoir for a regenerating ecosystem, helping to prevent the 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 burnt 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 burnt logs and in bare soil areas. Despite the relatively slow decay rates in this Mediterranean climate (*ca.* 10% of dry weight lost after four years), N and P were progressively released by logs, accounting for *ca.* 40% and 65% of the initial content respectively after 4 years. The presence of burnt logs consistently increased soil organic matter by around 18%, total C and N by 42% and 26%, respectively, dissolved organic C and N by 47%, inorganic P by 68%, and microbial biomass and nitrogen by 36% and 48%, respectively. By contrast, soil bulk density decreased by *ca.* 18% under logs compared to bare areas. Thus, the burnt wood was a useful natural element in the recovery of soil fertility and nutrient availability. Therefore, leaving the burnt wood onsite can enhance biogeochemical sustainability, microbiological processes and soil ecological functioning. The detrimental effect of post-fire salvage logging on soil fertility should therefore be considered when making management decisions.

Keywords

Carbon sequestration, salvage logging, silvicultural treatments, wildfire, wood decay, wood nutrient release.

1. 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 Conrand, 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 *et al.,* 2005; Iglesias *et al.,* 1997; Wan *et al.,* 2001; Yang *et al.,* 2003), as deposited nutrients can be lost by leaching and erosion especially in steep areas or sandy soils (DeBano and Conrand, 1978; Fernández *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 *et al.,* 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, 2010b; 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 in poor soils and yet with great nutrient demands (Costa-Tenorio *et al.,* 1998; Sardans *et al.,* 1995). 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 “hot spots” that foment 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 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 (Fernández *et al.,* 2007; Thomas *et al.,* 1999).

Since dead wood and coarse woody debris have been demonstrated to represent a major 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). However, 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 standing burnt 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, burnt 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 pool in burnt logs might be comparable to that reported for unburnt dead wood. Despite the potential relevance of this nutrient source via burnt 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 burnt wood (Grove *et al.,* 2009; Shorohova *et al.,* 2008; Wei *et al.,* 1997). Moreover, the effect of burnt wood on soil nutrient availability after a wildfire has not been specifically studied.

In this study, we seek to analyse the role of burnt wood on the soil nutrient availability and pools 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 burnt wood and soil. We hypothesise that the presence of burnt 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 burnt wood. As a result, the burnt wood 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 burnt pine wood during the first four years of decomposition in a Mediterranean mountain ecosystem across an altitudinal gradient; 2) assess the effect that burnt wood left over the ground exerts on the soil nutrient concentrations and pools; and 3) determine its 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 burnt wood on soil fertility and nutrient cycling.

2. MATERIAL AND METHODS

2.1. 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. 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 1465 m a.s.l.). Snow falls during winter, usually persisting from November to March above 2000 m a.s.l. The mean annual temperature is 12.3±0.4ºC at 1652 m a.s.l. (State Meteorological Agency, period 1994-2008. Ministry of Environment) and 7.8±0.7ºC at 2300 m a.s.l. (data from meteorological station, period 2008-10). Current vegetation is composed mainly of grass and forbs with a cover of approximately 70% (Castro *et al.,* 2010b).

The burnt pine stands occupy an altitudinal gradient from *ca.* 1300 to 2000 m a.s.l. Across this gradient, we established 3 study sites of *ca*. 3 ha each located at 1477, 1698, and 2053 m a.s.l. (sites 1 to 3, respectively). The sites were homogeneous in terms of fire intensity (high), slope (25 to 35%), situation (southwest exposure), bedrock (micaschists) and soil characteristics (Table 1). The dominant pine species at each site changed according to climatic conditions, with

Pinus pinaster Aiton. at site 1, *P. nigra* Arnold. at site 2, and *P. sylvestris* L. at site 3. Burnt tree density was 1200±40 individuals per hectare. Basal tree diameter ranged from 15.7±0.1 at site 3 to 18.3±0.1 at site 2 (Castro *et al.,* 2010b).

Table 1 *Main soil characteristics of the upper 10 cm soil layer in bare areas without burnt wood. 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)*

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 ($cmol_c$ kg^{-1} suelo)	5.6±0.3	5.3±0.3	4.6±0.3

Between January and March 2006 (4-6 months after the wildfire), the Forest Service felled the trees with the use of 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*. 1x1 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.

2.2. WOOD SAMPLING

2.2.1. INITIAL WOOD NUTRIENTS AND DRY WEIGHT

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", hereafter) are considered a representative sample of the initial characteristics of the burnt 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 70ºC 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 A). 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 of subsequent decayed wood discs by means of a regression equation established with the morphometric variables of the initial wood discs (Appendix A).

2.2.2. 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 per sampling point) after 2 years (June 2008) and 4 years (June 2010). 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 A). As before, a sample of sawdust (<1 mm) was also taken from each wood disc for chemical analysis.

2.3. 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 x 2 positions x 3 sites x 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 4ºC. 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 2M KCl, 0.5M K_2SO_4, and 0.5M $NaHCO_3$, respectively, and filtered through a Whatman GF-D filter. A 30 g subsample was oven dried at 105ºC 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 0.5M K_2SO_4 and 0.5M $NaHCO_3$ and filtered as above. Fumigated and nonfumigated extracts were frozen at -20ºC 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.

2.4. Chemical analyses

Carbon and nitrogen concentrations of the sawdust samples were determined using the combustion furnace technique at 850ºC (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 105ºC 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 550ºC 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 850ºC (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±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. Inorganic P (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). All nutrient fractions were referred to the corresponding dry weight of the soil.

2.5. 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 A). 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 A). The fragmentation of logs has a delay time of at least 25 years (Harmon, 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). For this, 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 remaining wood 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 effects 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}). Pools 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.

3. RESULTS

3.1. INITIAL WOOD NUTRIENTS AND DRY WEIGHT

Initial wood density varied 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 A). The initial N concentration in wood was also different among sites (P=0.0004, one way ANOVA), being 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 99.7±2.8 mg kg^{-1} (all sites pooled) and did not differ among sites (P=0.2011, one way ANOVA).

3.2. DECOMPOSITION AND TIME COURSES OF NUTRIENTS IN WOOD

The estimated percentage of the initial wood weight decreased mostly during the first two 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 two years and 10% after four 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).

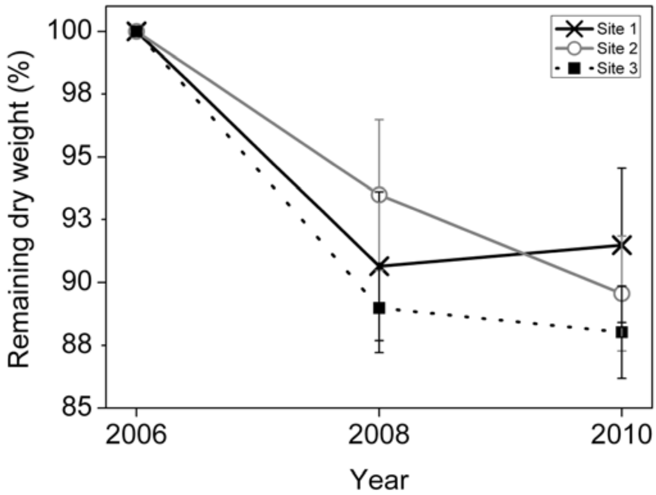

Figure 1: *Time course of the wood dry weight remaining after four years of decomposition under field conditions. Dry weight is expressed as percentage of the initial dry weight of the wood discs. Initial dry weight was estimated with regression equations constructed with the volume and dry weight of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

The composition of burnt wood varied over time at all study sites for all elements analysed (Table 2). Overall, the wood N and P concentrations and content decreased as wood decayed (Fig. 2). In the case of N, concentrations changed slightly during the first two years of decay, but then sharply fell within four years (*ca.* 35% of the initial concentration, Fig. 2A). Nonetheless, net N losses were detected even after the first two years of decay when expressed as N content per mass unit of remaining wood, reaching *ca.* 10% and 40% of the of the initial N content lost after two and four 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 within two and four years, respectively

(Figs. 2B and E). By contrast, the C concentration increased sharply within four years, despite an initial decrease during the first two 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 two years (Table 2, 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 2, 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 2).

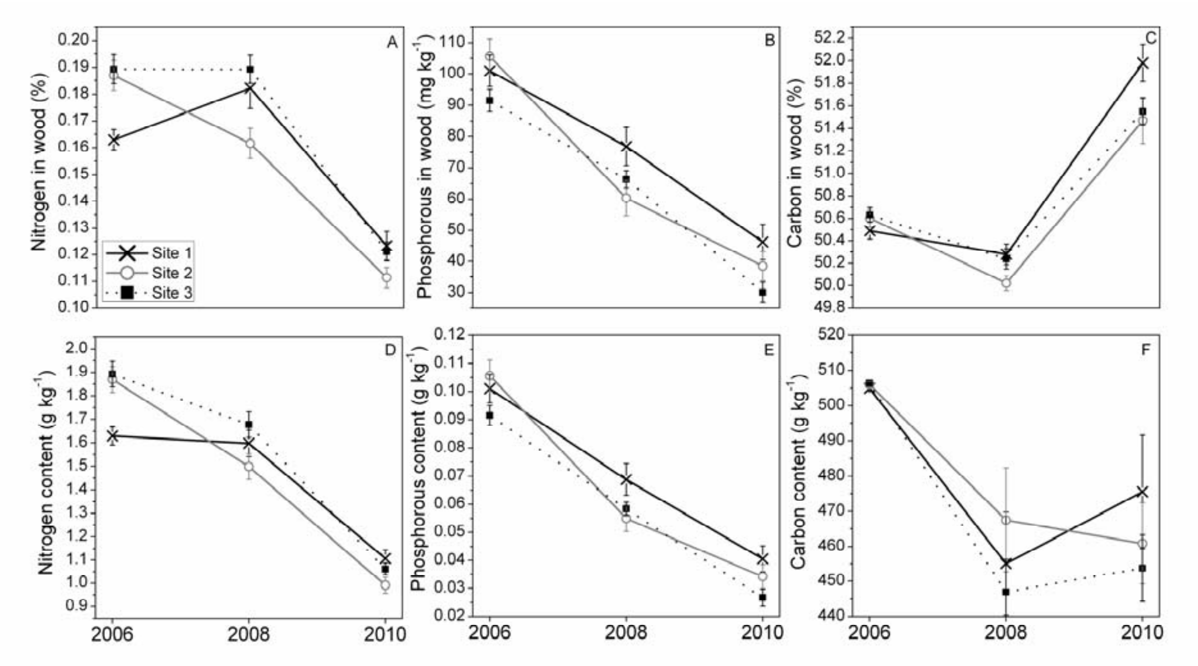

Figure 2: *Time courses of the nutrient and carbon concentrations and contents in the burnt wood. Panels A, B, and C refer to the nutrient and carbon concentrations; and panels D, E, and F refer to nutrient and carbon content per kg of burnt wood remaining. Nutrient content was calculated for each wood disc with the proportion of the initial dry weight remaining and its nutrient concentrations.*

Table 2: *Results of tests on wood nutrient concentrations and contents. Values of the F statistic are presented. df: degrees of freedom.*

		Nutrient concentration				Nutrient content			
Source	Site	C	N	P	C/N	C	N	P	df
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	

Critical probabilities of the correlations (P) are indicated:
**0.01<P≤0.05; †0.001<P≤0.01; ‡P≤0.001*

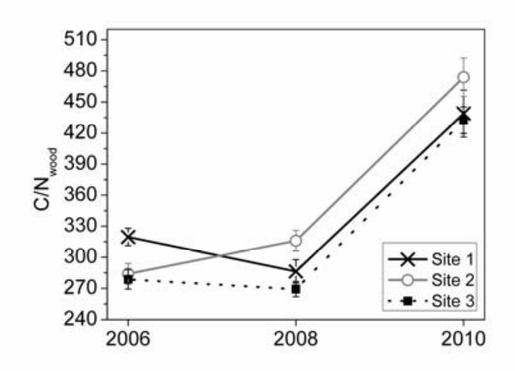

Figure 3: *Time courses of the C/N ratio of burnt wood during four years of decomposition under field conditions.*

3.3. EFFECT OF BURNT WOOD ON SOIL AND MICROBIAL FRACTIONS

Overall, the presence of burnt 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), 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 3, Fig. 4). This happened at all sites and either within two or four years, with no interactions with these factors (Table 3). 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 3). The pH was also slightly more basic under logs, although in this case the pattern varied across sites (Table 3, Fig. 4). By contrast, bulk density was lower under logs (Table 3, 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 3). 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 4) 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 3), all being higher in 2010 than in 2008 with the exception of N_{micro} (Fig. 5).

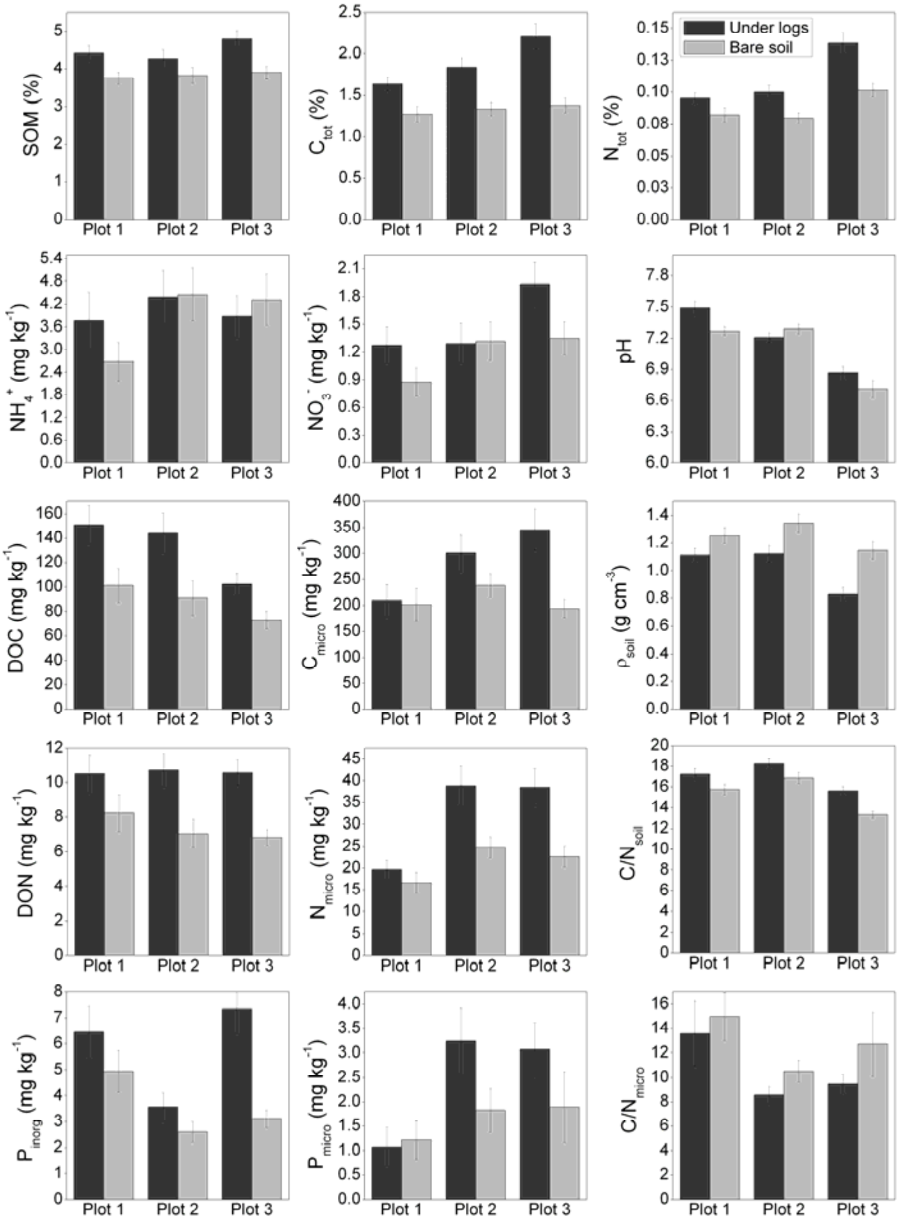

Figure 4: *Effects of the presence of burnt wood on the soil and microbial fractions, soil pH and bulk density. Bars represent mean soil pH, bulk density, organic matter (SOM), soil fractions (C_{tot}, N_{tot}, C/N_{soil}, NH_4^+, NO_3^-, DOC, DON, and P_{inorg}) and microbial fractions (C_{micro}, N_{micro}, 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 from 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.*

Table 3: *Results of tests on soil and microbial fractions. The effects of sampling years ("year"), experimental sites ("sites"), position in relation to the burnt logs (under or in bare areas; "position") and their interactions are shown. 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}), 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}). Values of the F statistic are presented. df: degrees of freedom.*

	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}	df
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

*Critical probabilities of the correlations (P) are indicated: *0.01<P≤0.05; †0.001<P≤0.01; ‡P≤0.001.*

Table 4: *Pools of soil and microbial fractions in positions located under logs and in bare areas for the upper 10 cm of soil. Values represent means±standard errors. UL: under logs, BS: bare 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

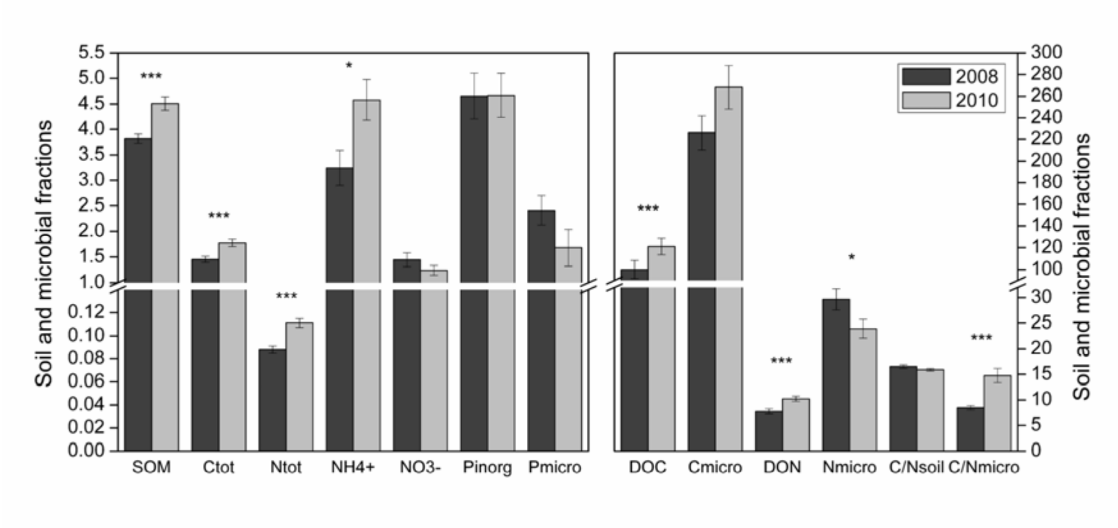

Figure 5: *Differences in soil and microbial fractions between sampling years. Different sites and positions (under logs and bare areas) are pooled. Significant differences among years are indicated: *0.01<P≤0.05, **0.001<P≤0.01, ***P≤0.001. Concentration units are % for SOM, C_{tot}, and N_{tot}, and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

4. DISCUSSION

Despite the relative slow decay rates of pine wood in this Mediterranean climate (*ca.* 10% of the initial wood weight was lost after four years) nutrients were progressively released from wood over the first four years of decay. Most of the soil and microbial fractions were radically affected by the presence of burnt wood scattered over the ground, with consistent increases in areas under burnt logs. Moreover, these effects became noticeable after two years of wood decomposition regardless of 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 burnt wood 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.

4.1. Decomposition and time courses of nutrients in wood

The results show that the burnt wood still had a high concentration of N (*ca.* 0.18%) and P (*ca.* 100 ppm), with similar or even higher values than those reported for unburnt wood (Alriksson and Eriksson, 1998; Augusto *et al.,* 2008; Merino *et al.,* 2005; Palviainen *et al.,* 2010a, 2010b). 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 remains unaffected (Stocks *et al.,* 2004; Wei *et al.,* 1997). Moreover, there was a strong release of nutrients contained in the burnt wood during the first four 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 two 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 microorganisms colonizing 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 burnt wood 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 (Garret *et al.,* 2008; Preston *et al.,* 1998; Sandström *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), since 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 decomposer activity (Ouro *et al.,* 2001; Weedon *et al.,* 2009). In summary, burnt wood 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.

4.2. EFFECTS OF BURNT WOOD ON SOIL AND MICROBIAL FRACTIONS

Overall, most of the soil and microbial fractions were higher and the pH more basic under burnt logs. This may be attributed either to the nutrient release by burnt wood (Hafner *et al.,* 2005; Kuehne *et al.,* 2008; Wei *et al.,* 1997) or to 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, burnt wood 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, 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 proportionally, 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 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 burnt 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, 2000). On the other hand, this implies that the nutrient pool 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 pools 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.

4.3. IMPLICATIONS FOR MANAGEMENT AND ECOSYSTEM PROCESSES

There is currently intense debate concerning the appropriate management of burnt trees after forest fires (Beschta *et al.,* 2004; Donato *et al.,* 2006; Lindenmayer *et al.,* 2004; McIver and Starr, 2001). Postfire salvage logging (felling and removing burnt 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.,* 2009; 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 burnt 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 burnt wood on the postfire soil fertility and nutrient mobilization has not been tackled to the date.

The present study shows that the burnt wood has a relevant role for nutrient cycling and the recovery of the soil fertility. Burnt wood biomass at the study site has been estimated at 43,052 kg ha^{-1} (66% aboveground and 34% belowground), according to allometric equations based on pine density and tree size (three sites pooled; Castro *et al.,* 2010b). This implies an initial pool of 76.2 kg ha^{-1} of N and

4.3 kg ha^{-1} of P, of which 31.8 kg ha^{-1} of N and 2.8 kg ha^{-1} of P were released after only four years. Moreover, its effect may be long lasting (Smaill *et al.,* 2008), as the nutrient release is slow and progressive. The reduction of the soil bulk density may also help to compensate for the detrimental effects that soil compaction can have on soil properties (Merino and Edeso, 1999). On the contrary, the removal of burnt wood, as during salvage logging operations, would translate to 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 can have detrimental effects on nutrient cycling and ecosystem functioning that should be considered when making management decisions.

5. CONCLUSIONS

The burnt wood after a wildfire still contains a great amount of nutrients that are released through decomposition, augmenting soil fertility and accelerating microbiological processes. Burnt logs therefore provide a valuable ecosystem service, as they enhance the biogeochemical sustainability, resilience, and functioning, which are key ecological properties for regeneration success.

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APPENDIX A : Estimation of the initial dry weight of the wood discs to calculate the dry weigh lost by the burnt 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 A1) 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 A1 *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. 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. Different letters indicate significant differences among sites at level α=0.05.*

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			

[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.

CHAPTER 3:

POST-FIRE SALVAGE LOGGING INCREASES WATER STRESS AND REDUCES SEEDLING GROWTH AND PERFORMANCE OF *Pinus Pinaster* IN THE SIERRA NEVADA (SE SPAIN)

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ABSTRACT

Intense debate surrounds the most suitable post-fire management related to the burnt wood for forest regeneration, but scant support is available from experimental studies. In this study, we experimentally analyze the effect of three post-fire management treatments on the growth and performance of seedlings of a serotinous pine (*Pinus pinaster*) in the Sierra Nevada (SE Spain), a Mediterranean mountain range. Treatments were applied 7 months after the September 2005 fire and differ in the degree of intervention, ranging from "Non Intervention" (NI, all trees left standing) to "Cut plus Lopping" (CL, felling most of the trees, cutting off the main branches, and leaving all the biomass *in situ* without mastication), and "Salvage Logging" (SL, felling and pilling up the logs, and masticating the woody debris). After three years, a random sample of naturally regenerating young pines was harvested (aboveground biomass) and analysed for growth, biomass, nutrient content, and leaf $\delta^{13}C$ and $\delta^{15}N$. Total aboveground pine seedling biomass was similar among treatments, although it tended to be higher in CL. The height growth and biomass increase during the second and third growing seasons (years 2007 and 2008) was also higher in CL and NI treatments, and lowest in SL. Leaf nutrient concentrations were similar among treatments. Pines from SL also showed higher leaf $\delta^{13}C$ values, indicating more severe water stress in this treatment. By contrast, the leaf $\delta^{15}N$ tended to show the opposite pattern, with the lowest values in SL, suggesting less N sources and mineralization in the soil. Overall, the results support the contention that salvage logging has a detrimental effect on pine growth and performance in relation to treatments where burnt logs and branches are left *in situ.* This is likely associated with the amelioration of microsite conditions by the presence of remaining wood, which increases soil moisture and nutrient availability through wood decomposition.

Key words: Burnt wood, facilitation, shelter structures, *Pinus pinaster* regeneration, post-fire restoration, salvage harvesting, pine nutrient status, microclimate amelioration, wood nutrient release.

1. INTRODUCTION

A current controversial issue among restoration ecologists and forest managers concerns the appropriate management of dead burnt trees after fire. Post-fire salvage logging (*i.e.:* the felling and removal of the burnt tree trunks, also often eliminating the remaining woody debris [branches, logs, and snags] by chipping, mastication, fire, etc.) has historically been routinely and widely practiced by forest administrations around the world (Bautista *et al.*, 2004; Beschta *et al.*, 2004; Lindenmayer and Noss, 2006; McIver and Starr, 2000; Spanos *et al.*, 2005), particularly in the case of burnt conifer forests. However, there is currently intense debate about the suitability of this approach, and an increasing number of studies are showing that the felling and removal of burnt trees using ground-based yarding techniques may impact plant regeneration in several ways (Beschta *et al.*, 2004; Donato *et al.*, 2006; Lindenmayer and Noss, 2006; McIver and Starr, 2000, 2001; Stark *et al.*, 2006). For example, salvage logging may increase soil erosion and compaction (Fernández *et al.* 2007; McIver and McNeil, 2006; Purdon *et al.*, 2004; Wondzell, 2001), precluding seedling emergence and establishment (Donato *et al.*, 2006). Indeed, the bank of seedlings or resprouters usually present (or starting to appear) at the moment of salvage operations can be also damaged, thus reducing seedling density at the starting point of succession (Fernández *et al.*, 2008; Greene *et al.*, 2006; Martínez-Sánchez *et al.*, 1999; McIver and Starr, 2000, 2001), with the consequent reduction of the regeneration capacity. As a result, there are increasing calls to implement less aggressive post-fire treatment policies and actions, including non-intervention, associated with evidence that snags and decaying burnt wood are important components of natural systems that promote ecosystem recovery and diversity (Beschta *et al.*, 2004; DellaSala *et al.*, 2006; Hutto, 2006; Lindenmayer *et al.*, 2004).

The factors that enhance seedling recruitment, as well as the later growth and performance after a perturbation will vary depending on the species and the limiting factors at each particular site. Mediterranean ecosystems are particularly characterised by moisture limitation and are frequently established over poor soils with low nutrient availability (Costa-Tenorio *et al.,* 1998; Sardans *et al.*, 1995). Therefore, the reduction of drought severity and the supply of a source of nutrients would bring to a higher probability of vegetation survival (Castro *et al.*, 2011; Jiménez *et al.*, 2007; Querejeta *et al.*, 2008; Matías *et al.*, 2011; Siles *et al.*, 2010). Water limitation can be especially accentuated after a stand replacing fire, since soil permeability and albedo decrease whereas radiation incidence and soil heating intensifies over the soil (Certini, 2005). In this regard, woody debris, remains of thinning, litter and mulching have been widely considered and used as elements to maintain soil moisture (Devine and Harrington, 2007; Harmon *et al.*, 1986; Jiménez *et al.*, 2007; Lindenmayer *et al.*, 2008; Martínez-Sánchez *et al.*, 1999; McIver and Starr, 2000; Smaill *et al.*, 2008; Stoddard *et al.*, 2008). In any case, organic materials covering the soil surface contribute in general to increase water availability for plant uptake, and specifically, the burnt wood scattered over the soil similarly increased soil moisture during the summer drought at this study site (Castro *et al.*, 2011).

Fires also provoke a sharp loss of nutrients from the ecosystem, which are contained in the nutrient-rich organic pools with low to medium temperature of ignition (litter, leaves, twigs and branches of small diameter) (Carter and Foster, 2004; DeBano and Conrad, 1978; Neary *et al.*, 1999; Trabaud, 1994; Whelan, 1995). Nonetheless, a great amount of logs and coarse woody debris of greater diameter usually remain after a wildfire (Brais *et al.*, 2005; Wei *et al.*, 1997). In fact, they can represent a potential nutrient reservoir (Harmon *et al.*, 1986; Johnson *et al.*, 2005; Kappes *et al.*, 2007; Merino *et al.*, 2003; Zhou, 2007), as a result of the high biomass and nutrient concentrations similar to that of unburnt wood in cases when only the bark and the outer layer have been scorched (Wei *et al.*, 1997). Nutrients contained in wood are progressively released as decomposition occurs (Brown *et al.*, 1996; Ganjegunte *et al.*, 2004; Ouro *et al.*, 2001; Wei *et al.*, 1997), being retained by the soil (De Marco *et al.*, 2005; Pérez-Batallón *et al.*, 2001; Smaill *et al.*, 2008) and becoming available for the regenerating vegetation (Augusto *et al.*, 2000; Jiménez *et al.*, 2007; Stoddard *et al.*, 2008). Thus, burnt wood may improve plant regeneration both by microclimatic amelioration as well as by the nutrient supply to the soil.

In this study, we seek to determine the effect of burnt-wood management on the growth and performance of pine seedlings naturally regenerating after a fire. In September 2005, the Lanjarón fire burned *ca.* 3500 ha in 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 by the maritime pine before fire (*Pinus pinaster* Aiton), a serotinous pine that often regenerates abundantly after fire (Fernandes and Rigolot, 2007; Fernández *et al.*, 2008; Rodrigo *et al.*, 2004; Tapias *et al.*, 2001). Three silvicultural treatments that differed in the degree of ecosystem intervention were established, ranging from no intervention to the conventional salvage logging. In a previous study, we demonstrated that salvage logging reduced the recruitment of pines and affected survival (Castro *et al.*, 2011). Here, we explore the mechanisms that provoked differences among treatments in three years old seedlings. We hypothesized that burnt logs and branches left *in situ* could improve soil fertility through the nutrient release by wood decomposition. Seedlings could have more access to nutrients, resulting in a higher growth and/or nutritional status. We also hypothesize that the presence of burnt trees and woody debris will improve the water status of pine seedlings due to the shade provided at the ground level (lower soil heating, reduction of evapotranspiration, retention of soil moisture; Castro *et al.*, 2011). This would translate to a lower water stress in seedlings that grow under the shelter of burnt trees and coarse woody debris, which will be reflected in its carbon isotopic signal. Altogether, this will imply a relatively lower vigour of seedlings growing in the salvaged area.

2. METHODS

2.1. STUDY SITE AND SPECIES

The study site is located in Sierra Nevada Natural and National Park (SE Spain), in an area that burned in September 2005 in the Lanjarón Fire. The fire burned *ca.* 1300 ha of pine forests of different species with trees 35 to 50 years old, depending on the stand, distributed along an elevational / moisture gradient according to their ecological requirements. The maritime pine (*Pinus pinaster*) was common at lower elevations (*ca.* 1400 m a.s.l.). This species is native in the area, although it was extensively planted about 50 years ago to re-establish the tree cover on long-deforested hillslopes, using terraces made with bulldozers, previously a common reforestation practice on hillsides in Spain. Each terrace stairstep is composed of a steep cutslope or "backslope" (~90 cm high), and the nearly flat area of the terrace ("terrace" hereafter) of ~3 m in width. The climate of the area is Mediterranean-type, with rainfall concentrated in spring and autumn, alternating with hot, dry summers. Mean annual precipitation was 470±50 mm, with summer precipitation (June, July and August pooled) of 17±4 mm (1988-2008 period; climatic data from a near meteorological station). The mean annual temperature was 12.3±0.4ºC at 1652 m a.s.l. (State Meteorological Agency, period 1994-2008; Ministry of Environment).

Pinus pinaster Aiton grows in the western Mediterranean basin and Atlantic area 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 (Tapias *et al.*, 2001) that protect the seeds from intense heat (Reyes and Casal, 2002). Seeds may still be viable after short heat pulses of above 100ºC (Herrero *et al.*, 2007; Martínez-Sánchez *et al.*, 1995), and the regeneration of the species after fires relies mostly on the aerial seed bank. An abundant seedling bank emerged from late February 2006 (*ca.* 6 months after the fire), and thus maritime pine naturally regenerated in the area (Castro *et al.*, 2011). Accompanying post-fire vegetation was composed mainly of grass and forbs, with a mean cover of approx. 70%. (Castro *et al.*, 2010). The most common perennial species were *Ulex parviflorus, Festuca scariosa, Dactylis glomerata*, and *Euphorbia flavicoma*.

2.2. Experimental design

From 21 April 2006 to 10 May 2006 (*ca.* seven months after the 2005 forest fire), a plot of 17.7 hectares was established at 1400 m a.s.l. approx., where three replicates of each of the following treatments were implemented in a random spatial distribution: 1) “Non Intervention” (NI), leaving all of the burnt trees standing. 2) “Cut plus Lopping” (CL), a treatment where about 90% of burned trees were cut and felled, with the main branches also lopped off, but leaving all the cut biomass *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), tress were cut and the trunks cleaned of branches with the use of chainsaws. Trunks were manually piled (groups of 10-15) and the woody debris was masticated using a tractor. The Forest Service planned to remove the trunks with a log forwarder in this treatment, but this step was later cancelled due to difficulties in precisely operating machinery within the spatial arrangement of the plots.

The resulting 9 experimental replicates had a size that averaged 2 hectares and was similar among treatments (Kruskal-Wallis test, P>0.05). Salvage logging is the usual post-fire action taken by the local Forest Service, and it was fully implemented throughout the rest of the burnt area where the experimental plots were located (removing the logs with a log-forwarder in this case). The three treatments differed therefore in the degree of intervention (maximum in SL, intermediate in CL, minimum in NI) and in the habitat structure generated (minimum habitat complexity in SL). The CL treatment differed from NI in the above-ground habitat structure; we hypothesize that wood decomposition would be faster in CL due to contact of burnt wood with the soil, prompting nutrient cycling and increasing soil fertility. All replicates were homogeneous in terms of orientation (SW), slope (*ca.* 30%), fire intensity (high intensity) and bedrock (micaschist).

The fire was moderate to high in severity, consuming or totally scorching most of the tree crown. Burnt tree density before treatment application was 1477±46 individuals per hectare (estimated by counting the number of trees in four 25x25 m quadrats per experimental replicate two months after the fire) and did not differ among treatments (Kruskal-Wallis test, P=0.66). Basal trunk diameter was 17.1±0.2 cm in NI, 17±0.2 cm in SL and 18.1±0.2 in CL (estimated for 30 random trees per quadrat, thus 120 trees per replicate). Burnt trees fell in the course of consecutive years. The fallen fraction (measured in February of each year) was 0.0% in 2006 and 2007, and 13.3±0.3% in 2008 (last year of this study; measured from 100 marked trees per replicate in NI and CL; Castro *et al.*, 2010). Thus, the NI treatment kept a vertical structure of standing trees throughout the study period.

2.3. SEEDLING SAMPLING

For each experimental replicate, we harvested 12 seedlings (cut at the ground level; 108 seedlings in total). Harvesting was performed in September 2008 (after three growing seasons) in order to ensure that the shoot elongation period of that year had finished. Seedling density was very low on the backslopes (Castro *et al.*, 2011), and thus we restricted the seedling harvesting to the flat area of the terraces. Seedlings were chosen following a stratified random procedure, starting from a initial random point and alternating among the centre and side positions of the terrace close to the backslopes, along the width of the terrace. In only one isolated case was a clearly damaged pine seedling discarded and replaced by another seedling. In order to avoid possible effects of herbivory in the seedling growth pattern, we initially planned to discard those affected by herbivory, but no herbivory was detected (see also Castro *et al.*, 2011) and this was finally not needed. For each seedling, we monitored the following variables:

1) Growth parameters, that included i) total height, ii) leader shoot elongation during the growing season of 2007 (measuring the length achieved in this season), iii) leader shoot elongation during growing season of 2008 (measured in a similar way), iv) basal trunk diameter, v) total biomass, vi) biomass of shoots of 2007, vii) and biomass of shoots of 2008. Biomass was estimated after oven-drying at 60ºC to constant weight (> 48 h).

2) Carbon and nutrient concentration (N, P, Ca, Mg, K, Na, Fe, Mn, Zn, and Cu) in pine needles. After drying, two subsamples of needles were taken from the leader shoot corresponding to the elongation of 2007 and 2008 of each seedling, they were ground with a dry ball-mill and homogenized. Total C and N were analysed by combustion at 850ºC with a Leco TrueSpec Autoanalyzer (St. Joseph, MI, USA). Ground samples were ignited to 750ºC 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] with a Perkin Elmer 2400 spectrophotometer (Waltham, MA, USA). The rest of nutrients were analysed only for needles of the shoot of 2008 by atomic absorption with a Perkin Elmer 5100 spectrometer.

3) Carbon and nitrogen isotopic composition. Another subsample of the needles from the leader shoot of 2008 was ground and its isotopic C and N was analysed with a micromass isotope ratio mass spectrometer GV Instruments Iso Prime (Youngstown, OH, USA). 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‰. Analyses were performed on whole-leaf tissue rather than extracted cellulose, because of strong positive correlations observed between $\delta^{13}C$ of whole tissue and cellulose (Ehleringer and Osmond, 1989; West *et al.*, 2001). The abundance of stable isotopes is presented in delta notation (δ), relative to a standard:

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

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

The C isotope analysis has been used as an integrative method to estimate the long term water use efficiency (*WUE*) of plant tissue over time in response to drought (Lajtha and Marshall, 1994). *WUE* is defined as:

$$WUE = A/g \qquad (2)$$

where A is the photosynthetic rate and g is the stomatal conductance (Scheidegger *et al.*, 2000). While both A and g can be negatively affected by water stress, *WUE* and $\delta^{13}C$ increase in response to drought, as g usually decreases more sharply than does A (Querejeta *et al.*, 2008). However, A is determined by biochemical factors (amount and activity of Rubisco), which are driven by temperature, irradiance and nutrient availability (Scheidegger *et al.*, 2000). Leaf N concentration is nonetheless a good indicator of the maximum carboxylation capacity (Adams and Kolb, 2004; Field and Mooney, 1986).

The $\delta^{15}N$ has been frequently used as an integrator of N cycle processes in soil (Peñuelas *et al.*, 1999; Robinson, 2001), where in general, an enrichment in ^{15}N is indicative of higher mineralization and more active N cycling (Nadelhoffer and Fry, 1994; Craine *et al.*, 2009). Despite the limitations related to the absence of $\delta^{15}N$ values in the soil, discrimination during N uptake by plants is considered not to be relevant in ecosystems where N is limiting (Nadelhoffer and Fry, 1994), as in this case (available inorganic N in soil, as a sum of NH_4^+ and NO_3^-, is <4.3±0.5 ppm). Thus, the $\delta^{15}N$ signatures of the soils are imprinted in the $\delta^{15}N$ of plants that utilize the soil N pools for their nutrition. Foliar $\delta^{15}N$ therefore have the potential to characterize N turnover in the soil and the source of N used by plants as an integrative proxy (Kahmen *et al.*, 2008; Querejeta *et al.*, 2008).

3. 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 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.

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 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 parameters of the shoot were also explored by Pearson correlations.

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.

4. RESULTS

4.1. GROWTH PARAMETERS

Overall, the growth parameters measured in the whole seedling (total biomass and height and basal trunk diameter) proved higher in CL, although only the total height showed significant differences among treatments, due to the relatively high random variance among replicates (Table 1; Fig. 1).

On the other hand, the annual growth (both as elongation and biomass of shoots) was the lowest in SL (Table 1; Fig. 2). This pattern was consistent in the shoots of the second and third growing season (2007 and 2008), but differences were significant only in the shoots of the last year (Table 1; Fig. 2).

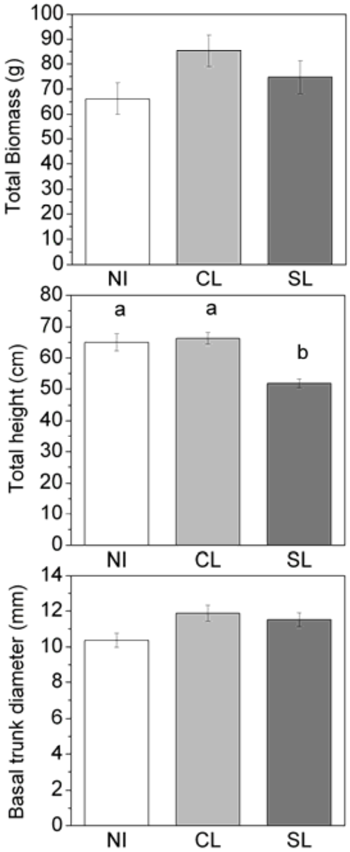

Figure 1: *Growth parameters of pine seedlings three growing seasons after the wildfire in the different post-fire treatments of burnt wood. NI: non intervention, CL: cut plus lopping, SL: salvage logging. Different letters above bars indicate significant differences among treatments (Tukey HSD test after mixed ANOVAs).*

Table 1: *Summary of the effects on the growth parameters and the carbon isotopic composition of the pine seedlings. Contrasts were performed by the method of the restricted maximum likelihood (REML). 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.*

Growth Parameter		**Treatment Effect**			**% Variance of the Total Random Components**	
		F	df	*P*	Replicate	Residual
Total biomass (g)		0.87	2, 5.99	0.4643	17.74	82.26
Total height (cm)		7.86	2, 6.00	0.0211	7.55	92.45
Basal trunk diameter (mm)		1.00	2, 5.98	0.4211	20.44	79.56
Leader shoot elongation (cm)	2007	3.37	2, 6.00	0.1046	5.24	94.76
	2008	14.80	2, 6.01	0.0047	-1.36	101.36
Shoot Biomass (g)	2007	3.01	2, 6.00	0.1241	-0.80	100.80
	2008	8.71	2, 5.88	0.0175	0.29	99.71
$\delta^{13}C$ (‰)	2008	17.58	2, 6.04	0.0030	6.26	93.74

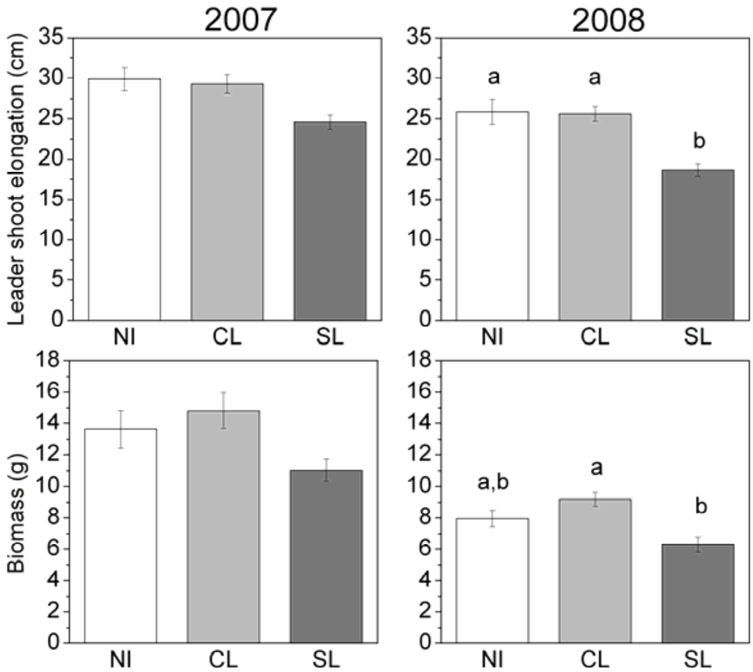

Figure 2: *Growth parameters of the shoots of pine seedlings corresponding to the second (2007) and third (2008) growing season after the wildfire in the different post-fire treatments of burnt wood NI: non intervention, CL: cut plus lopping, SL: salvage logging. Different letters above bars indicate significant differences among treatments (Tukey HSD test after mixed ANOVAs)*

4.2. Nutrient concentrations in pine needles

Carbon and nutrient concentrations in the pine needles did not differ among treatments, neither for the shoot part elongated during the second growing season (2007), nor for the corresponding one of the third growing season (2008) (Table 2).

In addition, no significant correlations were found between nutrient concentrations and biomass or shoot elongation in 2008. An exception was the correlation between the growth parameters of shoots and needle N concentration, although in these cases correlations were not very strong (R^2=-0.22, P=0.021 for shoot biomass; R^2=0.21, P=0.030 for shoot elongation; all treatments pooled).

Table 2: *Concentrations of carbon, nutrients and isotopic N in the pine shoot needles and their effects. Contrasts were performed by the method of the restricted maximum likelihood (REML). 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). Means±standard errors of each parameter in the different treatments are also presented. Different letters indicate significant differences among treatments (Tukey HSD test after mixed ANOVAs). F: value of the F 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. NI: non intervention, CL: cut plus lopping, SL: salvage logging.*

Shoot	**Parameter**	**Treatment**						**% Variance of the Random Components**	
		NI	CL	SL	F	df	P	Replicate	Residual
2007	C (%)	51.96±0.16	52.35±0.14	52.41±0.20	0.57	2, 5.93	0.5954	22.14	77.86
	N (%)	0.98±0.04	1.02±0.03	1.00±0.03	0.05	2, 5.98	0.9465	24.43	75.57
	P (ppm)	496.91±43.48	598.78±50.29	577.65±52.43	0.18	2, 6.02	0.8384	38.32	61.68
2008	$\delta^{15}N$	1.03±0.32	0.76±0.28	0.19±0.39	0.36	2, 6.01	0.7116	31.63	68.37
	C (%)	49.50±0.09	49.43±0.07	49.79±0.07	3.02	2, 6.01	0.1239	5.96	94.04
	N (%)	1.00±0.04	0.91±0.02	0.93±0.03	1.76	2, 5.99	0.2507	5.86	94.14
	P (ppm)	492.74±23.50	457.70±18.49	485.91±20.43	0.20	2, 6.02	0.8256	27.28	72.71
	Ca (ppm)	1762.53±64.24	1724.60±70.39	1678.65±58.10	0.63	2, 5.73	0.5678	-2.68	102.68
	Mg (ppm)	889.66±43.66	832.31±27.51	876.74±26.93	0.34	2, 5.99	0.7272	11.57	88.43
	K (ppm)	6034.75±243.52	6363.65±181.57	6187.55±245.84	0.08	2, 6.00	0.9268	35.17	64.83
	Na (ppm)	593.26±93.97	330.54±31.79	323.10±28.16	0.68	2, 6.01	0.5427	32.98	67.02
	Fe (ppm)	51.31±3.56	63.19±2.71	64.69±3.52	2.13	2, 5.78	0.2032	11.00	89.00
	Mn (ppm)	48.81±5.01	48.13±5.14	61.86±4.79	1.54	2, 5.80	0.2911	7.67	92.33
	Zn (ppm)	16.63±1.31	13.69±0.72	14.17±1.13	0.35	2, 5.95	0.7199	24.53	75.47
	Cu (ppm)	3.12±0.26	3.01±0.24	3.50±0.27	0.39	2, 6.07	0.6926	19.84	80.16

4.3. CARBON AND NITROGEN ISOTOPIC COMPOSITION

The C isotopic composition of pine needles of 2008 was the lowest in NI, followed by CL and SL (Table 1, Fig. 3). The $\delta^{13}C$ was not correlated with the N concentrations in needles (P=0.0969; all treatments pooled). Furthermore, an inverse correlation was found among $\delta^{13}C$ and shoot growth (R^2=-0.21, P=0.030 for shoot biomass; R^2=-0.40, P<0.0001 for shoot elongation; all treatments pooled).

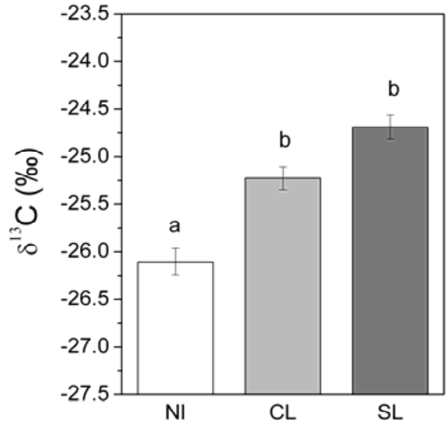

Figure 3: *Carbon isotopic composition of pine needles from the part of leader shoot elongated in 2008 in the different post-fire treatments of burnt wood. NI: non intervention, CL: cut plus lopping, SL: salvage logging. Different letters above bars indicate significant differences among treatments (Tukey HSD test after mixed ANOVAs).*

Conversely, the pattern of isotopic N in the same pine needles was inverse, with the highest values in NI and the lowest in SL, although in this case differences among treatments were not significant (Table 2).

5. DISCUSSION

Results of this study highlight the important role that the remaining burnt wood can have over the growth and performance of regenerating pine seedlings after a wildfire. After three growing seasons, pine seedlings growing in the CL treatment tended, overall, to have greater vigour and size. Moreover, their annual growth (both as annual shoot elongation and biomass) was also higher in CL and NI compared to SL. On the other hand, the nutrient status of pine seedlings did not vary with the silvicultural treatment, likely due to the low plasticity of the nutrient composition of the maritime pine (Bará, 1990; Martins *et al.*, 2009). However, these results would imply greater nutrient uptake by seedlings in the treatments where burnt wood was left *in situ.*

Standing burnt trees and coarse woody debris scattered over the ground can act as shelter structures for the understorey and regenerating vegetation (Perry *et al.*, 1989; Purdon *et al.*, 2004). In a previous study, we verified that the radiation incidence was reduced by the presence of burnt wood by *ca.* 30%. As a consequence, the soil temperature was ameliorated and the soil moisture increased (Castro *et al.*, 2011). In this study, the lowest C isotopic discrimination of pine seedlings in SL is indicative of higher water use efficiency. In the absence of additional measurements (*i.e.:* water potential, oxygen isotopic composition), this could be attributed to either a higher photosynthetic capacity or a reduction in stomatal conductance (Scheidegger *et al.*, 2000). However, the growth of seedlings was also the lowest in SL, and the nutritional status neither differed among treatments or was correlated with its isotopic signal. Thus, the evidence does not support the hypothesis of a higher photosynthetic capacity in SL and likely denotes a stronger control of the water losses through evapotranspiration. Therefore, pine seedlings in all probability undergo higher water stress in SL, whereas this limitation is alleviated by the presence of burnt wood in the other treatments.

Burnt wood can also represent a potential source of nutrients for the soil that will be progressively released during its decomposition (Brown *et al.*, 1996; Ganjegunte *et al.*, 2004; Harmon *et al.*, 1986; Palviainen *et al.*, 2010a, 2010b; Wei *et al.*, 1997). In fact, the tendencies in the N isotopic composition of needles point to a higher mineralization in the soil where burnt wood was present and ultimately, to more active N cycling among soil, plants, and soil microorganisms (Craine *et al.*, 2009). Trends in isotopic N could, however, be influenced by possible differences in the contribution of symbiotic N fixation among treatments, where in general, plants that rely on soil N are more enriched in ^{15}N than plants that obtain N from symbiotic fixation (Nadelhoffer and Fry, 1994; Craine *et al.*, 2009). Mycorrhization rates are generally higher in poor soils, since the shortage of carbohydrates and available N in soil increase the dependence of the symbiotic association between mycorrhizas and plants to satisfy their requirements (Côrrea *et al.*, 2011; Blanke *et al.*, 2005; Kazantseva *et al.*, 2009). Therefore, the lower values in SL could be also due to the higher mycorrhization rates in pine roots compared to the other treatments, which would be another indication of higher limitation of C and N sources to the soil in this treatment. This would represent further evidence of improved soil conditions for seedling performance provided by the presence of burnt wood. Consequently, pine seedlings incorporate available nutrients from soil while keeping their nutritional status constant. Thus, the nutrient supply provided by woody debris also contributes to faster seedling growth and biomass gains, as well as to higher rates of nutrient uptake and mobilization. Moreover, the accentuated differences in growth parameters in the shoots of the last year suggest that the facilitative effect provided by the remaining wood could be cumulative over time, as the remaining wood releases its nutrients and ameliorates the soil microclimate.

The degree of post-fire intervention and management of the remaining wood after a wildfire also determines the magnitude of the prevailing biomass pool, the diameter of wood fractions, and the degree of contact between wood and soil.

These factors can exert an influence on several ecosystem processes and, in turn, on vegetation recovery (Beghin *et al.*, 2010; Fernández *et al.*, 2008; Martínez-Sánchez *et al.*, 1999). As an example, in CL a higher degree of contact between wood and soil compared to NI will facilitate the colonization by decomposers and will help to retain in the wood substrate the level of moisture needed for their activity (Harmon *et al.*, 1986). Thus, during the early stages of regeneration, pine seedlings could take advantage of the higher decomposition rates and nutrient releases in this treatment, as shown by the trends of greater total aboveground biomass and basal diameter. Nevertheless, standing burnt trees will fall in the near future, as the basal part of their trunks is also decomposed (Harrington, 1996; Maser and Trappe, 1984), thereby offsetting the differences between NI and CL.

In summary, salvage logging implied the removal of most of the wood biomass, thus eliminating this physical protection against extreme microclimatic conditions and extracting the potential source of nutrients that would be released otherwise. This increased water stress in naturally regenerating pine seedlings after the wildfire, and hindered their annual growth and nutrient uptake. By contrast, less aggressive forms of burnt wood management can have important implications for post-fire regeneration in the long term, as their beneficial effects could be cumulative throughout the regeneration process.

6. CONCLUSIONS

The results of this study support the contention that salvage logging has a detrimental effect on the growth and performance of pine seedlings in relation to treatments where burnt logs and branches are left *in situ*. Moreover, the wood remaining after a fire provides two main ecosystem services, ameliorating the microsite conditions, and increasing nutrient availability through wood decomposition. The more favourable conditions generated as a result not only enhance pine seedling recruitment and survival at early stages (Castro *et al.*, 2011), but also their later growth and performance. This is a key point in Mediterranean and other water- and nutrient-limited ecosystems, where the amelioration of these limiting factors could have important benefits for the regeneration of vegetation (Querejeta *et al.*, 2008; Sardans *et al.*, 2005; Siles *et al.*, 2010). The results of this study should be considered for less intensive management policies devoted to encourage the natural regeneration of vegetation after forest fires.

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CHAPTER 4:

POST-FIRE SOIL RESPIRATION IN RELATION TO BURNT WOOD MANAGEMENT IN A MEDITERRANEAN MOUNTAIN ECOSYSTEM

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ABSTRACT

After a wildfire, the management of burnt wood may determine microclimatic conditions and microbiological activity with the potential to affect soil respiration. To experimentally analyze the effect on soil respiration, we manipulated a recently burned pine forest in a Mediterranean mountain (Sierra Nevada National and Natural Park, SE Spain). Three representative treatments of post-fire burnt wood management were established at two elevations: 1) "Salvage Logging" (SL), where all trees were cut, trunks removed, and branches chipped; 2) "Non Intervention" (NI), leaving all burnt trees standing; and 3) "Cut plus Lopping" (CL), a treatment where burnt trees were felled, with the main branches lopped off, but left *in situ* partially covering the ground surface. Seasonal measurements were carried out over the course of two years. In addition, we performed continuous diurnal campaigns and an irrigation experiment to ascertain the roles of soil temperature and moisture in determining CO_2 fluxes across treatments. Soil CO_2 fluxes were highest in CL (average of 3.34±0.19 µmol $m^{-2}s^{-1}$) and the lowest in SL (2.21±0.11 µmol $m^{-2}s^{-1}$). Across seasons, basal values were registered during summer (average of 1.46±0.04 µmol $m^{-2}s^{-1}$), but increased during the humid seasons (up to 10.07±1.08 µmol $m^{-2}s^{-1}$ in spring in CL). Seasonal and treatment patterns were consistent at the two elevations (1477 and 2317 m a.s.l.), although respiration was half as high at the higher altitude.

Respiration was mainly controlled by soil moisture. Watering during the summer drought boosted CO_2 effluxes (up to 37±6 µmol $m^{-2}s^{-1}$ just after water addition), which then decreased to basal values as the soil dried. About 64% of CO_2 emissions during the first 24 h could be attributed to the degasification of soil pores, with the rest likely related to biological processes. The patterns of CO_2 effluxes under experimental watering were similar to the seasonal tendencies, with the highest pulse in CL. Temperature, however, had a weak effect on soil respiration, with Q_{10} values of *ca*. 1 across seasons and soil moisture conditions. These results represent a first step towards illustrating the effects of post-fire burnt wood management on soil respiration, and eventually carbon sequestration.

Keywords: Rain events, salvage logging, silvicultural treatments, soil CO_2 fluxes, soil pore degasification, soil temperature, wildfire.

1. INTRODUCTION

Wildfires radically disturb carbon pools, leading to a sudden release of carbon to the atmosphere by combustion of vegetation and litter in soil (Brais *et al*., 2000; Conard *et al*., 2002; Page *et al*., 2002; Trabaud, 2004; Van der Werf *et al*., 2003). Furthermore, after the fire the ecosystem acts as a source of carbon for months to years as soil respiration exceeds photosynthesis (Amiro *et al*., 2003; Bond-Lamberty *et al*., 2007; Harden *et al*., 2000; Litvak *et al*., 2003). The magnitude of the soil CO_2 efflux after the fire depends on climatic factors (Almagro *et al*., 2009; Davidson *et al*., 1998; Kirschbaum, 2000; Lloyd and Taylor, 1994) and the recovery of the vegetation (Irvine *et al*., 2007; Litton *et al*., 2003; Yanai *et al*., 2000). Overall, post-fire soil respiration increases with improving soil microclimatic conditions (non-limiting soil moisture and warm temperatures; Carlyle and Bathan, 1988), with the presence of carbon substrates in soil (Coleman *et al*., 2004; Franzluebbers *et al*., 2001), and with primary productivity of vegetation (Craine *et al*., 1998; Janssens *et al*., 2001; Knapp *et al*., 1998; Mkhabela *et al*., 2009).

Studies of the effects of fire on soil respiration are relatively abundant and often compare a burnt area *versus* a reference ecosystem (e.g. Dore *et al*., 2010; Hamman *et al*., 2008; Hubbard *et al*., 2004; Kobziar, 2007; McCarthy and Brown, 2006) or address the progression of soil CO_2 fluxes during ecosystem recovery (e.g. Gough *et al*., 2007; O´Neill *et al*., 2006; Yermakov and Rothstein, 2006). Despite the need to assess the impact of different forest management practises for sustainable carbon management (Peng *et al*., 2008), there is scant information about the effects of burnt wood management on soil respiration after wildfire (see Irvine *et al*., 2007; Mkhabela *et al*., 2009). Post-fire wood management has the potential to strongly affect the magnitude of the soil CO_2 efflux, as burnt logs, snags or coarse woody debris can determine key factors for respiration. For example, microclimatic conditions (soil moisture, soil temperature) can differ depending on the amount of woody debris scattered on the ground (Castro *et al.*, 2011; Smaill *et al.*, 2008; Stoddard *et al.*, 2008). Burnt wood also has a high nutrient content (Johnson *et al.*, 2005; Kappes *et al.*, 2007; Merino *et al.*, 2003), which might improve soil fertility by providing nutrients and organic substrates (Coleman *et al.*, 2004; Grove and Meggs, 2003; Harmon *et al.*, 1986), thus favouring microbial abundance and soil respiration rates (Hamman *et al.*, 2008; Mabuhay *et al.*, 2006; Trumbore *et al.*, 1996). As a consequence of the above processes, vegetation cover and development may differ with burnt-wood management (Stark *et al.*, 2006), which will also affect soil respiration (Burton *et al.*, 2000; Nadelhoffer, 2000; Tang *et al.*, 2005).

Salvage logging is a common post-fire silvicultural management practice for burnt wood around the world (Castro *et al.*, 2010; Donato *et al.*, 2006; Lindenmayer and Noss, 2006; Van Nieuwstadt *et al.*, 2001). This practice consists of felling and removing burnt trunks, and is often combined with the elimination of the remaining woody debris (branches, logs, and snags) by chipping, grinding, mastication, or fire (Beschta *et al.*, 2004; McIver and Starr, 2001). Salvage logging is employed for numerous reasons including silvicultural (*e.g.*: site improvement for plantation or natural regeneration, access, fire risk prevention), economic (value of the salvaged wood products), aesthetics, and safety (Castro *et al.*, 2010; McIver and Starr, 2001). Some of these justifications are controversial, however (Castro *et al.*, 2010; DellaSala *et al.*, 2006; Donato *et al.*, 2006; Lindenmayer and Noss, 2006), and there is increasing support for less aggressive management policies for burnt wood in the post-fire landscape, based on the contention that burnt wood can enhance ecosystem functioning (Beschta *et al.*, 2004; Castro *et al.*, 2010, 2011; Donato *et al.*, 2006; Lindenmayer and Noss, 2006). However, we are not aware of any study on the impact of salvage logging on soil CO_2 effluxes. This is a key question for optimizing post-fire forest restoration plans to mitigate the destruction of natural CO_2 sinks by wildfires.

In this study, we analyze the effects of different post-fire wood managements on the magnitude of soil respiration in a burned pine forest. We established three experimental treatments that differed in degree of burnt wood management, ranging from the conventional salvage logging to non intervention. We hypothesize that this will influence the magnitude of soil respiration, as the treatments contrast sharply in ecosystem characteristics such as microclimatic conditions and nutrient availability. Different elevations also imply a variation in the climatic conditions, which also may determine the vegetation composition, decomposition rates and nutrient dynamic in the ecosystem. For that, measurements were performed at seasonal intervals over the course of two years, and at two altitudes to assess spatial and temporal variation in soil respiration. Continuous 24-h campaigns and a watering experiment were also performed to discern the main factor (soil temperature *versus* soil moisture) determining differences in CO_2 effluxes among treatments. The objectives of this study are: 1) to analyze the effect of post-fire burnt wood management on soil respiration at different altitudinal levels; 2) to determine the seasonal and daily patterns of soil CO_2 fluxes in this Mediterranean mountain ecosystem; and 3) to determine the roles of soil moisture and temperature on soil respiration across treatments.

2. MATERIAL AND METHODS

2.1. STUDY AREA

The study site is located in the Sierra Nevada Natural and National Parks (SE Spain), where the Lanjarón wildfire burned *ca.* 1300 ha of reforested pine between 35 and 45 years old in September 2005. Four sites of around 25 ha each along an altitudinal gradient were established to analyze the effect of burnt wood management on ecosystem regeneration and functioning (see Castro *et al*., 2011 for further details on experimental set-up). The lowest (LE hereafter) and highest (HE) elevations were selected for this study of soil respiration. LE is located at 1477 m a.s.l. (UTM position x, y: 456070; 4089811) and HE at 2317 m a.s.l. (UTM position x, y: 457719; 4091518). The pine species present before fire at each elevation differed, with *Pinus pinaster* and *Pinus nigra* dominating in LE and *Pinus sylvestris* in HE. The climate is Mediterranean-type, with rainfall concentrated in spring and autumn, alternating with hot dry summers. In LE, 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 beside the site). Snow falls during winter, usually persisting from November to March above 2000 m a.s.l. The mean annual temperature is 12.3±0.4ºC at 1652 m a.s.l. (State Meteorological Agency, period 1994-2008. Ministry of Environment) and 7.8±0.7ºC at 2300 m a.s.l. (data from metereological station placed in HE; period 2008-10). Both elevations were homogeneous in terms of fire intensity (high), aspect (southwest exposure), and bedrock (michaschists). The slope is between 25-30% in LE and 15-20% in HE. Tree density before burning was 1480±50 ha^{-1} for LE and 1060±50 ha^{-1} for HE, with a mean height of 6.36±0.06 m and a mean d.b.h. of 13.34±0.17 cm. No trees survived inside the study area, current vegetation is mainly composed of grasses and forbs. The most common perennial species were *Ulex parviflorus, Festuca scariosa, Dactylis glomerata* and *Euphorbia flavicoma* in LE, and *Genista versicolor, Festuca spp.*, and *Sesamoides prostrata* in HE.

2.2. Experimental design

From March to May 2006 (*ca.* seven months after the fire) we established in LE and HE three representative post-fire burnt wood managements that differed in degree of intervention (treatments hereafter): 1) "Salvage Logging" (SL), trees were cut and the trunks cleaned of branches by chainsaw. Trunks were piled manually in groups of 10-12, and the woody debris was chipped by machine. Trunks were later removed from the site with a log forwarder, 2) "Non Intervention" (NI), leaving all of the burnt trees standing. Trees fell naturally and progressively over the years, with ≥88.6±1.9% still standing during this study; and 3) "Cut plus Lopping" (CL), a treatment where trees were felled (100% felled in HE; *ca.* 90% felled in LE), the main branches lopped off, and all wood left *in situ* on the ground. Burnt logs and branches diffusely covered around 45% of the surface at ground level (Castro *et al.*, 2011). Each treatment was applied to a homogeneous area of at least 2 ha, adjacent to each other at each elevation.

In May 2007, 20 PVC collars per treatment at each elevation (diameter 10.5 cm x height 9 cm; 120 collars in total) were inserted in the soil to *ca.* 5 cm depth, randomly distributed over an area of *ca.* 1 ha and separated by at least 10 m. For CL, we used a stratified random procedure, in which the collars were randomly installed in areas below the burnt branches. Soil respiration measurements were performed on the collars for purposes of determining two types of patterns: seasonal and diurnal.

2.3. Soil respiration across seasons

Soil respiration was measured in summer 2007 (four times), autumn 2007 (twice), spring 2008 (twice), summer 2008 (once), and autumn 2008 (once) in every elevation and treatment (see Appendix A for dates). During winter, snow prevented the access to the study area. Summer measurements were done under typical drought conditions, whereas spring and autumn represented the humid season for the area. Thus, calendar definitions of the seasons coincided with the influence of rainfall on the campaigns (see Appendix B for distribution of rainfall over the study period). Measurements were usually performed simultaneously in LE and HE (occasionally separated by one day), from *ca.* 9 am to 3 pm. We used two CO_2 analyzer systems: the manual EGM-4/SRC-1 (PP-Systems, Hitchin, UK); and an automated Li-Cor 8100 (Lincoln, NE, USA). CO_2 measurements made with the PP-Systems were calibrated against the Li-Cor 8100. A comparison was performed on 31 October 2007 in which simultaneous soil respiration records were taken alternatively with both instruments on the same collars (n=48, using collars of the three treatments). Data from the two different devices were correlated (R^2=0.88), and those from the EGM-4 (PP-Systems) were corrected using the resulting linear regression (offset=0.197 μmol $m^{-2}s^{-1}$; slope=1.095). Soil CO_2 fluxes were taken together with soil temperature at *ca.* 5 cm depth (two measurements per collar; digital thermometer probe). The order of measurement was rotated among the three treatments over the campaigns. Vegetation inside the collars was not removed since it was considered an effect of the management treatment. Thus, soil respiration reported in this study could include some above-ground autotrophic respiration. Vegetation cover was estimated visually from 0 to 100% for each campaign (Sutherland, 1996). The effect of soil water content on soil respiration was explored using the rewetting index parameter (I_R) which has shown good correlation with CO_2 effluxes in a Mediterranean ecosystem (Almagro *et al.*, 2009): $I_R=P/t$, where P is precipitation (mm) and t is time elapsed (days) between rainfall event and soil respiration measurements.

2.4. Diurnal patterns of soil respiration

Measurements of the diurnal CO_2 fluxes allowed us to investigate the complete daily pattern of soil respiration in the different treatments and to isolate the dependence on temperature from other interacting environmental variables that can influence soil respiration (*e.g.*: herbaceous cover, phenological differences, soil moisture, microbial biomass and diversity, SOM content) remained relatively constant. For this purpose, soil respiration was measured over a cycle of 24 hours in one representative collar of each treatment in HE, using the Li-Cor 8100 programmed to take a measurement every 30 min. Soil temperature was measured every 10 min at 5 cm depth with 4 thermistors (TMC-HD, Onset Computer Corporation, Massachusetts, USA) connected to data loggers (HOBO H8, Onset Computer Corporation, Massachusetts, USA) within *ca.* 10 cm of the collar. Temperature was averaged and synchronized every 30 min with the corresponding CO_2 flux value. Measurements were performed during the mid-summer (07/10-12/2007, representing dry conditions), late summer (09/16-19/2007, dry conditions before the end of the drought period, Appendix B) and late spring (06/27-29/2009, during the period of highest soil respiration according to the observed seasonal values from the previous year).

2.5. EXPERIMENTAL ANALYSIS ON THE EFFECT OF SOIL MOISTURE

Given the evidence of strong effects of water availability and weak response to soil temperature derived from seasonal and diurnal campaigns (see results), we performed a field experiment to disentangle the role of these two factors on soil CO_2 fluxes. In summer 2009, one week to prior the experiment, four additional collars were installed randomly in each treatment in HE, separated by at least 10 m from each other and from the previous collars. At the beginning of the experiment, an area of 50x50 cm^2 surrounding each of these collars was delimited and irrigated with 5 L of water, uniformly distributed over the 0.25 m^2 surface. The quantity of water (20 mm) was chosen to simulate a typical summer storm according to the record of storms registered for Sierra Nevada (Mendoza *et al*., 2009). Following water addition, soil CO_2 effluxes were measured on the irrigated collars to determine two types of patterns: across days and diurnal.

For patterns across days, we measured CO_2 fluxes (EGM-4), soil temperature (5 cm deep) and gravimetric soil moisture (10 cm deep) in three collars of each treatment one day before, just after, and 1, 3, 5, 7, 10, 15 and 20 days after irrigation (from 29-July to 19-August 2009), alternating the order of measurements in each treatment. Gravimetric soil moisture was calculated as the difference between wet and dry weight of the soil fraction <2 mm after oven-drying at 60ºC to constant weight. For this, one soil sample at 0-10 cm depth was taken from within the delimited perimeter surrounding each collar on every sampling date. Simultaneously, CO_2 fluxes and soil temperatures were also measured in five non-irrigated collars in each treatment, which were taken as a drought-condition reference.

For diurnal patterns, we measured CO_2 fluxes (with the Li-8100) and temperature (with HOBO H8 loggers, 5 cm deep) at one collar of each treatment synchronized as described above. These measurements were carried out one day prior to irrigation, on the same day of the irrigation, and 3, 5 and 7 days after the irrigation. Three soil samples per collar (10 cm deep) were also taken on each of these days to determine gravimetric soil moisture.

3. DATA ANALYSIS

3.1. Effects of treatments, seasons and altitudinal levels on soil respiration

The treatment effect on soil CO_2 effluxes and its variation across seasons was analyzed with a repeated-measure analysis of variance (rmANOVA) split-plot design, in which Treatment was considered the *main plot* factor, and Season (with five levels; summer 2007 and 2008, autumn 2007 and 2008, and spring 2008) the *subplot factor* (Potvin, 2001). The analysis was thus run with mean values per collar for each season. This allowed us to balance the design for the season factor and also produce integrated data of soil respiration per season. In any case, we also performed rmANOVA considering each date as a within factor level (10 campaigns), yielding similar results (data not shown; see Appendix A for values per date). Differences between elevations were tested for each season with one-way ANOVAs pooling data of the three treatments.

The relationship between soil CO_2 effluxes and herbaceous cover inside the collars was analyzed using a Spearman-rank correlation. The analyses were restricted to the two campaigns in the spring period (15-April and 19-May 2008: mean of 35.1±2.3%; all treatments, dates and elevations pooled), since herbaceous cover was very low in other seasons (summer: mean of 0.51±0.24%; autumn: mean of 9.0±0.8%; all treatments, dates and elevations pooled). Differences in herbaceous cover among treatments were tested with a one-way ANOVA for each date and elevation. The relationship between the mean CO_2 flux for each date (all treatments pooled) and the rewetting index was tested using a Spearman-rank correlation.

3.2. Effect of experimental watering

The effect of experimental water addition on soil CO_2 effluxes and their variation across treatments and days after irrigation (time) was analyzed with a rmANOVA, with time defined as a within factor and treatment and irrigation as between factors (day before water addition were excluded of the analysis). Differences between treatments and time in soil moisture among the irrigated collars were similarly tested with rmANOVA. The relationship between soil moisture and CO_2 efflux in the irrigated collars was explored by Spearman-rank correlation. For this correlation, data measured in the first 2 h after irrigating were excluded from the analysis since we interpreted their rapid exponential decay as resulting from degassing of the CO_2 in soil pores displaced by water, an emission not directly associated with biological processes. This was evaluated by log-transforming the data of continuous CO_2 effluxes and fitting linear equations to the time course of these measurements (see Appendix C).

3.3. EFFECT OF SOIL TEMPERATURE

The effect of temperature on soil CO_2 fluxes was analyzed for all the continuous diurnal measurements, both in irrigated and non-irrigated collars. For this purpose, F_c from each campaign was fitted *versus* soil temperature (T_s) using the following equation describing the response of soil respiration to soil temperature (Curiel-Yuste *et al*., 2004):

$$F_c = R_{15} Q_{10}^{(Ts-15)/10} \quad (1)$$

with two fitting parameters: R_{15} is the respiratory flux predicted at 15ºC and Q_{10} is the factor of increasing respiration for a 10ºC rise in soil temperature.

Data were log- or angular-transformed when required to improve normality and homoscedasticity (Quinn and Keough, 2009). Statistical analyses and models were made with JMP 7.0 software (SAS Institute). Throughout the paper, values of soil respiration are expressed in units of µmol $m^{-2}s^{-1}$. Mean values are followed by ±1SE.

4. RESULTS:

4.1. SOIL RESPIRATION ACROSS TREATMENTS, SEASONS AND ALTITUDINAL LEVELS

Soil respiration differed among treatments and seasons in both elevations (Table 1). At the lower elevation, respiration was overall higher in CL (5.1±0.4; all campaigns pooled) than in NI (3.52±0.24) and SL (3.28±0.22; Fig. 1). The same pattern was registered at the higher elevation, with higher values in CL (2.29±0.16) than NI (2.07±0.17) and SL (1.50±0.10; Fig. 1). Among seasons, fluxes were much lower during summer than during spring and autumn for both elevations (mean of 2.08±0.10 in summer, 6.8±0.6 in spring and 4.45±0.18 in autumn for LE; 0.79±0.05 in summer, 2.35±0.17 in spring and 2.91±0.13 in autumn for HE; Fig. 1). An interaction emerged between treatment and season (Table 1), with CL clearly identified as the treatment with the highest soil CO_2 fluxes in spring (Fig. 1). Respiration was always higher in LE than in HE in all seasons ($P \leq 0.001$, Fig. 1; mean of 3.97±0.17 and 1.95±0.09, respectively; treatments pooled).

Table 1: *Summary of repeated measures analysis of variance (rmANOVA) for the seasonal CO_2 fluxes. Analyses were performed with the mean value of CO_2 fluxes measured at each collar by season. df: degrees of freedom of the numerator and denominator, respectively. F: value of the F statistic. Approximate value of F adjusted for the Season*Treatment interaction (Wilk`s-Lambda multivariate test). P: critical probability of the analysis.*

Source	**Low Elevation**			**High Elevation**		
	df	F	*P*	df	F	*P*
Between-subject						
Treatment	2, 57	9.51	0.0003	2, 56	5.41	0.0071
Within -subject						
Season	4, 54	96.29	<0.0001	4, 53	227.65	<0.0001
Season*Treatment	8, 108	5.10	<0.0001	8, 106	9.77	<0.0001
Error	57			56		

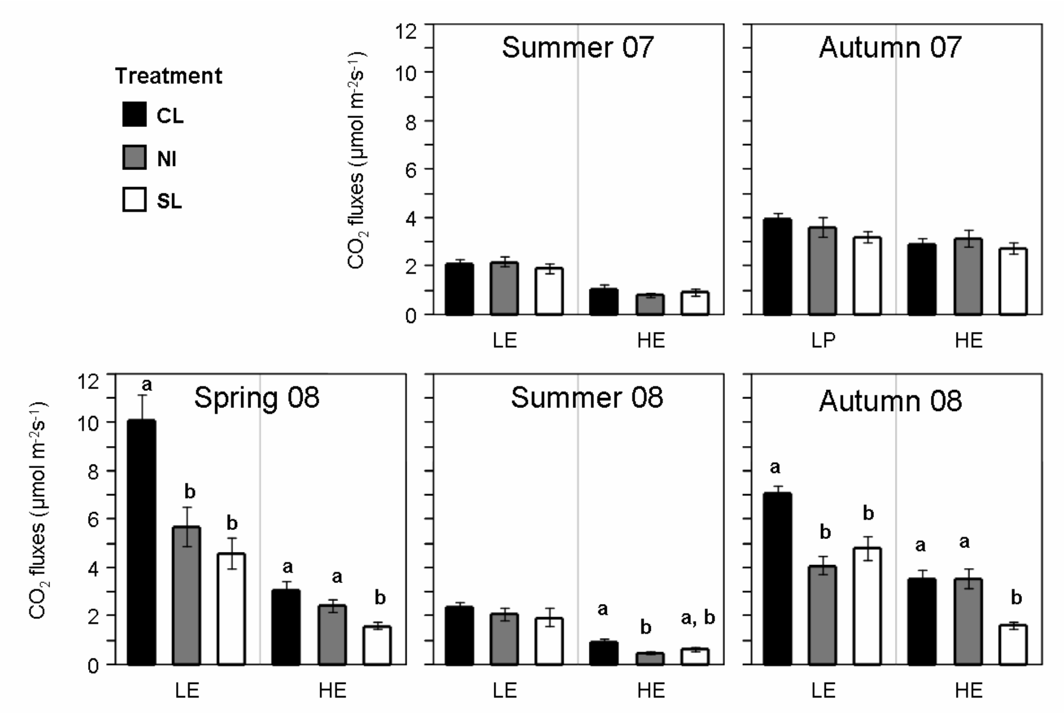

Figure 1: *Mean soil CO_2 effluxes in the different altitudinal levels and post-fire silvicultural treatments over the seasons. Abbreviations for altitudinal levels and treatments: LE: low elevation (1477 m a.s.l); HE: high elevation (2317 m a.s.l.); SL: salvage logging; NI: non intervention; CL: cut plus lopping. Each bar represents the mean CO_2 efflux for the 20 collars per treatment and elevation. Standard error of each mean is represented over each bar. Different letters above bars indicate significant differences between treatments within elevation and season according to Tukey test after one way-ANOVA.*

Soil CO_2 fluxes were positively correlated with green herbaceous cover inside the collars for the spring campaigns (ρ=0.41, P<0.0001, n=119 in LE and ρ=0.28, P<0.0028, n=109 in HE). Herbaceous cover inside the collars differed among treatments. On 15 April, it was higher in CL than SL and NI for both elevations (76±8%, 46±8% and 35± 5% respectively for LE; 47±9%, 12±2% and 11±4% for HE; P≤0.0004). On 19 May, the herbaceous cover in HE was also higher in CL than in NI and SL (24±5%, 8±2% and 4±1%, respectively; P=0.0002), whereas there were no differences among treatments in LE (56±8%, 38±5% and 50±8%, respectively; P=0.1828). For both elevations, soil fluxes were positively correlated with the rewetting index (ρ=0.83 in LE and ρ=0.98 in HE, P<0.0001).

4.2. Effect of experimental watering

Soil moisture differed between sampling dates (P<0.0001) and was similar among treatments (P>0.05, no significant interactions). It peaked on the day of irrigation, and then decreased gradually in all cases (Fig. 2A). Irrigation stimulated soil CO_2 effluxes in the three treatments, with a strong effect of date (Table 2). For the irrigated collars, soil CO_2 effluxes spiked within 60 s after water addition, reached a peak on the same day (*ca*. 47 times the previous value before water addition) and fell rapidly during *ca*. 2 h due to soil pore degasification, which accounted for *ca*. 51-87% of emissions, depending on treatment, during the first 24 h after water addition (Fig 3; see Appendix C). Respiratory fluxes then decreased toward basal values prior to the irrigation (Fig. 2B). Soil efflux peaks following irrigation were highest in CL, followed by SL, and were lowest in NI (Fig. 2B). Soil CO_2 effluxes in the reference collars without irrigation also varied with date (Table 2) but these effects can be attributed to a precipitation event that occurred thirteen days after the beginning of the experiment (12 August), which stimulated CO_2 effluxes and soil moisture measured on days 15 and 20 (14 and 19 August) of the experiment (Fig. 2C). Soil CO_2 effluxes in the irrigated collars were positively correlated to gravimetric soil moisture (ρ=0.62, P<0.0001).

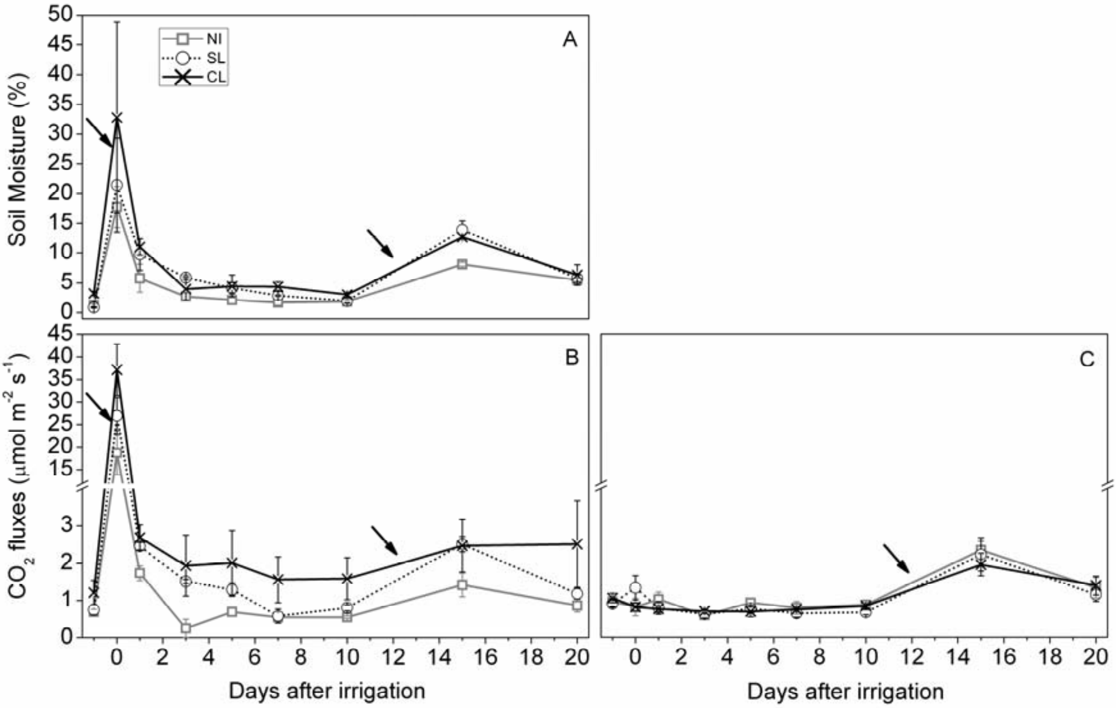

Figure 2: *(A) Soil moisture, (B) CO_2 effluxes in irrigated collars, and (C) CO_2 effluxes in reference collars not stimulated by water addition) in the different post-fire silvicultural treatments several days after the experimental watering. Arrows indicate the days when the water addition was performed and when the natural rain event occurred. CL: cut plus lopping; NI: non intervention; SL: salvage logging.*

Source	df	F	*P*
Between-subject			
Irrigation	1, 16	13.93	0.0018
Treatment	2, 16	5.83	0.0125
Irrigation*Treatment	2, 16	6.94	0.0068
Within -subject			
Time	7, 10	32.04	<0.0001
Time*Irrigation	7, 10	41.68	<0.0001
Time* Treatment	14, 20	3.79	0.0023
Time*Irrigation*Treatment	14, 20	3.76	0.1037
Error	16		

Table 2: *Summary of repeated measures analysis of variance (rmANOVA) for CO_2 fluxes after experimental irrigation. df: degrees of freedom of the numerator and denominator, respectively. F: value of the F statistic. Approximate value of F adjusted for the Time*Treatment and Time*Treatment*Elevation interactions (Wilk`s-Lambda multivariate test). P: critical probability of the analysis.*

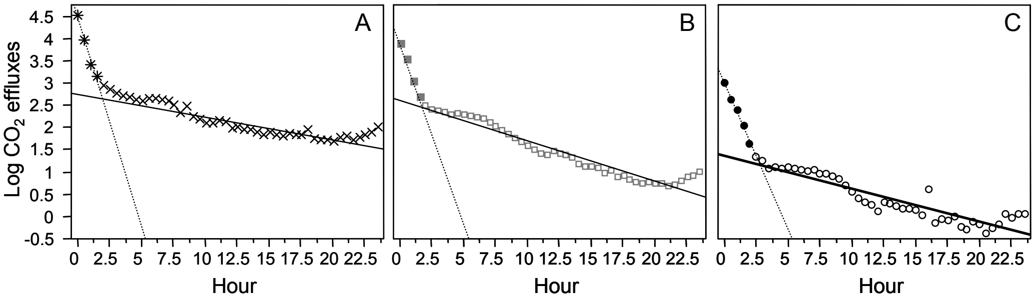

Figure 3: *Soil CO_2 effluxes (logarithmic scale) just after the water irrigation (9:00 am, local hour) over the first 24 h in (A) cut plus lopping (CL), (B) non intervention (NI) and (C) salvage logging (SL). Open symbols and continuous lines correspond to effluxes and linear regressions during the respiration period (r) respectively, solid and asterisks symbols and dotted lines correspond to the linear regressions during the degassing period (d) respectively (see Appendix C). (Linear fitted equations for the respiration period: Y=2.752-0.0512*X, R^2=0.81 in CL; Y=2.591-0.0904*X, R^2=0.93 in NI; Y=1.352-0.0736*X, R^2=0.82 in SL; and for the degassing period: Y=4.456-0.9341*X, R^2=0.97 in CL; Y=3.851-0.8021*X, R^2=0.99 in NI; Y=3-0.6621*X, R^2=0.99 in SL)*

4.3. Soil respiration sensitivity to diurnal temperature oscillations

Fitted values for the parameter Q_{10} were very low for all treatments and seasons (between 1.29 and 0.98, R^2<0.10 and P>0.05 for most cases). Due to this lack of temperature dependence (Fig. 4), the parameter R_{15} showed the same pattern as the mean values of CO_2 fluxes, with the highest values registered in CL for all campaigns. Soil CO_2 fluxes under experimental watering also showed low temperature sensitivity (Fig. 5). Overall, the temperature dependence of CO_2 fluxes increased very slightly in the absence of water limitations (3 days after irrigation) and fell again as the soil dried out (7 days after irrigation, Table 3). Again, R_{15} showed the same pattern as mean of the fluxes for every date, being always higher in CL, followed by NI and then SL (Table 3).

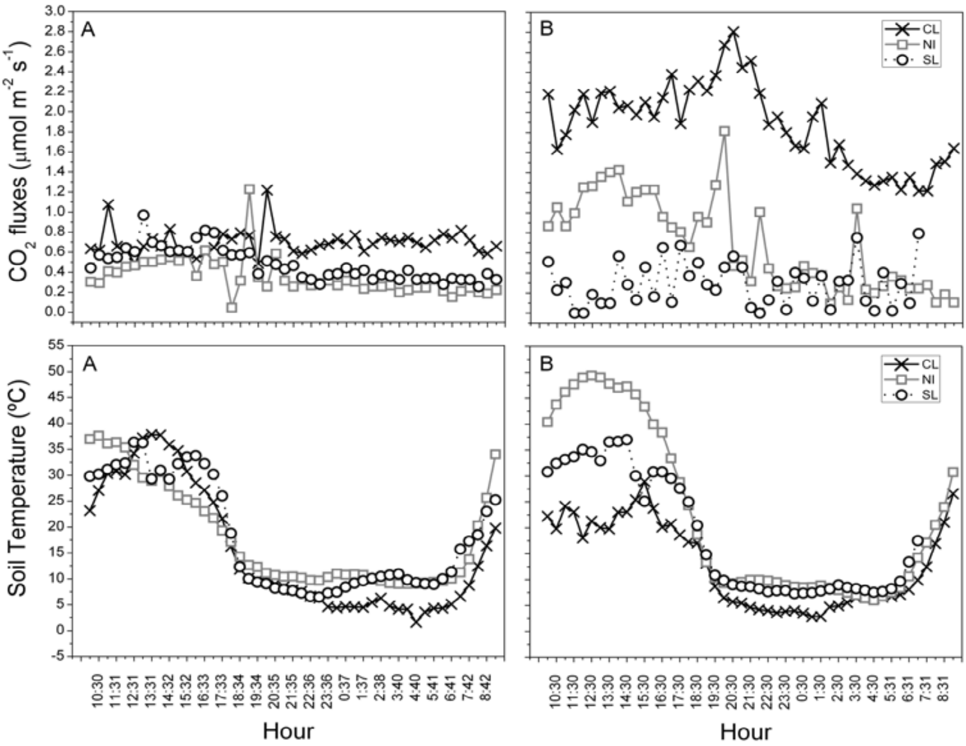

Figure 4: *Half-hourly soil CO_2 effluxes and soil temperatures in the highest elevation over 24 hours. Two sampling dates are represented: (A) Late summer (16-19 September 07); (B) late spring (27-29 May 09). Measurements started at 11:00 am (local hour) and lasted 24 h. (GMT is displayed in the x axes). CL: cut plus lopping; NI: non intervention; SL: salvage logging.*

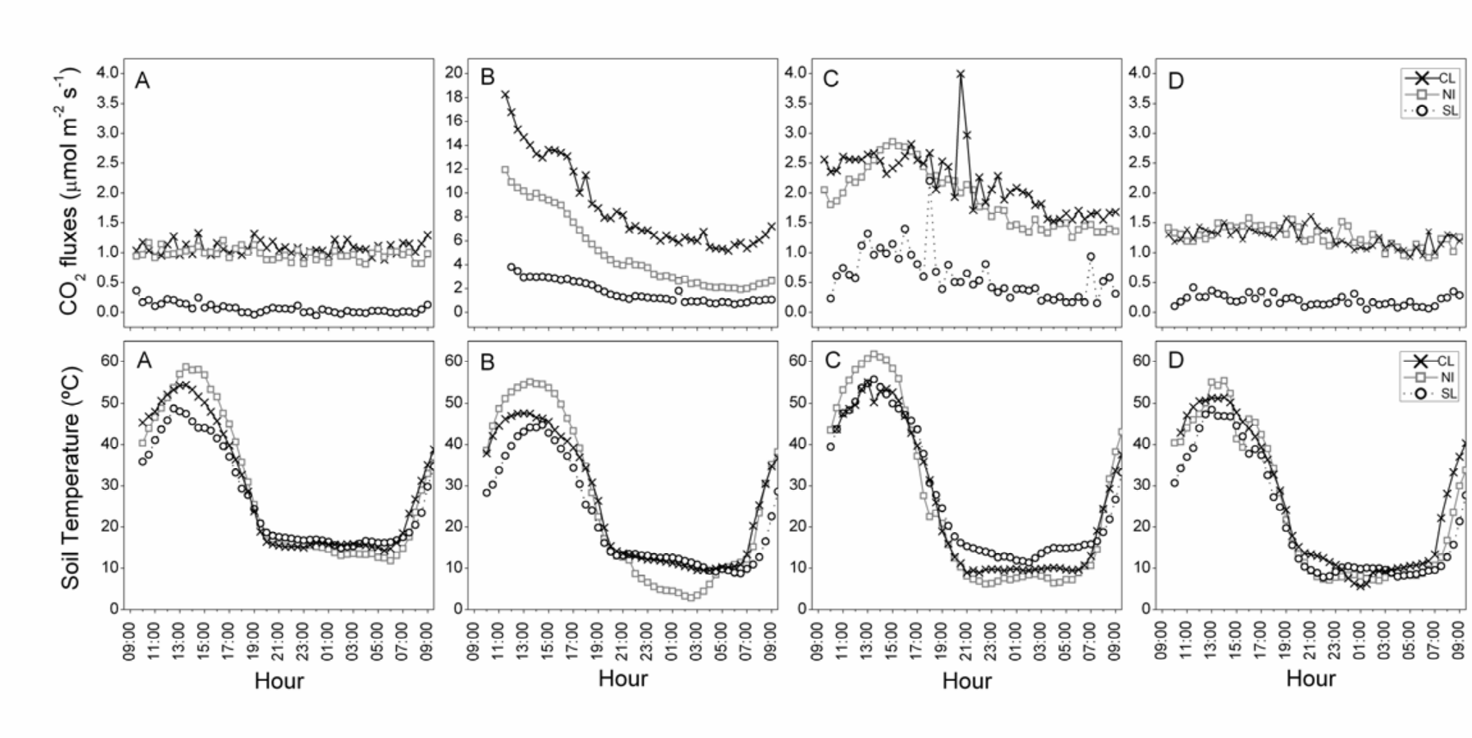

Figure 5: *Half-hourly measurements of soil CO_2 effluxes and soil temperature following the irrigation field experiment in the highest elevation over 24 hours. Data from four sampling dates are represented: (A) before irrigation, (B) the day of irrigation, (C) three days after irrigation, and (D) seven days after irrigation. Measurements started at 9:00 am (local hour) and lasted 24 h. CO_2 effluxes measures in B) from 9:30-11:30 am are not shown since they cannot be directly attributed to biological emissions (see Appendix C). CL: cut plus lopping; NI: non intervention; SL: salvage logging.*

Table 3: *Temperature sensitivity of daily soil CO_2 fluxes several days after the water addition treatment. Values of Q_{10} and R_{15} parameters were obtained by fitting measured CO_2 fluxes and simultaneous soil temperature to the exponential model of the Eq. (1) dependent of soil temperature. R^2 is the coefficient of correlation between measured and modelled data. Parameters for soil CO_2 fluxes during the day of water addition were not calculated, now that theses fluxes are not temperature dependent but soil moisture dependent. CL: cut plus lopping; NI: non intervention; SL: salvage logging.*

Treatment	Days after water addition	Soil moisture (%)[1]	Q_{10}	R_{15}	R^2
CL	1 day before (summer drought)	3.20±0.35	1.00±0.01	1.07±0.02	0.01
NI		1.24±0.20	1.02±0.01	0.95±0.02	0.15
SL		0.86±0.08	1.75±0.19	0.02±0.01	0.55
CL	3 days after	9.29±1.54	1.07±0.02	1.99±0.08	0.25
NI		6.12±0.08	1.07±0.01	1.75±0.07	0.37
SL		5.71±0.82	1.10±0.05	0.48±0.06	0.29
CL	7 days after	4.02±0.81	1.03±0.01	1.23±0.02	0.15
NI		2.91±0.17	1.03±0.01	1.22±0.02	0.21
SL		1.94±0.09	1.16±0.04	0.17±0.01	0.35

[1]Mean *of the gravimetric soil moisture of three soil samples taken inside the delimited perimeter of one collar per treatment.*

5. DISCUSSION:

In this study we have analyzed post-fire soil respiration considering burnt wood management and other environmental factors with the potential to affect respiration. The pattern of soil respiration was variable in time and space. On one hand, differences in altitudinal level yielded *ca*. twofold differences in respiration. On the other hand, soil CO_2 fluxes exhibited strong seasonality, with highest values in spring and basal values during the summer drought (see Almagro *et al*., 2009; Rey *et al*., 2002; for similar patterns). Overall, this study shows three main noteworthy factors that determine rates of CO_2 effluxes after fire in this Mediterranean ecosystem: 1) soil respiration is mostly determined by water availability, whereas soil temperature has a marginal effect; 2) soil respiration is substantially and consistently affected by burnt wood management; and 3) rain events during the dry season strongly impact soil CO_2 effluxes and reinforce the role of burnt wood management.

5.1. EFFECT OF SOIL MOISTURE AND TEMPERATURE

Soil moisture and temperature are the main drivers of soil CO_2 effluxes (Davidson *et al*., 1998; Lloyd and Taylor, 1994). The combination of these two factors is particularly critical in Mediterranean ecosystems, where high temperature in summer is coupled with limiting soil moisture (Carlyle and Bathan, 1988; Davidson *et al*., 1998; Reverter *et al*., 2010; Xu and Qi, 2001). The effect of water availability on respiration was clear in this study as seen both indirectly (correlation with the rewetting index; seasonal variation of CO_2 fluxes, with basal values in summer and maximum values in spring) as well as by experimental manipulation of water availability (see Almagro *et al*., 2009; Liu *et al*., 2002; Rey *et al*., 2002; Xu *et al*., 2004; for similar results).

The effect of soil temperature was, by contrast, almost irrelevant. This is an expected result for the dry period (summer), when limiting soil moisture overshadows the role of temperature (Carlyle and Bathan, 1988; Davidson *et al*., 1998; Serrano-Ortiz *et al*., 2007; Sowerby *et al*., 2008; Xu and Qi, 2001). This result is reinforced by the restriction of the temperature sensitivity analysis to diurnal measurements at a single collar (per treatment), thus avoiding the potentially confounding and interacting effects of spatial variability, primary productivity and phenology (Curiel-Yuste *et al*., 2004; Janssens *et al*., 2001). In any case, soil fluxes at seasonal scales also showed very weak temperature sensitivity during drought conditions (data not shown). However, low values of Q_{10} were similarly encountered during spring (although slightly higher than in summer), as well as in the controlled irrigation experiment. This contrasts with results in most of the studies for both seasonal and diurnal fluxes in un-burnt Mediterranean climates (Raich and Schlesinger, 1992; Reichstein *et al*., 2002; Rey *et al*., 2002; Tang *et al*., 2003, 2005; Xu and Qi, 2001) and suggests that factors other than water limitation could be restricting the diurnal effect of soil temperature; these might include the repression of the microbial activity by the extremely high temperatures reached in the soil during the midday (Killham, 1994; Luo and Zhou, 2006; Tang *et al*., 2003) and during the fire (Garcia-Oliva *et al*., 1999; Saa *et al*., 1998; Zhang *et al*., 2005). In addition, heat and CO_2 transport processes can influence Q_{10} values calculated from regressions of surface flux and soil temperature measured at a single depth (Phillips *et al*., 2011; Xu and Qi, 2001). Thus, Q_{10} values could be higher at greater depths.

In any case, soil respiration almost halved at the higher elevation. Several factors can be involved in this pattern including lower rate of wood decomposition, lower primary productivity and subsequent root activity and litter deposition (Brischke and Rapp, 2008; Craine *et al*., 1998; Janssens *et al*., 2001; Knapp *et al*., 1998;), but it is very likely that colder temperatures at higher elevation influence respiration differences between altitudinal levels (Kane *et al*., 2003), whether directly or via interactions with the above-mentioned factors.

5.2. Effect of burnt wood management

Soil respiration was consistently affected by post-fire burnt wood management both across seasons and altitudinal levels, whatever the effects of moisture and temperature. Overall, respiration was highest in the treatment where trees were felled and lopped, leaving the soil partially covered with logs and branches (CL treatment). This may be explained by several factors. First, the decaying wood may supply the soil with nutrients that encourage microbiological activity (Coleman *et al*., 2004; Grove and Meggs, 2003; Harmon *et al*., 1986). The fact that trees were felled would facilitate wood-soil contact and hence decomposition (Harmon *et al*., 1986; Maser and Trappe, 1984), explaining the higher respiration rates in CL *versus* NI. Second, logs and branches spread on the ground can improve microclimate by reducing soil desiccation produced by the extreme soil heating (Castro *et al*., 2011; see also Smaill *et al*., 2008; Stoddard *et al*., 2008 for similar effects of non-burned woody debris). Third, vegetation cover was consistently higher in collars in CL than in the other treatments, which may increase both autotrophic (either above and belowground) and heterotrophic respiration (Reichstein *et al*., 2003; Tang *et al*., 2005). This is likely a consequence of higher nutrient availability and microclimatic amelioration (Burton *et al*., 2000; Irvine *et al*., 2007; Stark *et al*., 2006), but altogether exerted a direct effect on soil respiration during spring.

We are not aware of studies analyzing the effect of post-fire burnt wood management on soil respiration by means of an experimental design with different levels of intervention. However, Concilio *et al*. (2006) and Irvine *et al*. (2007) reported increases in soil respiration following a fire of high intensity due to the presence of slash on the forest floor. In these cases, the increases in soil respiration were attributed to regrowth and nutrient inputs. Burnt wood management alters microclimate, nutrient content or vegetation cover regardless of the ecosystem considered (*e.g*.: Castro *et al*., 2011; Coleman *et al*., 2004; Grove and Meggs, 2003; Harmon *et al*., 1986; Stoddard *et al*., 2008). Thus, it is likely that burnt wood would encourage soil microbial activity and respiration rates in the upper soil layers after a wildfire.

5.3. EFFECT OF RAIN EVENTS

In addition to the positive relationship between soil moisture and respiration, this study shows the strong impact of evenly distributed rain events on soil CO_2 effluxes of a Mediterranean ecosystem. The simulation of a summer rain event provoked a CO_2 peak that reached *ca.* 47 times the basal values before the experimental watering. Furthermore, the effects of post-fire treatments are highlighted by the coincident patterns, both in the seasonal measurements of soil respiration and following experimental watering, with the highest values reached in the CL treatment. Vegetation was senescent at the beginning of the irrigation experiment, and no changes in living vegetation cover were observed following irrigation, so the increased soil CO_2 effluxes after the first 2 h of the water addition could be attributed mainly to microbial activity. Thus, differences in soil carbon pools like those due to decaying burnt wood can alter both peak and basal respiration rates (Sanderman *et al*., 2003).

Our results strongly suggest that a large fraction (about 64% approx.) of the initial CO_2 emitted within *ca.* 2 h after water addition was related to degasification of CO_2-rich air trapped in soil pores. During the dry season, CO_2 from the past and from water-limited metabolism would be trapped in soil pores (Inglima *et al*., 2009; Liu *et al*., 2002) when the soil is very dry and the low connectivity of soil pores leads to CO_2 accumulation. After initial soil degassing, rewetting leads to a cascade of responses (enhanced microbial activity and soluble organic C availability; Luo and Zhou, 2006; Xiang *et al*., 2008) that mobilizes and metabolizes otherwise unavailable soil carbon. This would explain the high peaks and exponential decrease of CO_2 effluxes. Thus, even if differences in soil respiration among treatments were not of a high magnitude during summer, their effect can be cumulative and show up after rain events following a long dry period.

5.4. *MANAGEMENT IMPLICATIONS*

There is currently an intense debate concerning the appropriate management of burnt trees after forest fires (Beschta *et al*., 2004; Donato *et al*., 2006; Lindenmayer *et al*., 2004; McIver and Starr, 2001). Post-fire salvage logging is implemented worldwide (Castro *et al*., 2010; 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*., 2010, 2011; Donato *et al*., 2006; Lindenmayer and Noss, 2006). The present study highlights the capacity of burnt wood management to alter soil CO_2 effluxes. Overall, salvage logging was the treatment with the lowest soil respiration, probably because of harsher microclimatic conditions and reduced nutrient availability (see above). Since this pattern was consistent in the two contrasted altitudinal levels of the study, with different dominant tree species before fire disturbance, these results could be extrapolated to other forest ecosystems in water-limited climates.

Post-fire management strategies should also be considered for carbon sequestration policies. Their relevance is accentuated given the increase in wildfire intensity and frequency in recent decades due to human factors (Cerdá and Mataix-Solera *et al*., 2009; Conard *et al*., 2002) and predicted climatic change scenarios (IPCC, 2007). Post-fire wood management can determine the rhythm of natural recovery of the ecosystem and net carbon balance by modifying soil parameters. However, the higher soil respiration reported in the "cut plus lopping" treatment does not necessarily imply an increase in net carbon emissions of the burnt area, but rather can be interpreted as a comparative diagnostic tool for soil metabolic activity in relation to forest practices (Weber, 1990). Primary production can equilibrate increases in CO_2 effluxes (Irvine *et al*., 2007), since the herbaceous cover registered during spring was higher in this treatment. Furthermore, the effect of burnt logs, branches or coarse woody debris over the soil may be long-lasting

(Smaill *et al.*, 2008), helping to compensate ecosystems fluxes over longer time scales. In order to disentangle the role of the burnt wood management on soil carbon sequestration, complementary studies on ecosystem-atmosphere carbon exchange would be convenient. In any case, this study sets a baseline and is the first that experimentally examines the key importance of post-fire wood management practices on soil CO_2 fluxes.

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APPENDIX A:

Table A1: *Soil CO_2 effluxes in each sampling date in every treatment and elevation. Mean values of soil fluxes (µmol $m^{-2}s^{-1}$) are followed by ±1SE (n=20). CL: cut plus lopping; NI: non intervention; SL: salvage logging; HE: high elevation (2317 m a.s.l.); LE: low elevation (1477 m a.s.l.)*

Season	Sampling Date	Elevation	Treatment		
			CL	NI	SL
Summer 07	05-July	HE	1.19±0.08	1.31±0.12	0.97±0.12
		LE	2.04±0.16	2.17±0.22	1.69±0.16
	19-July	HE	1.07±0.21	0.71±0.07	0.76±0.07
		LE	2.37±0.30	2.16±0.25	1.90±0.28
	2-August	HE	1.10±0.22	0.60±0.06	0.75±0.11
		LE	2.02±0.25	2.26±0.30	2.03±0.23
	30-August	HE	0.88±0.20	0.52±0.08	1.12±0.40
		LE	1.92±0.19	2.00±0.29	1.93±0.32
Autumn 07	25-September	HE	3.87±0.37	4.27±0.55	4.85±0.41
		LE	5.46±0.30	4.79±0.50	4.21±0.26
	30-October	HE	1.92±0.12	2.00±0.20	0.83±0.06
		LE	2.45±0.21	2.42±0.33	1.83±0.15
Spring 08	15-April	HE	2.29±0.27	2.16±0.24	0.76±0.09
		LE	5.22±0.41	3.98±0.44	2.86±0.25
	19-May	HE	3.82±0.56	3.14±0.52	2.43±0.20
		LE	14.92±1.87	7.38±1.18	6.57±1.13
Summer 08	02-September	HE	0.92±0.14	0.47±0.05	0.62±0.09
		LE	2.38±0.19	2.07±0.26	1.93±0.36
Autumn 08	01-October	HE	3.51±0.34	3.55±0.41	1.61±0.14
		LE	7.08±0.27	4.08±0.38	4.79±0.51

APPENDIX B

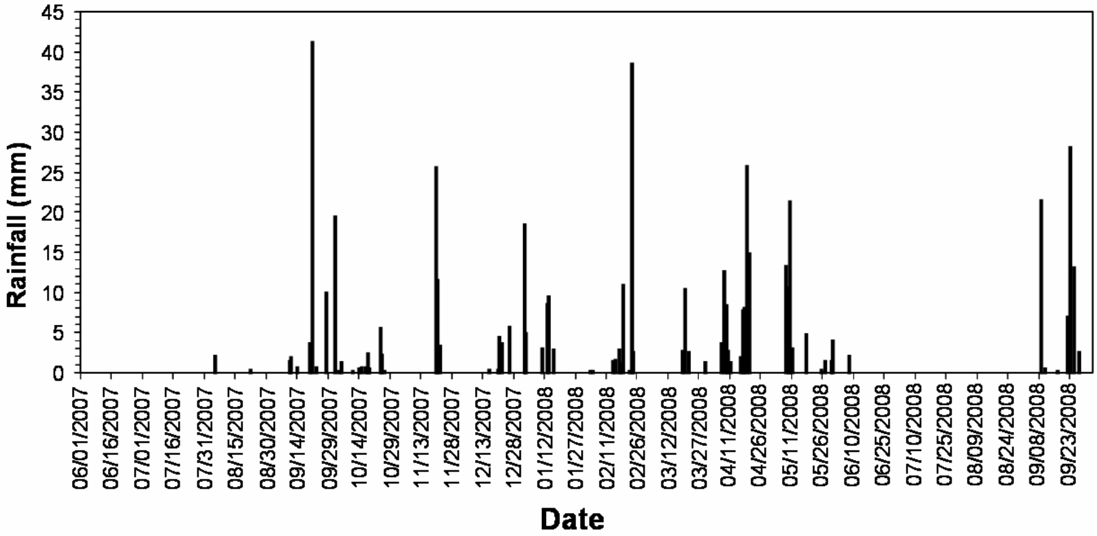

Figure B1: *Rain events during the measurement period. Data from a meteorological station near the low elevation (LE).*

APPENDIX C: Discrimination between the degassing period and the respiration period in continuous measurements of soil CO_2 fluxes after artificial irrigation.

The continuous CO_2 efflux data during the first 24 hours after irrigation consistently revealed two distinct periods, each displaying linear declines when plotted on a logarithmic scale (Fig. 5 of the manuscript) and thus corresponding to exponential decay.

Such linear relations can be expressed generally as

$$y = a + bt \, ,$$

where t is the time since irrigation, and the remaining variables correspond to the following assignations in the context of exponential decay:

$$y \rightarrow \ln(F)$$

$$a \rightarrow \ln(F_0)$$

$$b \rightarrow -\frac{1}{\tau}$$

In the above formulae, F is the CO_2 efflux (a function of t), F_0 the initial value (at t=0), and τ the time constant describing the exponential decay. These assignations are chosen such that the decline can be expressed as

$$\ln(F) = \ln(F_0) - \frac{1}{\tau} t \, .$$

When the above equation is equated in terms of the exponent of e (*ca*. 2.718), an exponential decay is described as

$$F = F_0 \exp^{-\left(\frac{1}{\tau}\right)t} ,$$

where τ is the time required for the flux to fall to *ca*. 37% (e^{-1}) of its initial value (F_0).

For every treatment, a rapid exponential decay was observed during the first 2 h, after which time a more slowly decaying efflux proceeded. We interpreted these periods as corresponding to two separate processes associated with the irrigation treatment: first, during the first couple of hours, physical degassing (period "d") as soil pores were filled by water (Luo and Zhou, 2006); and later, the decline of respiration (period "r") governed by enzyme kinetics (Inglima *et al*., 2009; Liu *et al*., 2002; Xiang *et al*., 2008) as the soil asymptotically returned to its water-limited state (Fig. 5). For each period, we determined linear fit parameters (a and b) by least-squares regression, and thereby the parameters F_0 and τ (summarized in Table C1) describing the different exponential decay processes.

The purpose of this analysis was merely to exclude the degassing period and thereby isolate the respiration period (excluding the first couple of hours), in order to explore the effect of soil moisture on biologically determined CO_2 fluxes in the irrigated collars.

Table C1. *Exponential decay parameters for post-irrigation declines in soil CO_2 effluxes. CL: cut plus lopping; NI: non intervention; SL: salvage logging.*

Treatment	Degassing period (d)		Respiration (r) period	
	$F_{0,d}$ (μmol m^{-2}s^{-1})	τ_d (h)	$F_{0,r}$ (μmol m^{-2}s^{-1})	τ_r (h)
CL	86.1	1.1	15.7	19.5
NI	47.0	1.2	13.3	11.1
SL	20.1	1.5	3.9	13.6

CHAPTER 5:

POST-FIRE SALVAGE LOGGING REDUCES CARBON SEQUESTRATION IN MEDITERRANEAN CONIFEROUS FOREST

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ABSTRACT

Post-fire salvage logging is a common silvicultural practice around the world, with the potential to alter the regenerative capacity of an ecosystem and thus its role as a source or a sink of carbon (C). However, there is no information on the effect of burnt wood management on the net ecosystem carbon balance. Here, we examine for the first time the effect of post-fire burnt wood management on the net ecosystem carbon balance by comparing the carbon exchange of two treatments in a burnt Mediterranean coniferous forest treated by "Salvage Logging" (SL, felling and removing the logs and masticating the woody debris) and "Non Intervention" (NI, all trees left standing) using eddy covariance measurements. Using different partitioning approaches, we analyze the evolution of photosynthesis and respiration processes together with measurements of vegetation cover and soil respiration and humidity to interpret the differences in the measured fluxes and underlying processes. Results show that SL enhanced CO_2 emissions of this burnt pine forest by more than 120 g C m^{-2} compared to the NI treatment from the period June-December 2009. Although soil respiration was around 30% higher in NI during growing season, this was more than offset by photosynthesis, as corroborated by increases in vegetation cover, evapotranspiration as well as reduced soil moisture in the NI treatment. Since SL is counterproductive to climate change and Kyoto protocol objectives of optimal carbon sequestration by terrestrial ecosystems, less aggressive burnt wood management policies should be considered.

Keywords: Burnt wood management, eddy covariance, forest carbon balance, photosynthesis, respiration, wildfire

1. INTRODUCTION

Wildfire is a frequent perturbation in Mediterranean-type ecosystems (Moreno *et al.*, 1998) inducing changes in land use/cover types (Lloret *et al.*, 2002; Quintana *et al.*, 2004; Viedma *et al.*, 2006) and thereby altering the balances of water, energy and carbon (Amiro *et al.*, 1999, 2006; Beringer *et al.*, 2003; Santos *et al.*, 2003). Although CO_2 emission immediately after fire can be reasonably estimated (Conard and Ivanova, 1997; Harden *et al.*, 2000; Page *et al.*, 2002; Van der Werf *et al.*, 2003), long-term effects on the carbon balance during ecosystems to regeneration are less certain and influenced by several factors. Enhanced rates of soil CO_2 efflux as well as large changes in the rate of ecosystem photosynthetic carbon uptake may also occur during several months after wildfire (Santos *et al.*, 2003). However, other studies suggest a reduction of soil CO_2 efflux in ecosystem to regeneration (Dore *et al.,* 2010; Irvine *et al.,* 2007) that could be attributed to the positive relation between aboveground productivity and respiration (Irvine *et al.,* 2007; Janssens *et al.,* 2001). Finally, some studies reveal decreased in evapotranspiration (*ET*) and a conversion from carbon sink to source with magnitudes differing over the years following wildfire (Amiro, 2001; Amiro *et al.*, 2003, 2006; Mkhabela *et al.*, 2009).

Post-fire management may affect the fluxes of carbon and hence the role of the ecosystem as a carbon source or sink. The capacity for carbon sequestration after a wildfire will depend on the regenerative capacity of the vegetation that determines net primary production. For example, reforestation soon after a stand-replacing disturbance accelerates the conversion from carbon source to sink (Magnani *et al.*, 2007) although natural regeneration may similarly increase carbon sequestration (Amiro, 2001). In addition, forest fires leave large amounts of partially burnt wood that may be handled in several ways according to ecological or management requirements, increasing productivity (Castro *et al.*, 2010a, 2011;

Donato *et al.*, 2006) and simultaneously enhancing C emissions due to decomposition (Jomura *et al.*, 2008; Marañón-Jiménez *et al.*, 2011). Therefore, the net carbon balance after a wildfire, may differ as a consequence of forest management (Stark *et al.*, 2006), whether by a direct effect on vegetation cover and development or as mediated by the presence of burnt wood.

One of the first and most important post-fire management decisions regards the fate of the burnt wood. After a fire, forest managers frequently apply salvage logging, removing the burnt tree trunks, and often eliminating the remaining woody debris by chopping, mastication, fire, etc. (Bautista *et al.*, 2004; Lindenmayer *et al.*, 2008; McIver and Starr, 2000). Post-fire salvage logging has been routinely practiced by forest managers worldwide, motivated by factors economic, silvicultural, or even esthetic (Castro *et al.*, 2009, 2011; Lindenmayer and Noss, 2006; McIver and Starr, 2000). However, there is increasing evidence that salvage logging degrades ecosystem function and structure in terms of vegetation regeneration, animal and plant diversity, watershed runoff and erosion, or nutrient cycling (Castro *et al.*, 2010a, 2010b, 2011; Donato *et al.*, 2006; Lindenmayer *et al.*, 2008). In the same way, post-fire burnt wood management can potentially alter the ecosystem carbon balance. On one hand, large amounts of carbon stored in the burnt wood can decompose and be emitted as CO_2 to the atmosphere. On the other hand, the presence of burnt wood can enhance regeneration capacity both by incorporating nutrients into the soil as it decomposes, and also by improving microclimatic conditions that benefit net primary productivity (Castro *et al.*, 2010a, 2011; Donato *et al.*, 2006; Lindenmayer *et al.*, 2008). Post-fire burnt wood management could therefore affect the net ecosystem carbon balance even during several years after the wildfire. To date however, there are no studies on the effects of bunt wood management on net carbon exchange after a wildfire.

The aim of this paper is to examine the effect of the post-fire salvage logging on the net ecosystem carbon balance. We compare the CO_2 exchange, measured during the fourth year following wildfire, of two treatments with different post-fire management treatments: “Salvage Logging” (SL) and “Non Intervention” (NI). We used the eddy covariance (EC) technique to directly measure net carbon, water vapor and energy exchanges between the atmosphere and the biosphere (Baldocchi, 2003; Wofsy *et al.*, 1993). In addition, soil CO_2 effluxes, vegetation cover and meteorological variables were measured to interpret the patterns of carbon fluxes and underlying processes. We hypothesized that post-fire burnt wood management would influence the magnitude of carbon exchange between the ecosystem and the atmosphere, as the presence of the burnt wood may alter both respiration rates and gross primary production. These measurements are critical to understand ecosystem carbon exchange at a global scale given the large areas of forest burned every year, and are a necessary step to ascertain the effect of management practices on the ecosystem carbon balance.

2. MATERIALS AND METHODS

2.1. STUDY AREA AND EXPERIMENTAL DESIGN

The study site is located in the Sierra Nevada National Park (SE Spain). In September 2005, a wildfire burned *ca.* 1300 ha of reforested pine between 35 and 45 years age. The area selected for this study is located at 2320 m a.s.l. (36°58'3.68"N; 3°28'37.04"W). The climate is Mediterranean-type, with precipitation falling mostly during autumn and winter, and by a dry summer. Mean annual temperature is 7.8±0.7ºC (period 2008–10) and the annual precipitation 470±50 mm (period 1988–2008; climatic data from a nearby meteorological station at 1500 m a.s.l). Snow falls during winter, usually persisting from November to March, and the growing season usually starts in the second half of May. The slope is between 15-20%. The dominant pine species present before the wildfire was

Pinus sylvestris with a density of 1060±50 ha^{-1} and 13.4±0.3 cm d.b.h. and 6.63±0.17 m height. Burnt wood biomass was estimated at 46.9 Mg ha^{-1} (70% above and 30% belowground), according to alometric equations based on pine density and tree size (Castro *et al.*, 2010a). This supposes a C stock in wood of 23.6 Mg ha^{-1} (C concentration was determined in the sawdust of 50 burnt logs with a Leco TruSpec autoanalyzer, St. Joseph, MI, USA). The fire was of high intensity and no trees survived inside the study area. Current vegetation is mainly composed by grass and forbs typical of disturbed areas in the Oromediterranean belt (Molero-Mesa *et al.*, 1996) the most common perennial species being *Genista versicolor*, *Festuca spp*. and *Sessamoides prostata*.

Nine months after the fire, two post-fire management treatments were applied to the burnt trees of two 35-ha stands: (1) “Non Intervention” (NI): all burnt trees were left standing and fell naturally and progressively over the years, with around 25% still standing at the beginning of this study; and (2) “Salvage Logging” (SL): trees were cut and the trunks cleaned of branches by chainsaw and piled manually in groups of 10-12, with woody debris chopped by machine and trunks removed from the site with a log forwarder. The two treatments were contiguous (Fig. 1) and showed similar characteristics in terms of tree size and density, slope, bedrock (michaschists) and soil type (Humic cambisols).

Figure 1: *Eddy tower locations as bull's eyes in Non intervention (white) and Salvage Logging (black) treatments. For each tower, according to the Flux-Source Area model of Schmid (1994) during periods of relative static stability (periods where measured fluxes are generated most distantly to the eddy tower) defined in terms of the friction velocity (0.2 m s^{-1}<u_*<0.4 m s^{-1}) and sensible heat flux (H<0), the maximum source location is denoted by the circle of grey dots. Similarly, the white circles denote the near- and far-limits of the 50% source area isopleths. According to Schmid (1997) a flux source point located on or outside the 50% source area boundaries would have to be from 5 to 10 times stronger than the point of maximum source weight, in order to achieve a similar response on the eddy covariance sensors. Consequently, maximum sources and near- and far-limits for other atmospheric conditions are inside the respective circles. Frequency (%) of each wind direction, over the measured period, is represented by number inside each octant.*

2.2. METEOROLOGICAL AND EDDY COVARIANCE MEASUREMENTS

An eddy covariance tower - with additional instrumentation for environmental and soil measurements - was installed in each treatment. Fluxes of CO_2, water vapor (or latent heat flux) and sensible heat were estimated from fast response (10 Hz) instruments mounted atop towers of 10 m (NI) and 2.5 m (SL). Densities of CO_2 and H_2O were measured by open-path infrared gas analysers (Li-Cor 7500, Lincoln, NE, USA) and calibrated periodically using an N_2 standard for zero and a 479.5 μmol (CO_2) mol^{-1} gas standard as a span for both treatments. Winds and sonic temperature were measured by three-axis sonic anemometers (for NI: Model 81000, R.M. Young, Traverse City, MI, USA; for SL: CSAT-3, Campbell Scientific, Logan, UT, USA). Comparison analyses between fluxes calculated by both anemometers have been already published and show good agreement (Loescher *et al.*, 2005; Tanny *et al.*, 2010). Measurements were made in 2009 (the 4th year after the fire), year-round in NI, and from early June to late December in SL.

Air temperature and humidity were measured by thermohygrometers (HMP 45C, CSI, USA) at 7 m (NI) and 2 m (SL) above the surface. Soil water content (SWC) was measured by two water content reflectometers (CS616, CSI) at 4 cm depth for NI treatments. Over a representative ground surface, photosynthetic photon flux densities were measured by quantum sensors (Li-190, Lincoln, NE, USA) for NI and SL treatments. In the NI treatment, a net radiometer (NR Lite, Kipp & Zonen, Delft, Netherlands) located 8 m above the surface and four heat flux plates (HFP01SC, Hukseflux, Delft, Netherlands) at 8 cm depth and two pairs of soil temperature probes (TCAV, Campbell Scientific, Logan, UT, USA) at 2 and 6 cm depth, were installed parallel to the surface to examine the energy balance closure (Wilson *et al.*, 2002). For both treatments, data loggers (CR3000, CSI) managed the measurements and recorded the data. For eddy covariance measurements, data were saved at 10 Hz by the logger which calculated and recorded means, variances and covariances on half-hour bases following Reynolds' rules. Eddy flux corrections for density perturbations (Webb *et al.*, 1980) and coordinate rotation (McMillen, 1988) were applied, as well as quality control checks following Reverter *et al.*, (2010) using an in-house program (PECADO) based on MATLAB routines.

2.3. DATA QUALITY CONTROL, GAP FILLING FOR LONG TERM INTEGRATION OF FLUXES, AND PARTITIONING

Half-hour statistics were computed when data eliminated by quality control did not exceed 25% of the total. Night-time data during periods with low turbulence (friction velocity, u_*<0.35 m s^{-1} for the NI treatement; u_*<0.25 m s^{-1} for the SL treatment) were rejected (Goulden *et al.*, 1996), as were three nights from February with unrealistic values. The Flux-Source Area footprint model (Schmid, 1994, 1997, 2002) was applied to verify that fluxes originated from well within the fetch (Fig. 1). Even during periods of relative static stability (0.2 m s^{-1}<u_*<0.4 m s^{-1}; sensible heat fluxes *(H)*<0), the estimated maximum source location was 101 m for NI and 36 m for SL; the maximum distance of the 50% source area isopleths (Fig. 1) was 228 m (NI) and 68 m (SL). In addition, the energy balance closure (ratio of the sum of sensible and latent turbulent fluxes, *H*+*LE*, to the difference between net radiation and the soil heat flux, R_n-*G*) was 90% (R^2=0.67; n=755) for the NI treatment and 96% (R^2=0.60; n=1225) for SL treatment. This value is in the range reported by most FLUXNET sites (Wilson *et al.*, 2002) and provides additional information regarding turbulent flux quality (Moncrieff *et al.*, 1997).

Data rejected due to environmental conditions or instrument malfunction amounted to 29% and 23% of the total measured period for the NI and SL treatments respectively. In addition, night-time low turbulence conditions rejected 18% and 13% of the data, resulting in 47% total data missing for NI and 36% for SL, requiring gap filling in order to estimate the annual CO_2 and water vapor exchanges. Gaps were filled using the ‘‘Marginal Distribution Sampling’’ (MDS) technique (Falge *et al.*, 2001; Reichstein *et al.*, 2005), replacing missing values using a time window of several adjacent days. The length of the time window depends on environmental conditions and meteorological data availability. In a parallel way and only for CO_2 fluxes, a semi-empirical gap filling method based on the response to temperature and photosynthetic photon flux density for respiration and photosynthesis respectively (Falge *et al.*, 2001; Lasslop *et al.*, 2010) was also applied. Results from this alternative gap-filling method are mentioned only when significant differences with the MDS method were detected ($P<0.05$). Random uncertainty and errors in net ecosystem carbon and water vapor exchanges introduced by the gap-filling processes were calculated using Monte Carlo simulations (Richardson and Hollinger, 2007); see Reverter *et al.,* (2010) for more information. Positive values of net ecosystem carbon exchange denote CO_2 release from the soil to the atmosphere while negative values denote CO_2 uptake.

Half hourly net CO_2 fluxes were broken into gross primary production (GPP) and ecosystem respiration (R_{eco}) components using two different techniques: the "night-time data-based estimate" (NB; (Reichstein *et al.*, 2005)) and the "daytime data-based estimate" (DB; (Lasslop *et al.*, 2010)) flux partitioning algorithms. The NB algorithm assumes that GPP is zero at night and models R_{eco} as a function of temperature using night-time data; this relationship is extrapolated to daytime, for which the difference between the modeled R_{eco} and measured CO_2 fluxes yields the estimated GPP (see Reichstein *et al.,* 2005 for more information). For the DB algorithm, the daytime measured CO_2 fluxes are modeled using a hyperbolic light–response curve (Falge *et al.*, 2001) for GPP and a respiration model depending on temperature for R_{eco} (Eq. (1)); where F_C is the measured CO_2 flux, α (µmol C J^{-1}) the canopy light utilization efficiency representing the initial slope of the light–response curve, β (µmol C $m^{-2}s^{-1}$;) the maximum CO_2 uptake rate of the canopy at light saturation adjusted for vapor pressure deficit limitations, R_g the global radiation (W m^{-2}) that can be easily estimated using the measured photosynthetic photon flux density (Ceulemans *et al.*, 2003), R_{15} (µmol C $m^{-2}s^{-1}$) the base respiration at 15ºC, E_0 (ºC) the temperature sensitivity and T_a (ºC) the air temperature (see Lasslop *et al.,* 2010 for more details).

$$F_C = \frac{\alpha\beta R_g}{\alpha R_g + \beta} + R_{15}\exp\left(E_0\left|\frac{1}{15-46.02} - \frac{1}{T_a + 46.02}\right|\right) \quad (1)$$

To track the respiratory and photosynthetic capacity of both treatments, mean monthly values of R_{15} and α estimated every two days from the DB partitioning algorithm were selected.

2.4. *PLANT COVER AND SOIL RESPIRATION AND MOISTURE MEASUREMENTS*

In order to determine possible causes of the differences in measured F_C between treatments, plant cover and soil CO_2 fluxes and humidity were measured. Plant cover was sampled with a point-linear method one and two years after the fire (June 2006 and 2007, respectively) as a surrogate for regenerative capacity and primary production. In June 2006, measurements were done in 12 randomly established linear transects of 25x2 m along the maximum slope of the terrain for each treatment. The number of individuals of perennial plants was counted within each transect. For June 2007 the methodology was changed due to the high plant cover that impeded the monitoring of all individuals. In that case, three points (central and transversal sides) at each 50 cm along the transect (n=150 points per transect) were sampled, observing the nature of contact (soil or vegetation). Plant height (if present) was measured at every central point of the transect. Differences between treatments were analyzed with one-way ANOVAs for each year.

Soil respiration and water content were measured six times throughout the spring of 2009 at three-week intervals from March to June. Twenty PVC collars per treatment were installed in the soil to *ca.* 5 cm depth, randomly distributed over an area of *ca.* 1 ha and separated by at least 10 m. Soil respiration measurements were performed on the collars from *ca.* 9 am to 3 pm using two CO_2 analyzer systems: the manual EGM-4/SRC-1 (PP-Systems, Hitchin, UK); and an automated

Li-8100 (Li-Cor; Lincoln, NE, USA). The two instruments were used in both treatments. A previous instrument intercomparison (Marañón-Jiménez *et al.*, 2011) allowed correction of the EGM-4/SRC-1 data to match the Li-8100. During these campaigns, soil water content was also measured at 10, 20, 30 and 40 cm depth at 15 points per treatment, using the PR-2 profile probe (Delta T, Services, Cambridge, UK). Soil CO_2 effluxes and their variation over sampling dates (time) were analyzed with a repeated-measure analysis of variance (rmANOVA), with sampling dates defined as the within-factor and treatment as the between-factor. Soil water content was similarly analyzed with rmANOVA. Throughout the paper mean values are followed by ±1SE.

3. RESULTS

3.1. Meteorological conditions

Meteorological conditions showed a strongly asynchronous pattern of rainfall and temperature throughout the year (Fig. 2). During summer (June, July, August), the mean daily air temperature (T_a) was 17.1ºC, while precipitation was almost negligible with only one rain event exceeding 5 mm. In winter (January, February, and December) mean daily T_a was 1ºC and the greatest precipitation fell, mostly as snow which persisted from December to March. During spring and fall, rain and T_a showed intermediate values compared with the other two seasons, with a mean daily T_a of 7.8ºC, and accumulated rainfall of 170 mm. Annual values of mean T_a and total rainfall in 2009 were 8.4ºC and 678 mm respectively.

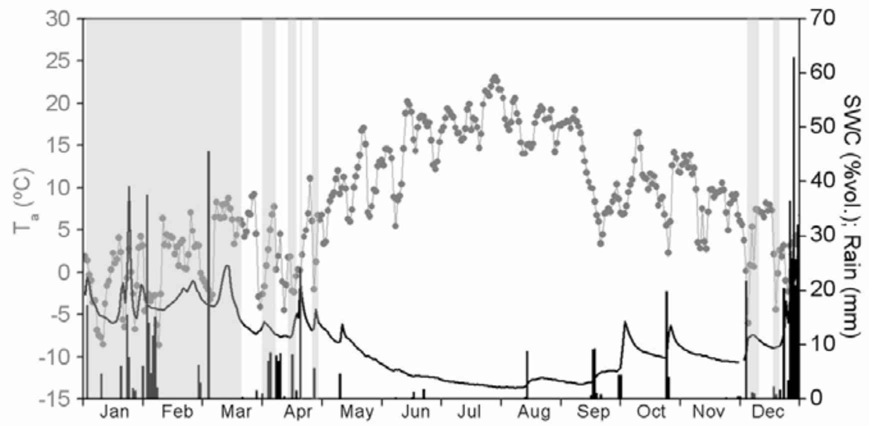

Figure 2: *Mean daily values of air temperature (T_a: ºC; grey dots), soil water content (SWC: % vol.; black line) and total precipitation (Rain; mm; black bars) during 2009. Shaded bars denote periods of snow cover [ratio of mean daytime reflected photon flux density to mean daytime incident photon flux density higher than 0.2]*

3.2. MONTHLY NET CARBON EXCHANGE AND EVAPOTRANSPIRATION

Overall, the Non Intervention (NI) treatment acted as a monthly net carbon sink during nearly the whole year 2009, whereas the Salvage Logging (SL) treatment acted consistently as a source following the June installation of the eddy system (Fig. 3). The most productive period for NI was the end of spring and beginning of summer, reaching the maximum value of carbon uptake in May (around 30 g C m^{-2}). Then, from August to October, NI emitted *ca.* 2 g C m^{-2} per month. In November (end of autumn, with fair weather) the ecosystem absorbed more than 10 g C m^{-2}. During winter, NI was very nearly carbon neutral. However, December and January are interpreted as carbon source months if gaps were filled using the semi-empirical approach, emitting 13 and 9 g C m^{-2} respectively. By contrast, SL consistently emitted carbon, with maximum emissions in July (more than 20 g C m^{-2}) and decreasing from then until the year's end. The semi-empirical approach could not be applied in SL due to the inability to correlate measured CO_2 fluxes with temperature or light (Lasslop *et al.*, 2010).

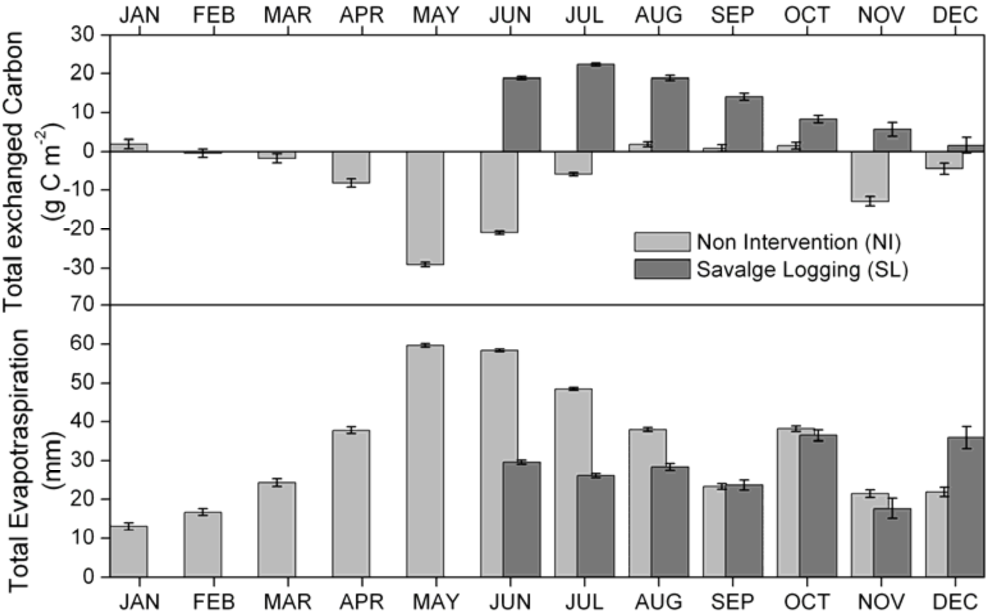

Figure 3: *Monthly totals of exchanged carbon (g C m^{-2}) and evapotranspiration (mm) by forest stands during 2009 for Non Intervention (NI, grey bars) and since June 2009 for Salvage Logging (SL, dark bars) treatments, using MDS gap-filling technique. Ecosystem CO_2 uptake is depicted as negative values while ecosystem CO_2 release is positive.*

During the measured period in both treatments, NI presented usually higher monthly evapotranspiration values (*ET*), with the exception of December (Fig. 3). Monthly *ET* for NI reached maximum values at the end of spring (May and June; *ca.* 60 mm) and minima at the beginning and end of the year (<25 mm). In early autumn (October), *ET* was similar to that of early spring (*ca.* 40 mm). In SL, during the measured period (June-December), maximum *ET* values where reached in October when the soil was moist and the temperature mild (Figs. 2 and 3). Nonetheless, monthly *ET* remained very low and stable over the measured period and never exceeded 40 mm. The monthly Bowen ratio (ratio of sensible to latent heat flux) increased from February to August for NI treatment and decreased afterwards (Table 1). For SL treatment the monthly Bowen ratio was higher than NI. Both treatments presented higher values in July and August (Table 1).

Table 1: *Monthly values of the Bowen ratio for Non Intervention (NI) and Salvage Logging (SL) treatments along 2009. The error (in parentheses) is calculated based on the standard errors of H and LE.*

	Bowen Ratio											
	Jan.	Feb.	Mar.	Apr.	May.	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
NI	-	0.4 (0.2)	1.4 (0.5)	2.2 (0.4)	1.9 (0.2)	2.1 (0.2)	3.6 (0.3)	3.1 (0.3)	-	1.6 (0.2)	1.2 (0.3)	-
SL	-	-	-	-	-	3.4 (0.5)	4.2 (0.5)	3..5 (0.6)	1.8 (0.4)	1.8 (0.3)	2.0 (1.1)	-

3.3. Diurnal trends of CO_2 fluxes across treatments

Diurnal trends of CO_2 fluxes were explored in three representative months for simplicity (Fig. 4). In general, during daytime NI acted as a consistent net CO_2 sink while SL acted as a source. During night-time both treatments acted as sources of CO_2. However, while SL presented values lower than 0.6 μmol $m^{-2}s^{-1}$, NI reached values exceeding 1 μmol $m^{-2}s^{-1}$ in June. Concretely, in June, daytime CO_2 uptake in NI was often near 3 μmol $m^{-2}s^{-1}$ while SL acted as daytime CO_2 source (*ca.* 1.5 μmol $m^{-2}s^{-1}$). In July, SL presented similar behavior to June whereas NI reduced its CO_2 assimilation by more than a half. In November, early daytime CO_2 uptake was measured in SL (F_C=-0.5 μmol $m^{-2}s^{-1}$). For the NI treatment, autumn values of daytime CO_2 uptake reached 2 μmol $m^{-2}s^{-1}$ and nighttime CO_2 release was considerably lower than June and July.

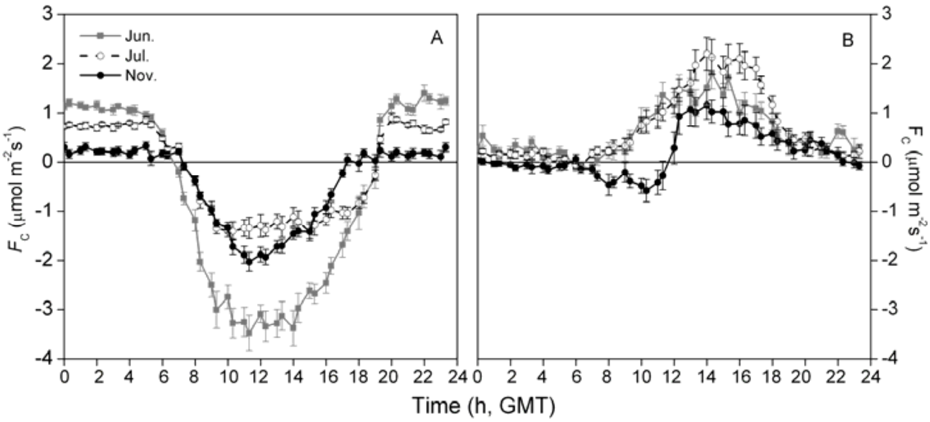

Figure 4: *Diurnal trends in CO_2 flux (F_c, μmol $m^{-2}s^{-1}$) for the monthly means (±SE) of June, July and November 2009 for (A) Non Intervention and (B) Salvage Logging treatments.*

3.4. ACCUMULATED CARBON EXCHANGE

Fig. 5 shows the accumulated carbon exchange estimated for NI and SL over the period when simultaneous measurements in both treatments are available (June–December of 2009). For the SL treatment, the accumulated carbon exchange showed a near constant slope (*a*) [a=0.6; R^2=0.995] from the start of the measurements (June) until October. During this period, this treatment acted as a constant daily carbon source, emitting between 80 and 110 g C m^{-2} and thereafter, it acted as near neutral C sink until the end of the year. The NI treatment acted as a net carbon sink during spring, absorbing 60 g C m^{-2} (from April to June; data not shown). After this productive period, the net carbon uptake capacity was reduced and the ecosystem absorbed 30 g C m^{-2} from June to July. From this point, the NI treatment behaved as near neutral C sink until the middle of November, when this treatment recovered its sink activity until the end of the year.

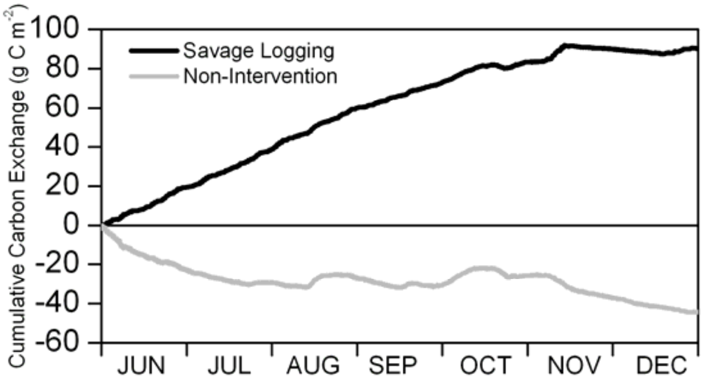

Figure 5: *Cumulative carbon exchange (g C m^{-2}) from June-December 2009 by burnt forest treated with Non intervention (NI, grey line) and Salvage Logging (SL, black line).*

Over the course of 2009 the NI treatment absorbed 77±11 g C m^{-2}. Such a confident value cannot be given for SL treatment, due to the absence of carbon exchange measurements from January to May 2009. However, crude annual estimation can be given assuming range of possible behaviors of SL treatment during the non-measured period. During winter, we can consider similar behavior for NI and SL, acting as a neutral net carbon sink due to the existence of snow cover (Harding *et al.*, 2001). For April and May, the accumulated carbon exchange could be considered as delimited by two extreme situations: (1) a neutral net carbon exchange, given the lack of net carbon assimilation throughout the measurement period (Fig. 3) and (2) a scenario of maximum carbon emission. For the estimations under this assumption we used the "daytime data-based estimate" (DB) respiration model (Lasslop *et al.*, 2010). The model was applied using maximum values of base respiration at 15ºC (R_{15}) and temperature sensitivity (E_0) estimated during the measured period (1.25 µmol m^{-2}s^{-1} and 335ºC, respectively). Thus, in any case considered under these preliminary assumptions, the SL treatment acts as a net annual carbon source, emitting between 90 and 120 g C m^{-2} in 2009.

3.5. Plant cover and soil respiration and moisture measurements

Plant cover in June 2006 was higher in NI (11.1±1.6 individuals m^{-2}) than in SL (7.5±1.1 individuals m^{-2}; F=3.24, d.f.=1, 22; P=0.086). Plant cover similarly differed between treatments in June 2007 (F=18.17, d.f.=1, 22; P<0.001), being higher in NI (61.2±1.7%) than in SL (46±4%; see also Fig. 6 for pictures of the study areas in 2009). Plant height also differed between treatments (F=4.69; d.f.=1, 453; P=0.031; log-transformed data), being likewise higher in NI (22.9±1.4 cm), than in SL (19.5±1.4 cm).

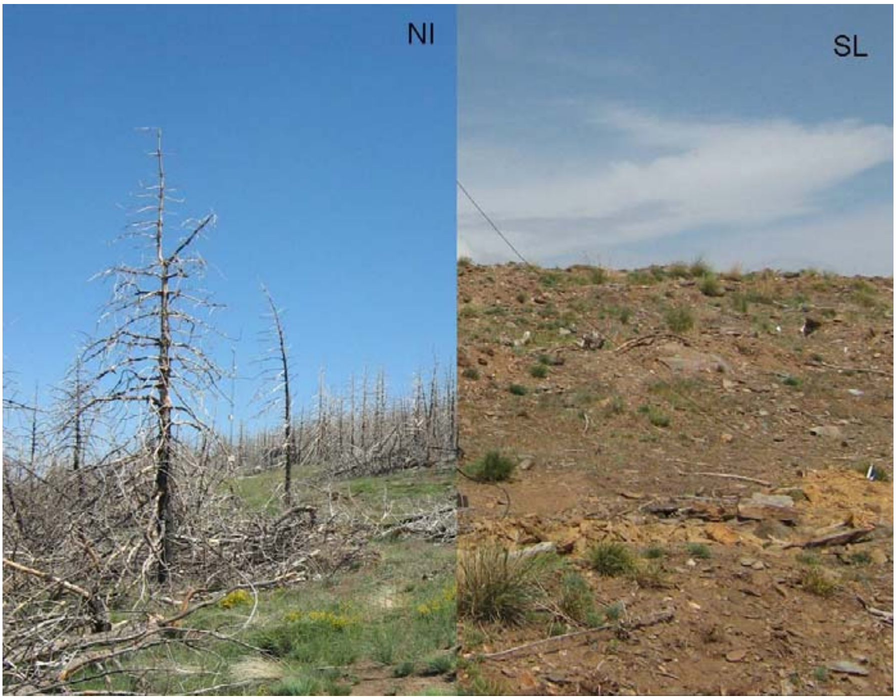

Figure 6: *Appearance of burnt forest treated by Non Intervention (NI) and Salvage Logging (SL) for the 27th and 28th of May 2009 respectively.*

Soil respiration was consistently higher in NI than SL (Fig. 7A, Table 2). Soil water content decreased throughout the growing season and was constantly higher in SL (Fig. 7B; Table 3).

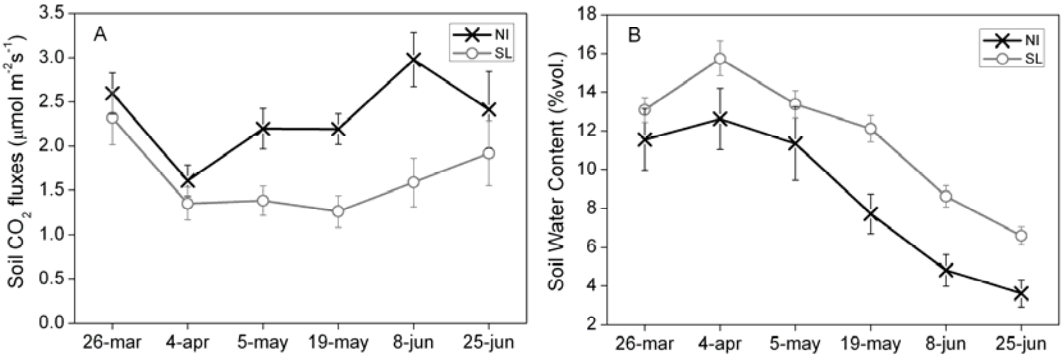

Figure 7: *Mean values (±SE) of (A) soil CO_2 effluxes of 20 PVC collars and (B) soil water content from 10 to 40 cm depth for Non Intervention (NI) and Salvage Logging (SL) treatments, for six campaigns in spring 2009.*

Table 2: *Summary of repeated measures analysis of variance (rmANOVA) for soil CO_2 fluxes measured throughout the spring 2009. df: degrees of freedom of the numerator and denominator respectively. F: Value of the F statistic. P: Critical probability of the analysis.*

Source	df	F	P
Between-subject			
Treatment	1, 28	7.34	0.0114
Within -subject			
Time	5, 24	4.76	0.0037
Time*Treatment	5, 24	2.07	0.1048
Error	28		

Table 3: *Summary of repeated measures analysis of variance (rmANOVA) for the soil water content measured throughout the spring of 2009. df: degrees of freedom of the numerator and denominator respectively. F: Value of the F statistic. Approximate value of F adjusted for the Time*Depth and Time*Treatment*Depth interactions (Wilk`s-Lambda multivariate test). P: Critical probability of the analysis.*

Source	df	F	*P*
Between-subject			
Treatment	13.61	1, 54	0.0005
Depth	0.41	3, 54	0.7464
Treatment*Depth	0.18	3, 54	0.9101
Within -subject			
Time	5, 50	156.61	<0.0001
Time*Treatment	5, 50	9.23	<0.0001
Time*Depth	15, 138.43	3.94	<0.0001
Time*Treatment*Depth	15, 138.43	1.10	0.3572
Error	54		

3.6. Photosynthesis and respiration partitioning

Mean estimated values of base respiration at 15ºC (R_{15}) and canopy light utilization efficiency (α) from the DB partitioning algorithm (Fig. 8) were used to track the respiratory and photosynthetic capacities of NI. Monthly trends of R_{15} and α were very similar, showing peaks at the end of spring (May) and in the fall, with lower values during the dry summer. However, R_{15} lagged α by about one month in reaching its fall maximum (in October, R_{15}=0.86 µmol $m^{-2}s^{-1}$) by which time α had dropped back to low values (*ca*. 0.008 µmol C J^{-1}). Relatively high values of R_{15} were also estimated in December, but were accompanied by only a slight increase in α. For SL, no dependence of GPP on light, nor of R_{eco} on temperature, was detected and thus, the DB partitioning algorithm could not been applied, except from mid-October to December, where early daytime CO_2 uptake was measured in

SL (see November 2009 in Fig. 4) and R_{15} reached values near 0.54 µmol m^{-2}s^{-1}. The estimated α was generally null, except for 22-24 October (0.0012 µmol C m^{-2} s^{-1}) and 5-7 November (0.0853 µmol C m^{-2}s^{-1}).

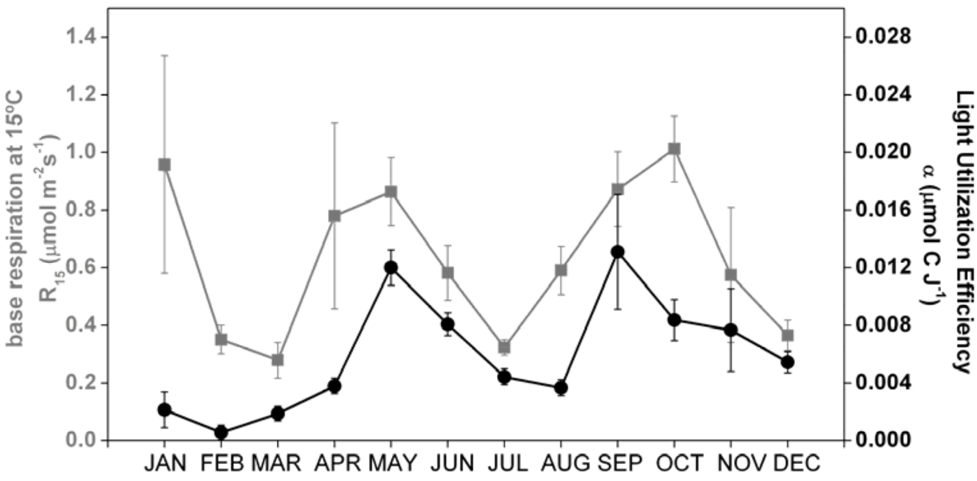

Figure 8: *Mean monthly values (±SE) of respiratory and photosynthetic parameters used to estimate both processes in Non Intervention (NI) treatment. Estimated values outside the range defined as "mean monthly value±SD" were rejected.*

Thus, due to the lack of measured CO_2 fluxes dependencies on light or temperature for SL, estimated values of gross primary production and ecosystem respiration are given only for NI. Using both algorithms, higher values of GPP were obtained in May and June, while lower values corresponded to cold winter months (January-March; Fig. 9). During end of summer, fall and beginning of winter the estimated GPP remained nearly constant according both algorithms. The same seasonal pattern for GPP was obtained using the NB algorithm. By contrast, modeled R_{eco} showed significant differences depending on the algorithm used. For "DB" algorithm, R_{eco} presented higher estimated values during the end of summer and early fall, and maximum in September (only for DB algorithm). A peak in R_{eco}

was also estimated in May. The beginning and end of the year (January and December) also presented high values similar to June and October respectively. Using the NB algorithm higher values of R_{eco} were estimated in May and June, and minimum values during winter.

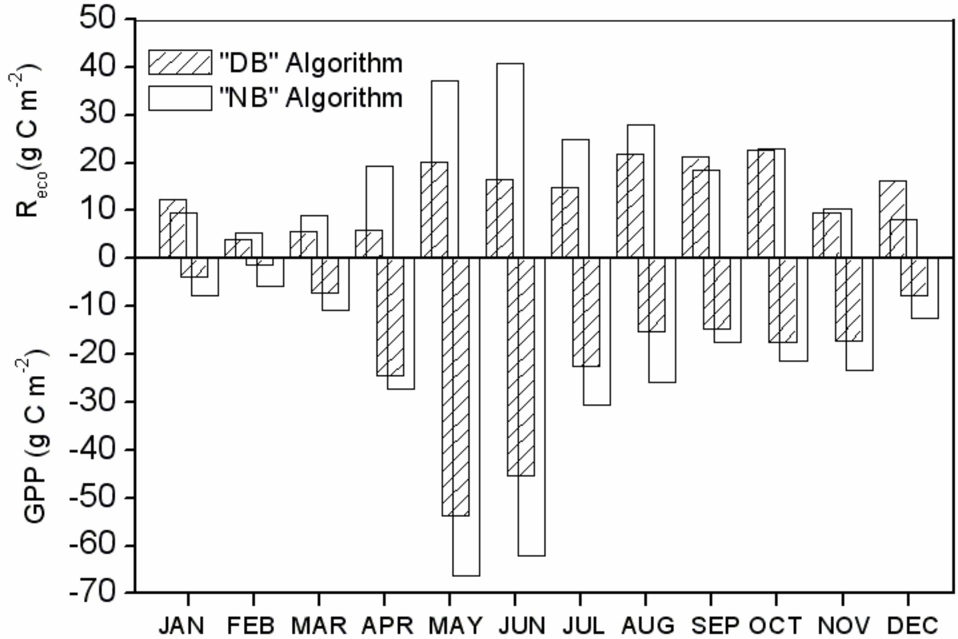

Figure 9: *Estimated monthly gross primary production (GPP; negative exchanges) and ecosystem respiration (R_{eco}; positive exchanges) using the "daytime data-based estimate" (DB; lined bars) and the "night-time data-bases estimate" (NB, white bars) flux partitioning algorithms for the non intervention treatment.*

4. DISCUSSION

During the fourth year after a fire, SL management hindered the recovery of carbon sequestration in the Mediterranean coniferous forest compared to the NI treatment. Photosynthesis and respiration processes also presented different patterns between post-fire treatments. Carbon loss was mostly constant in SL and not related to temperature at short time scales (30 min), with very small oscillations throughout the whole measurement period at both daily and seasonal scales, evidencing very low biological activity in the soil and vegetation. By contrast, the NI treatment showed more biological activity, with higher soil respiration rates and vegetation productivity, yielding higher daily and seasonal ranges of carbon exchange. In fact, the results of this study underline higher vegetation cover and performance for NI treatment, explaining the higher *ET* and lower Bowen ratio compared to SL treatment, with a consequent decrease in soil water content. Furthermore, while opposing processes in the carbon cycle (plant uptake and respiration) were both enhanced in NI, the additional contributions of CO_2 released by the wood decomposition (Gough *et al.*, 2004) was overwhelmed by photosynthesis such that annual carbon emissions were reduced considerably compared to the SL treatment. Thus, despite the limited temporal extent of data coverage, the strong impact of SL management on ecosystem CO_2 fluxes has been clearly demonstrated even at the initial stages of natural regeneration.

Several reasons may contribute to the marked differences in the net CO_2 fluxes between SL and NI treatments. First, burnt trees and coarse woody debris left after the wildfire represent a large pool of nutrients (Johnson *et al.*, 2005; Kappes *et al.*, 2007; Merino *et al.*, 2007; Wei *et al.*, 1997), that will be progressively incorporated to the soil as the trees fall and wood decomposes (Coleman *et al.*, 2004; Grove and Meggs, 2003; Harmon *et al.*, 1986), improving soil fertility. Second, burnt trees and branches (even after falling) act as nurse structures that improve microclimatic conditions for plant regeneration (Castro *et al.*, 2010a, 2011; Harmon *et al.*, 1986; Lindenmayer *et al.*, 2008; Smaill *et al.*, 2008; Stoddard *et al.*, 2008). Third, salvage logging may damage the banks of seedlings and shoots that regenerate soon after the fire (Lindenmayer *et al.*, 2008; Martínez-Sánchez *et al.*, 1999; McIver and Starr, 2000), reducing plant density. In addition, the presence of burnt logs and branches creates habitat complexity that may reduce herbivore damage to the vegetation (Ripple and Larsen, 2001; see also Relva *et al.*, (2009) for similar effect in non-burnt woody debris), and attract seed-dispersing birds (Castro *et al.*, 2010b; Rost *et al.*, 2009, 2010). All this may translate to a higher capacity in NI for vegetation productivity and hence carbon sequestration, while SL retards vegetation recovery and carbon uptake capacity. Differences could be more accentuated in the long term, as wood decomposes and progressively releases its nutrients (Irvine *et al.*, 2007).

These results are likely extensible to many other burnt coniferous forest ecosystems subjected to post-fire salvage logging. Coarse woody debris has been widely reported to contribute to soil fertility and soil microclimate improvement in different ecosystem types (Castro *et al.*, 2010a, 2011; Hafner and Groffman, 2005; Pérez-Batallón *et al.*, 1998; Smaill *et al.*, 2008; Stoddard *et al.*, 2008), and consequently to enhance primary productivity (Burton *et al.*, 2000; Irvine *et al.*, 2007; Stark *et al.*, 2006; Stoddard *et al.*, 2008). Since partially burnt woody debris (with charring limited to the bark and the superficial layers) has similar nutrient concentrations to unburnt wood (Wei *et al.*, 1997), the effects of burnt wood on soil fertility enrichment will be comparable to those reported for unburnt coarse woody debris. In addition, reductions in plant cover and regeneration capacity after salvage logging have been also reported in different forest types across the world (Beghin *et al.,* 2010; Castro *et al.,* 2011; Donato *et al.,* 2006; Greene *et al.,* 2006; Lindenmayer *et al.,* 2004; Lindenmayer and Noss, 2006; Stark *et al.,* 2006; Svoboda *et al.,* 2010), thus with the potential to reduce carbon uptake. Finally, the generalized increase of the erosion risk after a wildfire (Lindenmayer *et al.*, 2008; Spanos *et al.*, 2005; Thomas *et al.*, 1999; Yang *et al.*, 2003) leads to a negative synergic effect through the soil impoverishment, reinforcing the impact of salvage logging on carbon emissions. Thus, in general salvage logging applied after a wildfire in coniferous forests has the potential to alter soil properties, retarding vegetation recovery and thus the carbon uptake capacity.

4.1. Management implications

Fires destroy large areas of forest every year in many areas of the world (FAO, 2007). A key management decision after a forest fire is to determine the fate of the burnt wood, and an intense debate surrounds the practice of salvage logging as it has ecological, economical and silvicultural implications (Beschta *et al.*, 2004; DellaSala *et al.*, 2006; Donato *et al.*, 2006; Lindenmayer *et al.*, 2008). Our study demonstrates, for the first time, that the removal of burnt wood retards the capacity of such ecosystems to restore their carbon sink capacity in Mediterranean climates. Thus, in terms of policies for optimization of carbon sequestration in the context of the climate change, salvage logging should be discouraged. Potential implications at the global scale are aggravated by the predicted increase in wildfire incidence for climate change scenarios in Mediterranean and other semi-arid climates of the world (IPCC, 2007). Applying alternative management strategies for burnt wood following wildfire could therefore suppose a notable variation in carbon release to the atmosphere at a global scale, even without considering CO_2 emissions by the heavy machinery used in salvage logging operations (Stephens *et al.*, 2009).

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APPENDIX A:

Recently, a controversial correction has been proposed for eddy covariance measurements in cold environments (Burba *et al.*, 2008). This correction can increase by over 100 g C m^{-2} annual carbon exchange integrations (Reverter *et al.*, 2010) but does not change the relative difference between treatments in an identical climate. Burba *et al.,* (2008) argued that density measurements by an open path IRGA may be biased when the instrument significantly heats the air that it measures, particularly in cold conditions. Despite the correction proposed by Burba *et al.,* (2008), other scientists (Wohlfahrt *et al.*, 2008; Järvi *et al.*, 2009; Amiro, 2010) consider such an *a posteriori* correction to be somewhat premature, with no simple adjustment that can be applied universally.

For our data, Table A1 shows monthly values of F_C and *ET* both with and without the "self-heating correction" applied. The correction reduces CO_2 uptake in NI such that only two months of net CO_2 absorption are observed, and increases emissions by more than three times for SL. Notice that this result modifies substantially the absolute values of both annual net carbon exchange values, but changes relative differences between treatments only slightly. In addition, monthly GPP and R_{eco} values, estimated by the DB algorithm, are shown in Table A1 for NI. While values of GPP do not change with the correction, monthly R_{eco} increases dramatically as a result of the influence of the "self-heating correction" on flux partitioning algorithms. As previously reported (*e.g.*, Reverter *et al.,* 2010), *ET* is found to be comparatively insensitive to the "self-heating correction".

Table A1: *Monthly values of carbon fluxes (F_C, g C m^{-2}), and evapotranspiration (ET, mm) estimated in Non Intervention and Salvage Logging treatments, and gross primary production (GPP, g C m^{-2}) and ecosystem respiration (R_{eco}, g C m^{-2}) for Non Intervention, corrected by instrument heating (C) and not corrected (NC).*

	Salvage Logging				Non Intervention							
Month	***F*C**		**ET**		***F*C**		**GPP**		**Reco**		**ET**	
	NC	**C**	**NC**	**C**	**NC**	**C**	**NC**	**C**	**NC**	**C**	**NC**	**C**
1	-	-	2	20	2	20	9	5	19	42	13	13
2	-	-	0	16	0	16	2	2	6	29	17	17
3	-	-	-2	16	-2	16	10	6	9	27	24	25
4	-	-	-8	12	-8	12	25	23	14	32	38	38
5	-	-	-29	-10	-29	-10	59	59	28	55	60	62
6	19	57	-21	-3	-21	-3	48	48	20	48	58	60
7	22	63	-6	14	-6	14	25	26	15	46	49	50
8	19	58	2	19	2	19	24	26	26	57	38	42
9	14	53	1	17	1	17	25	21	36	50	23	25
10	8	50	2	19	2	19	25	22	31	51	38	39
11	6	46	-13	5	-13	5	18	16	9	29	21	22
12	2	43	-4	15	-4	15	20	9	33	36	24	22
TOTAL	**90**	**371**	**-77**	**139**	**-77**	**139**	**290**	**264**	**245**	**502**	**403**	**416**

DISCUSIÓN GENERAL

DISCUSIÓN GENERAL

El papel fundamental de los restos gruesos de madera muerta en el capital de nutrientes y los ciclos biogeoquímicos ha sido ampliamente discutido para el caso de bosques vivos poco perturbados. De este modo, se los ha considerado como elementos clave para asegurar la sostenibilidad de los ecosistemas (Harmon *et al.*, 1986), para el mantenimiento de su productividad (Brewer, 2008; Graham *et al.*, 1994; Jurgensen *et al.*, 1997), así como generadores de diferentes hábitats y microclimas que promueven la mayor abundancia y diversidad de organismos (Franklin *et al.*, 2002; Grove y Meggs, 2003; Kappes *et al.*, 2007; McCay y Komoroski, 2004; Reynolds *et al.*, 1992). Sin embargo, a pesar de la controversia existente sobre el manejo más adecuado de la madera quemada tras un incendio forestal, pocos trabajos se centran en el análisis de los efectos del manejo post-incendio de la madera quemada sobre la dinámica de nutrientes (Brais *et al.*, 2000; Johnson *et al.*, 2005), el balance del carbono y el funcionamiento biogeoquímico del ecosistema (Lindenmayer *et al.* 2008; Lindenmayer y Noss, 2006; McIver y Starr, 2000). Además, la mayor parte de estos estudios se centran en el efecto de la extracción intensiva de la madera frente a la ausencia de intervención, a pesar del amplio abanico de posibilidades intermedias existentes.

Durante las primeras etapas de establecimiento de un bosque, las plántulas dependen fundamentalmente de los nutrientes existentes en el suelo para su crecimiento y desarrollo, mientras que a medida que se cierra el dosel arbóreo las demandas se satisfacen mediante una mayor proporción de reciclaje interno y retranslocación de nutrientes (Imbert *et al.*, 2004; Landsberg y Coger, 1997). Por ello, la disponibilidad de nutrientes en el suelo en proporciones adecuadas resulta especialmente clave durante las primeras etapas de la sucesión ecológica. Sin embargo, esta condición es particularmente limitante en ecosistemas montaña mediterránea, cuyos suelos son frecuentemente poco desarrollados y pobres en nutrientes (Costa-Tenorio, 1998; Sardans *et al.*, 2005), y más aún cuando esta limitación se acentúa tras las pérdidas asociadas a un incendio (Trabaud, 1994; Yang *et al.*, 2003; Capítulo 1).

A pesar de que las plantas pueden reflejar cierta limitación de nutrientes en el caso de que esta sea muy acusada, concentran en sus tejidos los elementos minerales existentes en el suelo en las proporciones necesarias para su desarrollo, absorbiendo preferentemente los nutrientes que más limitan su crecimiento (Ingestad, 1979; Capítulo 1). Aún después de un incendio de alta intensidad, en el que se queman la totalidad de las fracciones finas de vegetación con mayor concentración de nutrientes, la mayor parte de la biomasa leñosa permanece en el ecosistema (Johnson *et al.*, 2005; Stocks *et al.*, 2004; Tinker y Knight, 2000; Wei *et al.*, 1997) con su composición química casi inalterada. Esto conlleva la existencia de un gran capital de nutrientes contenido en la madera quemada (Capítulo 1). De este modo, la madera puede actuar en una primera etapa como reservorio y almacén de nutrientes, amortiguando el impacto del incendio sobre la economía de nutrientes del ecosistema. Más aún, en el Capítulo 1 de esta tesis se observa cómo la relevancia de la madera como fuente potencial de nutrientes coincide bastante con aquellos nutrientes que son deficitarios en el suelo para satisfacer los requerimientos de un bosque maduro de coníferas.

Sin embargo, estos nutrientes no son utilizables por la vegetación hasta que no son liberados de forma progresiva mediante la descomposición de la madera y retenidos por el suelo. En el Capítulo 2 mostramos cómo a pesar de las lentas tasas de descomposición típicas de ecosistemas mediterráneos, en los que la humedad es limitante durante los periodos de mayores temperaturas, la madera libera N y especialmente P desde etapas tempranas. Así, durante el periodo transcurrido de este estudio la liberación de N y P por la madera quemada se estima en unos 8 kg ha^{-1} $año^{-1}$ y 0.7 kg ha^{-1} $año^{-1}$ respectivamente, aunque esta cifra puede variar considerablemente entre años. Esto supone alrededor de un 20% de los requerimientos anuales de N y P de los bosques de coníferas (*ca.* 40 kg ha^{-1} $año^{-1}$

de N y 4 kg ha^{-1} año^{-1} de P; Cole y Rapp, 1981; Helmisaari, 1995; Johnson y Lindberg, 1992; Miller, 1986). Estos aportes superan además las contribuciones de otras posibles entradas en el ecosistema, como las asociadas a la deposición atmosférica (*ca.* 6.3 kg ha^{-1} año^{-1} año de N y 0.2 kg ha^{-1} año^{-1} de P; Morales-Baquero *et al.*, 2006), o las debidas a la fijación de N en las raíces de leguminosas como *Adenocarpus decorticans*, presentes en la zona de estudio (*ca.* 1 kg ha^{-1} año^{-1} de N; Moro *et al.*, 1996). La presencia de la madera quemada provoca, ya sea de forma directa a través de los aportes de nutrientes de la madera, o indirectamente, mediante la reducción de las pérdidas de nutrientes por erosión (Thomas *et al.*, 2000) o mejora del microclima (Bros *et al.*, 2011; Castro *et al.*, 2011), un aumento efectivo del contenido en materia orgánica, de la biomasa microbiana, de la disponibilidad de nutrientes, y en su retención por parte de los microorganismos del suelo. Estos factores, unidos a la reducción de la densidad aparente del suelo, suponen un aumento de la fertilidad, el fomento de los procesos de reciclaje de nutrientes y, en definitiva, la mejora de las funciones ecológicas del suelo (Capítulos 2 y 3). Todo ello nos lleva a considerar la madera quemada como un elemento del ecosistema que desempeña importantes servicios ecosistémicos (Millennium Ecosystem Assessment [MEA], 2003), dado el beneficio que reporta al conjunto de la sociedad por su capacidad reguladora de procesos ecosistémicos clave (servicio de regulación) sobre la degradación del suelo y la erosión, así como el suministro de servicios de base, como la formación del suelo, el secuestro de carbono y los ciclos de los nutrientes.

La mayor calidad del suelo y la mejora del microclima por la presencia de restos de madera tienen implicaciones directas sobre la regeneración de la vegetación tras el incendio. De este modo, y tal como queda de manifiesto en el Capítulo 3, las plántulas de pino establecidas en los tratamientos con restos de madera quemada tienen un mayor crecimiento, biomasa y vigor, probablemente asociados a la reducción del estrés hídrico, por un lado, y a la mayor disponibilidad de nutrientes en el suelo (Capítulo 2), por otro. Sin embargo, al igual que en la madera de los árboles quemados (Capítulo 1), las concentraciones de nutrientes en las acículas de las plántulas de pino reflejaron deficiencias en micronutrientes (Fe, Mn, Zn, Cu), siendo estas muy bajas comparadas con los valores encontrados en la literatura para las mismas especies (Bonneau, 1995; López Varela *et al.*, 2008; Merino *et al.*, 2005; van Wesemael, 1993). Entre los macronutrientes, las acículas también mostraron carencias de P y, en menor medida, de N (Álvarez-Álvarez *et al.*, 2011; Augusto *et al.*, 2008; Bará, 1991; Bonneau, 1995; Dumbrell y McGrath, 2003; Merino *et al.*, 2005; Montero *et al.*, 1999; Warren *et al.*, 2005) prevaleciendo estas deficiencias independientemente del tratamiento. A pesar de que la madera quemada ha demostrado mejorar la fertilidad y disponibilidad de nutrientes en el suelo (Capítulo 2), la incorporación de estos nutrientes por las plantas estará condicionada por su existencia en formas asimilables y en proporciones adecuadas. De este modo, la carencia de un determinado nutriente en sus formas asimilables o su existencia en proporciones muy diferentes a las necesarias para las plantas puede interferir en la incorporación de otros nutrientes y provocar incluso una ralentización del crecimiento (Chapin *et al.*, 2002; Clarkson y Hanson, 1980, en Schlesinger, 1997). Los aportes de estos nutrientes limitantes en los tratamientos donde no se extrajo la madera quemada explicarían, en parte, el mayor crecimiento y biomasa de los pinos a pesar de la ausencia de diferencias en su estado nutricional entre los diferentes tratamientos. Estos resultados implican además una mayor incorporación de nutrientes por las plántulas en presencia de madera quemada, lo que sugiere la mitigación de esta limitación aunque no desaparezca por completo. En definitiva, los resultados muestran que la presencia de madera se traduce en una mejora de las condiciones microclimáticas (Castro *et al.*, 2011) y edáficas (Capítulo 2) para el desarrollo de las plántulas de pino. Las ramas y troncos quemados actúan así como estructuras nodriza que facilitan la regeneración tras el incendio sin añadir con ello una competencia por los recursos a nivel de las raíces (Castro *et al.*, 2011).

El manejo post-incendio de la madera quemada tiene también implicaciones de gran relevancia en el ciclo del carbono, ya que este elemento es el principal componente de la madera. En este estudio, la cantidad de carbono existente inicialmente tras el incendio en la biomasa aérea de madera quemada y las raíces se estimó en unos 22.000±3.000 kg ha^{-1}, mientras que los primeros 10 cm del suelo albergaron unos 20.000±5.000 kg ha^{-1} de carbono (Capítulo 1). Por tanto, la madera quemada supuso, en aquellos tratamientos en los que no se extrajo, un 54% aprox. del carbono total contenido en ambos reservorios. Parte de este carbono es emitido de forma directa y progresiva a la atmósfera como CO_2 (Gough y Seiler, 2004; Progar *et al.*, 2000; Wang *et al.*, 2002), y otra parte es liberada al suelo en forma de sustratos orgánicos potencialmente mineralizables por los microorganismos (Hafner *et al.*, 2005; Kuenhe *et al.*, 2008; Spears y Lajha, 2004). Así, durante la primera etapa de descomposición recogida en este estudio, se estima que la madera quemada libera anualmente unos 430 kg ha^{-1} de carbono al suelo y a la atmósfera, aunque esta cantidad es también bastante variable entre años, siendo esperable que decrezca exponencialmente a medida que disminuye su cantidad y se hace más recalcitrante (Brown *et al.*, 1996; Weedon *et al.*, 2009; Capítulo 2). Así, la presencia de la madera incrementó la concentración de materia orgánica en el suelo en un 18%, el carbono total un 42% y el carbono orgánico disuelto un 49% (Capítulo 2). Por tanto, dada la lenta descomposición de la madera y la difícil mineralización de los compuestos orgánicos liberados al suelo, éstos pueden constituir un importante almacén potencial de carbono en el ecosistema (Laiho y Prescott, 2004; Mackensen y Bauhus, 2003).

Por otro lado, la presencia de la madera quemada favorece el aumento de las tasas de actividad biológica, lo cual se refleja tanto en la productividad de la vegetación como de la respiración del suelo, como se discute en los Capítulos 3, 4 y 5. Esto se interpreta como un incremento de las tasas de mineralización, incorporación y reciclaje de nutrientes y, por tanto, del funcionamiento ecológico del suelo. Este hecho también se constata en el Capítulo 2, en el que se muestra cómo la biomasa microbiana y la incorporación de nutrientes por parte de los microorganismos se ven favorecidas bajo los troncos de madera quemada. Además, la relación C/N en los microorganismos del suelo también desciende, a pesar de que el incremento de la relación C/N en el suelo puede acentuar la limitación de N para los microorganismos (Hafner *et al.*, 2005; Magill y Aber, 2000). No obstante, la mineralización de la materia orgánica del suelo y, por tanto, la liberación de nutrientes en formas asimilables por las plantas, sería comparativamente más lenta que en casos de aportes de materia orgánica de menor ratio C/N y/o fácilmente mineralizables (Phillips *et al.*, 2011). De hecho, la adición de sustratos orgánicos lábiles y nutrientes (N y P) puede estimular la descomposición del carbono orgánico ya existente en el suelo (Kuzyakov, 2010; Milcu *et al.*, 2011) y, por tanto, incrementar la emisión de CO_2 (Heath *et al.*, 2005), lo cual resultaría, por otro lado, contraproducente para el mantenimiento de la capacidad de secuestro de carbono del suelo (Hoosbeek *et al.*, 2004). Los aportes de sustratos orgánicos de difícil mineralización, sin embargo, posibilitan el aumento de la capacidad de retención del suelo por la mayor persistencia de la materia orgánica (Capítulo 2), lo que ayudaría a reducir las pérdidas de nutrientes por lavado y lixiviación.

La madera quemada además desempeña una importante función ayudando a amortiguar y favorecer las condiciones microclimáticas del suelo. En este tipo de ecosistemas mediterráneos la disponibilidad de agua puede resultar particularmente limitante para el desarrollo de la vegetación y la actividad microbiana (Almagro *et al.*, 2009; Casals *et al.*, 2000; Sardans *et al.*, 2005; Xu y Baldocchi, 2004; ver Capítulos 3 y 4). Además, tras un incendio, las temperaturas que alcanza el suelo durante las horas centrales del día pueden llegar a ser muy elevadas, debido al color oscuro de los restos vegetales carbonizados y la consiguiente reducción del albedo (Amiro *et al.*, 1999; Majorowicz y Skinner, 1997; ver temperaturas del suelo en Capítulo 4 y razón de Bowen en el Capítulo 5). La presencia de madera quemada contribuye a reducir el calentamiento del suelo y al mantenimiento de la humedad, particularmente cuando los restos de madera quemada se encuentran en contacto con el suelo (Castro *et al.*, 2011; Bros *et al.*, 2011). Como se ha mencionado, esta función ecosistémica de la madera quemada contribuye a reducir el estrés hídrico de las plantas (Capítulo 3) y los microorganismos del suelo (Capítulo 4), contribuyendo a acelerar el desarrollo y crecimiento de la vegetación y las tasas de respiración y mineralización de los microorganismos (Capítulos 3 y 4).

Desde el punto de vista de las emisiones globales de CO_2, la productividad primaria supone un sumidero de carbono, mientras que la respiración del suelo y las emisiones directas de carbono a la atmósfera por la descomposición de la madera constituyen fuentes de emisión de CO_2. Al constituir flujos contrapuestos, estos procesos son contrarios en cuanto sus implicaciones para el ciclo del carbono, aunque se verán favorecidos simultáneamente por los mismos factores (disponibilidad nutrientes, agua, temperatura, etc.; Irvine *et al.*, 2007; Janssens *et al.*, 2001; Mkhabela *et al.*, 2009). Por tanto, la evaluación del efecto neto resultante de la presencia de la madera quemada en las emisiones de carbono a nivel de ecosistema no resulta sencilla. En el Capítulo 5, se muestra cómo el aumento de la productividad primaria de la vegetación en presencia de madera quemada contribuye a compensar las mayores emisiones de CO_2 por respiración (vistas en el Capítulo 4) y descomposición de la madera, inclinando el balance hacia un mayor secuestro de carbono.

Para la evaluación de las implicaciones que los diferentes tratamientos de manejo de la madera quemada tendrían en el balance neto del carbono debería incluirse además el consumo de combustibles fósiles durante los trabajos de extracción de la madera, su transporte y su procesado (Stephens *et al.*, 2009). Esto llevaría a incrementar aún más las diferencias existentes en el balance global del carbono entre la extracción intensiva de la madera y la ausencia de intervención. Además, en el caso de la retirada de la madera, el uso final que se le da a la madera quemada y la proporción de los productos destinados a los reservorios de carbono de corto (*i.e.*: papel, biomasa, etc.) o largo plazo (*i.e.*: mobiliario, estructuras, etc.) también será determinante (Lindenmayer *et al.*, 2008), aspectos que no han sido considerados en la presente tesis.

Otros aspectos a tener en cuenta cuando se interviene en un bosque tras un incendio, y que no se han considerado específicamente en este trabajo, son el impacto que produce la introducción de maquinaria pesada en el ecosistema. A menudo, los trabajos de corte y extracción de la madera coinciden con el periodo de emergencia de las plántulas (Donato *et al.*, 2006; Fernández *et al.*, 2008; Greene *et al.*, 2006; Martínez-Sánchez *et al.*, 1999), sobre todo en el caso de especies pirófitas como son los pinos procedentes de semillas liberadas de piñas serotinas (Tapias *et al.*, 2001). Esto implica con frecuencia una mayor mortalidad de las plántulas emergentes (Donato *et al.*, 2006; Fernández *et al.*, 2008; Martínez-Sánchez *et al.*, 1999). Además, la compactación del suelo que se produce en las zonas donde se introduce la maquinaria pesada (McIver y McNeil, 2006; McIver y Starr, 2000, 2001) puede dificultar la penetración de las raíces (Schoenholtz *et al.*, 2000) y modificar la disponibilidad de agua (Gómez *et al.*, 2002), con el consiguiente detrimento en el desarrollo y supervivencia de las plántulas. La persistencia de la madera quemada *in situ* sin la utilización de maquinaria pesada puede provocar, sin embargo, una reducción de la densidad aparente del suelo (Capítulo 2) y dar lugar, por tanto, a una mayor porosidad y aireación (Merino y Edeso, 1999; Schoenholtz *et al.*, 2000). Ello favorece la penetración de las raíces y el agua de lluvia con lo que se reduce la escorrentía y arrastre del suelo. Más aún, la disposición de los troncos, ramas quemadas y otros restos orgánicos sobre el suelo ha demostrado actuar como barreras de contención que reducen el arrastre y pérdida de suelo y cenizas que se depositan tras el incendio, ya sea cuando estas se disponen estratégicamente con esta finalidad (Fox, 2011; Kim *et al.*, 2008; Robichaud, 2005; Robichaud *et al.*, 2008; Wagenbrenner *et al.*, 2006) o bien simplemente debido a su presencia sobre el suelo (Fernández *et al.*, 2007; Shakesby *et al.*, 1996; Thomas *et al.*, 2000; observación personal). Esta función de los restos de madera quemados reporta, por tanto, beneficios al ecosistema tanto desde el punto de vista biogeoquímico, al reducir la pérdida de nutrientes (Beschta *et al.*, 2004; McIver y McNeil, 2006), como hidrológico, al reducir la concentración de sedimentos y de estos elementos en las aguas (Karr *et al.*, 2004; Wondzell, 2001).

En resumen, los resultados de esta tesis doctoral ponen de manifiesto que la madera quemada tras un incendio forestal desempeña un papel esencial en la regulación de la disponibilidad de nutrientes y la protección física del suelo, mejorando el microclima y reduciendo el riesgo de erosión y arrastre. Estas funciones contribuyen a la recuperación de funcionalidad ecológica y el mantenimiento de procesos ecológicos clave, como son la fertilidad del suelo, la actividad microbiológica y la movilización de nutrientes, lo que favorece el desarrollo de la vegetación y la recuperación de la capacidad de secuestro de carbono del ecosistema. Por el contrario, la retirada intensiva de la madera quemada supone una perturbación adicional al ecosistema que se añade a las perturbaciones ya ejercidas por los incendios. Su efecto acumulado puede tener un impacto sinérgico negativo sobre el ecosistema (Lindenmayer *et al.*, 2008), aumentando el riesgo de superar el umbral de impacto reversible (Lindenmayer y Ough, 2006; Paine *et al.*, 1998). Los resultados de esta tesis pretenden servir de ayuda de manera directa en la toma de decisiones sobre el manejo de la madera quemada tras un incendio forestal. Las conclusiones que se extraen en el presente estudio son especialmente extrapolables a ecosistemas mediterráneos, así como a otros ecosistemas con similar limitación de nutrientes y humedad, en los que la persistencia de la madera quemada en el ecosistema actúe aliviando dichos factores limitantes para la regeneración de la vegetación.

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CONCLUSIONES / CONCLUSIONS

CONCLUSIONES

1. La madera quemada que queda tras un incendio forestal contiene aún una importante cantidad de nutrientes y actúa como reserva para el ecosistema en regeneración, lo cual resulta especialmente relevante en ecosistemas asentados sobre suelos pobres o degradados como es el caso. En este estudio, la magnitud de estas reservas fue especialmente importante en el caso del N, K y los micronutrientes Na, Mn, Fe, Zn y Cu, en los que el contenido en la madera quemada fue mayor respecto al existente en los primeros 10 cm de suelo. Es más, la relevancia de la madera como fuente potencial de nutrientes coincidió con buena parte de aquellos nutrientes que son deficitarios en el suelo para satisfacer los requerimientos de un bosque maduro.

2. A medida que se descompone sobre el suelo, la madera actúa como fuente de nutrientes para el ecosistema en regeneración. Ya en los primeros años de descomposición, se produjo una progresiva liberación de N y P, a pesar de la lenta descomposición de la madera en este ecosistema mediterráneo.

3. La presencia de la madera quemada sobre el suelo supuso un aumento efectivo del contenido en materia orgánica, de la biomasa microbiana, de la disponibilidad de nutrientes, y en su retención por parte de los microorganismos del suelo. Estos factores, unidos a la reducción de la densidad aparente del suelo, conllevan un aumento de la fertilidad, el fomento de los procesos de reciclaje de nutrientes y, en definitiva, la mejora de las funciones ecológicas del suelo, ayudando así a restaurar las pérdidas de nutrientes y de fertilidad asociadas a un incendio.

4. El tratamiento post-incendio de la madera quemada afectó, asimismo, la eficiencia de la regeneración natural del pino resinero. La presencia de la madera quemada tras el incendio incrementó el crecimiento, vigor y con ello, la asimilación de nutrientes de las plántulas durante las primeras etapas de crecimiento. Este efecto facilitador de la madera quemada se asocia probablemente a la reducción del estrés hídrico de las plántulas por la mejora del microclima y a la mayor disponibilidad de nutrientes en el suelo, lo cual supone la aminoración de los factores típicamente limitantes de los bosques de coníferas mediterráneos.

5. La presencia de madera quemada también incrementó la actividad respiratoria del suelo y, por tanto, la emisión de CO_2, especialmente en el tratamiento en el que la madera quemada se encuentra en contacto con el suelo. Esta mayor tasa de actividad microbiana en el suelo se interpreta como un indicador del restablecimiento de los procesos de mineralización de la materia orgánica, y de la mejora de la calidad, fertilidad y condiciones edáficas en respuesta a la amortiguación del microclima, al aporte de nutrientes y sustratos orgánicos por parte de la madera quemada y a las contribuciones directas o indirectas de la vegetación a través de la respiración de sus raíces o el suministro de exudados orgánicos fácilmente degradables por los microorganismos.

6. A pesar de las mayores emisiones de CO_2 existentes en el tratamiento en el que la madera no fue extraída, el aumento de la productividad primaria de la vegetación en presencia de madera quemada compensó estas emisiones y equilibró el balance neto hacia un mayor secuestro de carbono. Por tanto, en bosques de coníferas mediterráneos afectados por incendios, la extracción intensiva de la madera quemada no se encuentra en consonancia con los

objetivos de optimización del secuestro de C acordados en el protocolo de Kyoto.

7. En resumen, la madera quemada tras un incendio forestal es un elemento natural que puede proporcionar importantes servicios ecosistémicos, como son, entre otros, la regulación de la disponibilidad de nutrientes y la protección física del suelo, mejorando el microclima y reduciendo el riesgo de erosión y arrastre. Estas funciones favorecen la recuperación y reactivación de procesos ecológicos clave para la regeneración y sostenibilidad del ecosistema. Por el contrario, la retirada intensiva de la madera quemada supone una perturbación adicional que se añade a las perturbaciones ya ejercidas por los incendios, lo cual puede implicar un impacto negativo y sinérgico sobre el ecosistema y un aumento del riesgo de procesos de degradación irreversibles.

CONCLUSIONS

1. The burnt wood remaining after a forest fire still contains an important amount of nutrients and acts as a reservoir for the regenerating ecosystem. This is especially relevant in ecosystems located over poor or degraded soils as in the present case. In this study, the magnitude of these stocks was especially important in the case of N, K and the micronutrients Na, Mn, Fe, Zn and Cu, whose 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.

2. As decomposition occurs over the soil, the wood acts as a source of nutrients for the regenerating ecosystem. A progressive release of N and P occurred even during the first years of decomposition, despite the slow wood decay in this Mediterranean ecosystem.

3. The presence of burnt wood over the soil produced an effective increase in the organic matter content, in the microbial biomass, in the nutrient availability, and in its retention by soil microorganisms. These factors, together with the reduction of the soil bulk density, led to increased fertility, enhanced nutrient cycling processes and, ultimately improved soil ecological functions, helping therefore to restore the nutrients and fertility following the wildfire.

4. The post-fire treatment of burnt wood also affected the natural regeneration efficiency of maritime pine. The burnt wood remaining after the fire increased the growth, vigour and thus, the nutrient assimilation of seedlings during the first growing seasons. This facilitative effect of the burnt wood is

likely attributable to the reduction of the water stress of seedlings, due to the more favourable microclimate, and to higher soil nutrient availability. All this represents the amelioration of factors that typically limit Mediterranean coniferous forests.

5. The presence of burnt wood also increased soil respiratory activity and hence CO_2 emissions, especially in the treatment where the burnt wood was in contact with the ground. This higher microbial activity in the soil is interpreted as an indicator of the reestablishment of mineralization processes, and of the improvement of the quality and fertility of edaphic conditions. This is also the consequence of microclimatic amelioration, of the supply of nutrients and organic substrates by the burnt wood, and of the direct and indirect contributions of vegetation through root respiration or organic exudates that are easy for microorganisms to mineralize.

6. Despite the higher CO_2 emissions in the treatment where the wood was not removed, the increase in primary productivity in the presence of burnt wood compensated these emissions and pushed the net balance towards higher carbon sequestration. Therefore, in Mediterranean coniferous forests, salvage logging is not consistent with the Kyoto protocol objectives of optimizing carbon sequestration.

7. Summarizing, the burnt wood after a forest fire is a natural element that can provide important ecosystem services, such as the regulation of nutrient availability and soil physical protection, ameliorating the microclimate and reducing the risks of erosion and runoff. These functions stimulate the recovery and reactivation of key ecological processes for regeneration and ecosystem sustainability. On the contrary, burnt wood salvage logging represents an additional perturbation beyond those exerted by wildfires.

This can involve a negative and synergic impact on the ecosystem and a higher risk of irreversible degradation processes.

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