UNIVERSIDAD DE MURCIA

Departamento de Química Agrícola, Geología y Edafología

**Reservorios y flujos de carbono en un gradiente de
intensificación de usos del suelo de un ecosistema mediterráneo:
factores de control y capacidad de secuestro de carbono**

**Carbon pools and fluxes along a land use intensification
gradient in a Mediterranean ecosystem:
controls and carbon sequestration capacity**

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Centro de Edafología y Biología Aplicada del Segura

Tesis Doctoral

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A mis padres,
por su apoyo incondicional

"The nation that destroys its soil, destroys itself"

Franklin D. Roosevelt

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Resumen

Introducción general

Los ecosistemas terrestres juegan un papel clave en el ciclo global del carbono (C) porque almacenan grandes cantidades de C orgánico en el suelo (1550 Pg) y en la vegetación (750 Pg), intercambian CO_2 con la atmósfera (590 Pg) a través de la fotosíntesis y la respiración, y pueden actuar como fuentes o sumideros de CO_2 atmosférico en función del uso del suelo y de las condiciones climáticas (Batjes y Sombroek, 1997; Cox et al., 2000; Joos et al., 2001). Aunque la mayoría de los ecosistemas terrestres naturales actúan como sumideros de carbono, absorbiendo y almacenando más CO_2 del que emiten de vuelta a la atmósfera, es importante destacar la importancia de las masas de bosque en el balance global neto del carbono, ya que: i) almacenan grandes cantidades de carbono en la vegetación, los detritus y la materia orgánica del suelo, regulando la concentración atmosférica de CO_2 y el clima, y ii) porque la conversión de estos ecosistemas a campos de cultivo libera CO_2 a la atmósfera (Fahey et al., 2010).

El carbono almacenado en los ecosistemas terrestres representa un equilibrio dinámico de ganancias (productividad primaria neta aérea y subterránea) y pérdidas (a través de la respiración del suelo y de los procesos erosivos) que se dan dentro del ecosistema y actúan a escalas temporales diferentes (diaria, mensual, anual, centenaria). Una gran proporción del CO_2 absorbido por la vegetación a través de la fotosíntesis es asignado y almacenado en forma de carbono orgánico en los tejidos leñosos y foliares (hojas, ramas, tronco y raíces) (Figura 1). Otra fracción es asignada a la parte subterránea (TBCA, *Total Belowground Carbon Allocation*) para la producción de raíces y exudados y el mantenimiento de la actividad radicular y micorrízica (Raich y Nadelhoffer, 1989). El resto vuelve a la atmósfera a través de la "respiración del suelo", que incluye la respiración radicular (como subproducto de la fotosíntesis) y los procesos de descomposición de la hojarasca y la materia orgánica del suelo (Edwards et al., 1970; Schlesinger, 1997; Wiant, 1967). Las pérdidas de carbono a través de otros procesos como la erosión y la lixiviación, aunque generalmente resultan ser mucho menores que aquellas debidas a la respiración del suelo (Edwards y Harris, 1977; Forrester et al., 2006; Giardina y Ryan, 2002; Raich, 1983; Schlesinger 1977; 1984), pueden ser relevantes en el balance neto de carbono de ecosistemas limitados por el agua como los mediterráneos (Lal 2003; Smith et al., 2007). En este sentido, el papel del patrón espacial de la vegetación o el tipo de comunidad vegetal pueden ser determinantes en el balance neto de carbono del sistema, influyendo

sobre los distintos aportes (*inputs*) de carbono procedentes de la productividad primaria neta y la liberación (*outputs*) de carbono a la atmósfera a través de la respiración radicular y los procesos erosivos (Högberg et al., 2001; Lal 2003; Schlesinger y Litcher, 2001; Trumbore, 2006).
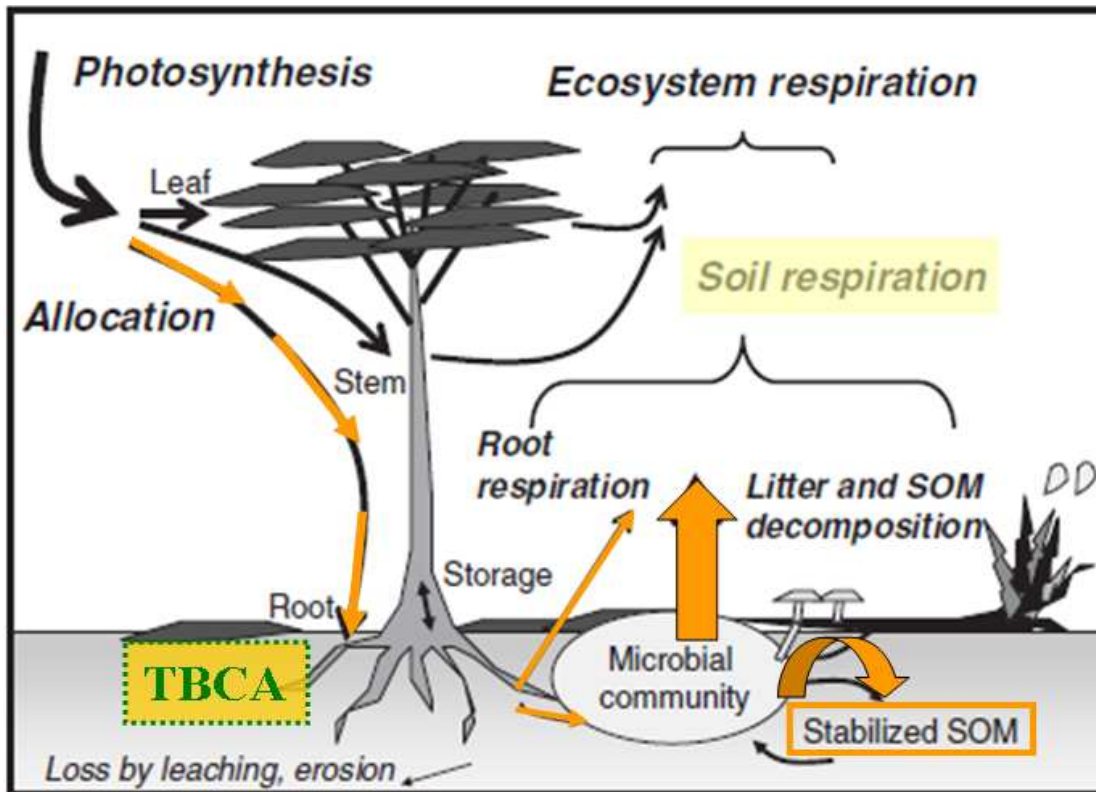
Figura 1. Flujos de carbono en ecosistemas terrestres. Adaptada de Trumbore (2006).

Entre los principales procesos de cambio global destacan los cambios de usos del suelo, el cambio climático, el aumento en las concentraciones de CO_2 atmosférico, el aumento de radiación solar ultravioleta (280-400 nm), la degradación del suelo y los procesos de desertificación, los cambios en los ciclos biogeoquímicos del nitrógeno y la proliferación de especies invasoras (Evaluación de los Ecosistemas del Milenio, 2005; Sala et al., 2000). De todos estos procesos, los cambios de uso del suelo se consideran la principal causa de la pérdida de carbono orgánico y de la degradación del suelo (Lal, 2004a; Post et al., 2000; Powlson et al., 2011), y son responsables del 20% de las emisiones antropogénicas de CO_2 a la atmósfera (Le Quéré et al., 2009; The Terrestrial Carbon Group, 2008).

El aumento de las emisiones de CO_2 procedentes del suelo y la disminución de los reservorios de carbono a nivel de ecosistema (suelo y vegetación) debidos a la conversión

de ecosistemas naturales a tierras agrícolas pueden ser compensados parcialmente cuando se produce el abandono de tierras agrícolas, ya que la regeneración de la vegetación natural lleva asociada la absorción de CO_2 atmosférico y la acumulación de carbono en el suelo. Sin embargo, el nivel de incertidumbre asociado a la estimación de las tasas de acumulación y pérdida de carbono como consecuencia de los cambios de uso del suelo está limitando nuestra comprensión acerca del papel de los diferentes usos del suelo como potenciales sumideros de carbono. Por lo tanto, cuantificar los reservorios de C así como estimar los flujos (entradas y salidas) de C en un gradiente de intensificación de usos del suelo es un paso previo para evaluar el impacto de los cambios de uso del suelo sobre el ciclo del C en la región mediterránea, y puede resultar de gran utilidad como apoyo en la toma de decisiones sobre la gestión territorial orientada a las medidas compensatorias (conservación de los reservorios de carbono) o de mitigación (reducción de las de emisiones de CO_2) ante la perspectiva del cambio climático (Evaluación de los Ecosistemas del Milenio, 2005; UNEP-UNDP-UNCCD, 2008¸ UNFCCC, 2008).

Los ecosistemas mediterráneos han mostrado ser especialmente sensibles a los cambios de uso del suelo, al aumento de la concentración atmosférica de CO_2 y al cambio climático (Sala et al., 2000; Schröter et al., 2005). Las proyecciones de los modelos de cambio climático, y las tendencias ya observadas durante las últimas décadas, apuntan a un incremento de la temperatura (4-5 ºC) y una menor disponibilidad de agua en el suelo (25-30%) para las próximas tres décadas como consecuencia de una disminución de las precipitaciones y cambios en la distribución de las mismas en la región mediterránea (IPPC 2007; Sabaté et al., 2002). En particular, el cuadrante suroriental de la Península Ibérica, de clima mediterráneo seco-subhúmedo y semiárido, ha sido identificado como una de las zonas más vulnerables, ya que los modelos apuntan a un incremento en la frecuencia y duración de los periodos de sequía, así como en el número de eventos de lluvia de intensidades extremas durante el periodo estival (Giorgi y Lionello, 2008). Este escenario afectará de manera significativa a la dinámica y estructura de los ecosistemas, repercutiendo negativamente en algunos de los servicios ecosistémicos tales como la retención de agua en el suelo o el secuestro de carbono (Evaluación de los Ecosistemas del Milenio, 2005; Foley et al., 2005).

Como resultado del cambio climático y de los cambios de uso del suelo, muchos ecosistemas están sufriendo alteraciones en los factores que controlan los flujos de carbono, afectando en última instancia a los procesos que regulan la capacidad de almacenamiento de carbono (Álvaro-Fuentes y Paustian, 2011; Fahey et al., 2009; Foley et

al., 2005; Quinton et al., 2010; Sala et al. 2000). Después de la fotosíntesis (PPB) la respiración del suelo (R_s) es el flujo más importante del balance de carbono (Schimel, 1995), ya que regula la cantidad de carbono que se almacena en el suelo (Valentini et al., 2000). Dado que la respiración del suelo es un parámetro muy sensible a los cambios de temperatura y humedad (Davidson et al., 1998; Lloyd y Taylor, 1994), resulta esencial investigar su respuesta ante las variables climáticas y los diferentes atributos del ecosistema en distintos usos del suelo para mejorar nuestro entendimiento del ciclo del carbono, y así poder predecir cómo responderán los diferentes usos del suelo a los cambios previstos por el clima. Sin embargo, la heterogeneidad propia de ecosistemas limitados por el agua, caracterizados por una cubierta vegetal escasa y que se distribuye en manchas discontinuas separadas por zonas de suelo desnudo (Noy-Meir, 1973), hace difícil establecer relaciones entre los patrones de distribución de la vegetación (manchas de vegetación y zonas de suelo desnudo), las propiedades del suelo y los flujos de carbono (Maestre y Cortina, 2003; Qi et al., 2010; Rey et al., 2010; Merbold et al., 2011). De modo que para evaluar la respuesta de los flujos de carbono a las fluctuaciones climáticas y los diferentes atributos del ecosistema es fundamental entender la respuesta relativa de cada componente del ecosistema (micrositio): suelos desnudos y manchas de vegetación.

Esto resulta de especial interés en éste y otros ecosistemas limitados por el agua (*drylands*), pues aunque no son muy relevantes en cuanto a la densidad de sus reservorios de carbono, ocupan entre el 41 y el 47% de la superficie terrestre, en ellos se concentra el 38% de la población mundial, contienen el 27% del reservorio mundial de carbono orgánico del suelo y presentan un gran potencial para el secuestro de carbono (Evaluación de los Ecosistemas del Milenio, 2005; FAO, 2004; Grünzweig et al., 2003, 2007; Lal, 2004b; Reynolds et al., 2007; UNEP-UNDP-UNCCD, 2008; WRI, 2002). Sin embargo, las características inherentes a los ecosistemas mediterráneos, tales como: i) precipitaciones escasas e irregulares; ii) presencia de especies leñosas con tasas de crecimiento lento; iii) altas tasas de mineralización de la hojarasca y la materia orgánica del suelo; iv) dificultad para recuperar el reservorio de carbono orgánico en el suelo después de haber sufrido una alteración; y v) una larga historia de intensificación agrícola (Albaladejo et al., 1998; Álvaro-Fuentes y Cantero-Martínez, 2010; Martínez-Mena et al. 2002; Vallejo et al., 2006), limitan su resiliencia tras la cesación de una perturbación. Estas características, junto con la duración y el nivel de intensificación del uso del suelo (Asner et al., 2003; Kauffman et al., 2009), determinarán las tasas de acumulación de C a escala de ecosistema

así como el tiempo necesario para alcanzar la capacidad máxima de almacenamiento de carbono.

De todo lo anterior se deduce que cuantificar los reservorios y los flujos de carbono, así como identificar los factores que controlan los principales flujos de carbono en diferentes usos del suelo es crucial para profundizar en el conocimiento del ciclo del C y la capacidad de secuestro de C de ecosistemas mediterráneos, y con ello optimizar la gestión territorial orientada a la implementación de medidas compensatorias y/o de mitigación de emisiones de CO_2 contempladas en el Protocolo de Kyoto (UNEP-UNDP-UNCCD, 2008; UNFCCC, 2008). El papel relativo de los distintos componentes del balance de carbono, así como de sus factores de control y las interacciones entre ellos, son temas sujetos a estudio y debate en la actualidad (Grace y Rayment, 2000; Lal, 2003; Trumbore, 2006; Throop y Archer, 2007; Valentini et al., 2000; Van Oost et al., 2007).

Hipótesis general, objetivos y estructura de la tesis

La hipótesis general de este estudio es que los cambios en los patrones (estructura y distribución espacial) y tipo de vegetación resultantes de la intensificación de los usos de suelo causarán alteraciones en las condiciones microclimáticas (temperatura y humedad del suelo, exposición a la radiación solar) y en las características del micrositio (comunidades microbianas del suelo, calidad de los detritos procedentes de la vegetación, patrones de escorrentía y erosión del suelo), que afectarán a los flujos de carbono (entradas y salidas), a los factores que controlan dichos flujos y a la capacidad de secuestro de carbono del ecosistema.

Conforme a esta hipótesis, el objetivo general de la presente memoria es la caracterización de los reservorios y los flujos de carbono, la evaluación de la importancia relativa de los diferentes componentes del balance de C y la identificación de los factores que controlan los flujos de C más importantes que regulan la capacidad subterránea de secuestro de carbono en un gradiente de intensificación de usos del suelo: i) un matorral mixto con individuos de pino carrasco intercalados, ii) un campo agrícola abandonado, y iii) un olivar de secano. Estos usos del suelo son representativos de los cambios ocurridos en el paisaje durante las últimas décadas del siglo XX en ésta y otras regiones de la cuenca mediterránea como consecuencia de los procesos de intensificación agrícola y posterior abandono de tierras. Se espera que esta investigación contribuya, en última instancia, a

profundizar en el conocimiento de los procesos y factores que modulan la capacidad de los diferentes usos del suelo para secuestrar carbono.

Para alcanzar este objetivo general, se plantearon cuatro objetivos específicos:

- Caracterizar (cuantificación y distribución) los reservorios de carbono y la productividad primaria neta, así como estimar y evaluar la importancia relativa de los flujos de C (entradas y salidas) en el balance de C de cada uso del suelo.

- Analizar la variabilidad temporal de la respiración del suelo e identificar los factores bióticos y abióticos que modulan dicha variabilidad.

- Explorar las relaciones entre la estructura de la vegetación y su distribución espacial, las propiedades del suelo y la respiración del suelo a escala de sitio; así como identificar los factores de control (abióticos y bióticos) de la variabilidad espacial de la respiración del suelo en cada uso del suelo.

- Cuantificar las tasas de descomposición de dos tipos de hojarasca predominantes en ecosistemas mediterráneos (*Pinus halepensis* Miller y *Rosmarinus officinalis* L.) y evaluar la influencia del tipo de hojarasca y las condiciones ambientales inherentes al sitio en las dinámicas de descomposición de la hojarasca en la superficie del suelo.

La memoria de tesis se compone de una introducción general, un primer capítulo con la descripción del área de estudio y el diseño experimental, cuatro capítulos que constituyen el cuerpo principal de la memoria, las conclusiones generales, la bibliografía y los anejos. A continuación se describe brevemente el contenido de cada capítulo:

Capítulo 1: **Descripción del área de estudio y diseño experimental**

En este capítulo se describen las características climáticas, los tipos de suelos y las comunidades vegetales presentes en cada uno de los usos del suelo seleccionados. Se presenta así mismo el diseño experimental general utilizado en el presente trabajo.

Capítulo 2: **Caracterización de los reservorios de carbono y estimación de la capacidad de secuestro de carbono en un gradiente de intensificación de usos del suelo**

El objetivo principal de este capítulo es la caracterización (cuantificación y distribución) de los reservorios de carbono y la estimación de la productividad primaria neta en un gradiente de intensificación de usos del suelo. Para ello, se estiman los flujos de entrada (caída de hojarasca o "desfronde" y producción de biomasa radicular) y salida (respiración y erosión) de carbono en el suelo, así como los cambios anuales en el carbono almacenado en el suelo, y se integran en una aproximación a un balance de carbono (*TBCA approach*) para evaluar la capacidad subterránea de secuestro de carbono en cada uno de los usos del suelo. Los contenidos de este capítulo se corresponden con los del artículo:

Almagro, M., López, J., Boix-Fayos, C., Albaladejo, J., Martínez-Mena, M. (2010). Belowground carbon allocation patterns in a dry Mediterranean ecosystem: A comparison of two models. *Soil Biology and Biochemistry* 42 (9), 1549-1557.

Capítulo 3: **Variabilidad temporal de la respiración del suelo: factores de control**

Este capítulo se centra en analizar la variabilidad temporal de la respiración del suelo, así como en evaluar la importancia relativa de la temperatura y la disponibilidad de agua en el suelo como factores que controlan dicha variabilidad. Además, se evalúa la influencia de la distribución y estructura de la vegetación en la respuesta de la respiración del suelo a la temperatura y disponibilidad de agua en cada uso del suelo. Los contenidos de este capítulo se corresponden con los del artículo:

Almagro, M., López, J., Querejeta, J.I., Martínez-Mena, M. (2009). Temperature dependence of soil CO_2 efflux is strongly modulated by seasonal patterns of moisture availability in a Mediterranean ecosystem. *Soil Biology and Biochemistry* 41 (3), 594-605.

Capítulo 4: **Relación entre el patrón espacial de la vegetación, las propiedades del suelo y la respiración del suelo**

Este capítulo tiene como objetivo explorar las relaciones entre la estructura de la vegetación y su distribución espacial, las propiedades del suelo y la respiración del suelo a escala de sitio, y comprobar si los patrones de correlación se mantienen en los distintos usos del suelo. Además, se identifican los factores de control de la variabilidad espacial de la respiración del suelo en cada uno de los usos del suelo. Los contenidos de este capítulo se corresponden con los del artículo:

Almagro, M., Querejeta, J.I., Boix-Fayos, C., Martínez-Mena, M. Soil carbon pools and respiration rate are decoupled from current vegetation patterns in a Mediterranean old-field. *Soil Biology and Biochemistry* (en revision).

Capítulo 5: **Factores de control en la dinámica de descomposición de la hojarasca de dos especies predominantes de ecosistemas mediterráneos: dependencia del sitio y del tipo de hojarasca**

El objetivo de este capítulo es comparar las tasas de descomposición de dos tipos de hojarasca que difieren en su composición química (*Pinus halepensis* Miller y *Rosmarinus officinalis* L.) y que son predominantes en ecosistemas mediterráneos, así como evaluar si los factores de control de la dinámica de descomposición difieren según el tipo de hojarasca. Los contenidos de este capítulo se corresponden con los del artículo:

Almagro, M., Martínez-Mena, M. Exploring the factors controlling leaf-litter decomposition dynamics in a Mediterranean ecosystem: dependence on litter type and site conditions. *Plant and Soil* (en revision).

Bibliografía

Albaladejo, J., Martínez-Mena, M., Roldan, A., Castillo, V., 1998. Soil degradation and desertification induced by vegetation removal in a semiarid environment. Soil Use and Management 14, 1-5.

Álvaro-Fuentes, J., Cantero-Martinez, C., 2010. Short communication. Potential to mitigate anthropogenic CO_2 emissions by tillage reduction in dryland soils of Spain. Spanish Journal of Agricultural Research 8 (4), 1271-1276.

Álvaro-Fuentes, J., Paustian, K., 2011. Potential soil carbon sequestration in a semiarid Mediterranean agroecosystem under climate change: Quantifying management and climate effects. Plant and Soil 338, 261-272.

Asner, G.P., Archer, S., Hughes, R.F., Ansley, R.J., Wessman, C.A., 2003. Net changes in regional woody vegetation cover and carbon storage in Texas Dryland 1937-1999. Global Change Biology 9, 316-335.

Batjes, N.H., Sombroek, W.G., 1997. Possibilities for carbon sequestration in tropical and subtropical soils. Global Change Biology 3, 161-173.

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408, 184-187.

Edwards, C.A., Reichle, D.E., Crossley, D.A.Jr., 1970. The role of soil invertebrates in turnover of organic matter and nutrients. In: Reichle, D.E. (Eds) Analysis of temperate forest ecosystems, Springer-Verlag, New York, 12-172 pp.

Edwards, N.T., Harris, W.F., 1977. Carbon cycling in a mixed deciduous forest floor. Ecology 58, 431-437.

Fahey, T.J., Woodbury, P.B., Battles, J.J., Goodale, C.L., Hamburg, S., Ollinger, S., Woodall, C.W., 2010. Forest carbon storage: ecology, management, and policy. Frontiers in Ecology and the Environment 8 (5), pp. 245-25.

Foley, J.A., De Fries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Zinder, P.K., 2005. Global consequences of land use. Science 309 (5734), pp. 570-574.

Forrester, D.I., Bauhus, J., Cowie, A.L., 2006. Carbon allocation in mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. Forest Ecology and Management 233, 275-284.

Giardina, C.P., Ryan, M.G., 2002. Total belowground carbon allocation in a fast-growing *Eucalyptus* plantation estimated using a carbon balance approach. Ecosystems 5, 487-499.

Giorgi, F., Lionello, P., 2008. Climate change projections for the Mediterranean region Global and Planetary Change 63, 90-104.

Grace, J., Rayment, M., 2000. Respiration in the balance. Nature 404 (6780), pp. 819-820.

Grünzweig, J.M., Lin, T., Rotenberg, E., Schwartz, A., Yakir, D., 2003. Carbon sequestration in arid-land forest. Global Change Biology 9, 791-799.

Grünzweig, J.M., Gelfand, I., Fried, Y., Yakir, D., 2007. Biogeochemical factors contributing to enhanced carbon storage following afforestation of semi-arid shrubland. Biogeosciences 4, 891-904.

IPPC, 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M and Miller HL, eds. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press, 1-996.

Kauffman, J.B., Hughes, R.F., Heider, C., 2009. Carbon pool and biomass dynamics associated with deforestation, land-use, and agricultural abandonment in the neotropics. Ecological Applications 19 (5), 1211-1222.

Lal, R., 2003. Soil erosion and the global carbon budget. Environment International 29 (4), pp. 437-450.

Lal, R., 2004a. Soil carbon sequestration impacts on global climate change and food security. Science 304 (5677), 1623-1627.

Lal, R., 2004b. Carbon sequestration in dryland ecosystems. Environmental Management 33, 528-544.

Le Quéré, C., Raupach, M.R., Canadell, J.G., Marland, G., *et al*., 2009. Trends in the sources and sinks of carbon dioxide. Nature Geosciences 2 (12), pp. 831-836.

Martínez-Mena, M., Álvarez Rogel, J., Castillo, V., Albaladejo, J., 2002. Organic carbon and nitrogen losses influenced by vegetation removal in a semi-arid soil. Biogeochemistry 61 (3), 309-321.

Middleton, N.J., Thomas, D.S.G., eds., 1997. World Atlas of Desertification. U.N. Environment Programme, Edward Arnold, New York.

Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Desertification Synthesis. World Resources Institute, Washington, DC.

Noy-Meir, I, 1973. Desert ecosystems: environment and producers. Annual Review of Ecoloy and Systematics 4, 25-51.

Post, W.M., Kwon, K.C., 2000. Soil carbon sequestration and land-use change: processes and potential. Global Change Biology 6: 317-327.

Powlson, D.S., Gregory, P.J., Whalley, W.R., Quinton, J.N., Hopkins, D.W., Whitmore, A.P., Hirsch, P.R., Goulding, K.W.T., 2011. Soil management in relation to sustainable agriculture and ecosystem services. Food Policy 36, 572-587.

Quinton, J.N., Govers, G., Van Oost, K., Bardgett, R.D., 2010. The impact of agricultural soil erosion on biogeochemical cycling. Nature Geoscience 3, pp. 311-313.

Raich, J.W., 1983. Effects of forest conversion on the carbon budget of a tropical soil. Biotropica 15, 177-184.

Raich, J.W., Nadelhoffer, K.J., 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology 70 (5), 1346-1354.

Sabaté, S., Gracia, C., Sánchez, A., 2002. Likely effects of climate change on growth of *Quercus ilex*, *Pinus halepensis*, and *Fagus sylvatica* forest in the Mediterranean region. Forest Ecology and Management 162, 23-37.

Sala, O.E., Chapin, F.S., Arnesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., *et al.*, 2000. Biodiversity: Global biodiversity scenarios for the year 2100. Science 287, pp. 1770-1774.

Schimel, D.S., 1995. Terrestrial ecosystems and the carbon cycle. Global Change Biology 1 (1), 77-91.

Schlesinger, 1997. An analysis of global change, 2nd edition, Academic Press, San Diego, U.S.A., pp.150.

Schlesinger, W.H., 1984. Soil organic matter: a source of atmospheric CO_2, in: Woodwell, G.M. (Ed.), The role of terrestrial vegetation in the global carbon cycle: measurement by remote sensing. John Wiley & Sons, Chichester, England, 111-127 pp.

Schlesinger, W.H., Litchter, J., 2001. Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO_2. Nature 411, pp. 466-469.

Schröter, D., Cramer, W., Leemans, R., Prentice, I.C., Araújo, M.B., Arnell, N.W., Bondeau, A., *et al*., 2005. Ecosystem service supply and vulnerability to global change in Europe. Science 310 (25): 1333-1337.

Smith, S.V., Bullock, S.H., Hinojosa-Corona, A., Franco-Vizcaíno, E., Escoto-Rodriguez, M., Kretzschmar, T.G., Farfán, L.M., Salazar-Ceseña, J.M., 2007. Soil erosion and significance for carbon fluxes in a mountainous mediterranean-climate watershed. Ecological Applications 17 (5), 1379-1387.

The Terrestrial Carbon Group, 2008. How to include terrestrial carbon in developing nations in the overall climate change solution, http://www.terrestrialcarbon.org

Throop, H.L., Archer, S.R., 2007. Interrelationships among shrub encroachment, land management, and litter decomposition in a semidesert grassland. Ecological Applications 17 (6), pp. 1809-1823.

Trumbore, S., 2006. Carbon respired by terrestrial ecosystems - recent progress and challenges. Global Change Biology 12, 141-153.

UNEP-UNDP-UNCCD, 2008. Carbon in Drylands: Desertification, Climate Change and Carbon Finance. Technical Note for Discussions at CIC 7, Istanbul, Turkey -03-14.

UNFCCC (United Nations Framework Convention on Climate Change), 2008. Kyoto Protocol reference manual. Climate Change Secretariat (UNFCCC), Bonn, Germany.

Valentini, R., Matteucci, G.R., Dolman, A.J., Schulze, E.D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404, 861-863.

Vallejo, R., Aronson, J., Pausas, J.G., Cortina, J., 2005. Restoration of Mediterranean woodlands, in: van Andel, J., Aronson, J. (Eds.), Restoration Ecology. The new frontier. Blackwell Science Ltd., pp. 193-207.

Van Oost, K., Quine, T.A., Govers, G., *et al.*, 2007. The impact of agricultural soil erosion on the global carbon cycle. Science 318: 326-329.

Wiant, H.V., 1967. Has the contribution of litter decay to forest soil respiration been overestimated? Journal of Forestry 65, 408-409.

Capítulo 2. Caracterización de los reservorios de carbono y estimación de la capacidad de secuestro de carbono en un gradiente de intensificación de usos del suelo.

Resumen

El objetivo principal de este capítulo es la caracterización (cuantificación y distribución) de los reservorios y de la productividad primaria neta en un gradiente de intensificación de usos del suelo. Así mismo se estiman los flujos de carbono y se evalúa la importancia relativa de los diferentes componentes del balance de carbono dentro de cada uso del suelo. Para llevar a cabo dicho objetivo se seleccionaron tres usos del suelo localizados en el Noroeste de la provincia de Murcia. Estos usos son representativos del mosaico actual de usos del suelo como resultado de los cambios ocurridos en el paisaje durante las últimas décadas del siglo XX, en ésta y otras regiones de la cuenca mediterránea, como consecuencia de los procesos de intensificación agrícola y posterior abandono de tierras: (i) un matorral mixto con individuos de pino carrasco intercalados que no ha sufrido ninguna intervención humana desde hace 150 años; (ii) un campo agrícola abandonado que fue cultivado con cereal y se abandonó hace aproximadamente 30 años; y (iii) un olivar de secano cuyos olivos tienen aproximadamente 100 años.

Para llevar a cabo la estimación de la capacidad subterránea (suelo y raíces) de secuestro de carbono de cada uso del suelo y evaluar la importancia relativa de los diferentes componentes del balance de carbono dentro de cada ecosistema se aplican dos aproximaciones basadas en la ley de conservación de la masa ("*steady-state*" y "*non-steady-sate*"):

1) El modelo estacionario ("*steady-state*") propuesto por Raich y Nadelhoffer (1989), asume que el reservorio de carbono (C) en el suelo se encuentra en estado de equilibrio, de modo que las entradas de carbono en el sistema han de ser iguales a las salidas de carbono del mismo. De esta forma el carbono liberado por las raíces, el suelo mineral y la capa de hojarasca a través de los procesos de descomposición y respiración (es decir, flujo de CO_2 emitido por el suelo o "respiración del suelo") o exportado a través de procesos de erosión debe ser igual a las entradas de carbono procedentes de la parte aérea ("desfronde" o caída de hojarasca, que comprende las hojas, los frutos y las ramillas) más las entradas procedentes de la parte subterránea (TBCA, *Total Belowground Carbon Allocation,* que

incluye la respiración total del suelo, los carbohidratos utilizados por las micorrizas o exudados, y la producción de raíces finas):

$$R_s + Erosión = Aportes\ hojarasca + TBCA \qquad\qquad Ec.1$$

Despejando TBCA de la ecuación 1, podemos estimar la cantidad de C que es asignada a la parte subterránea para un determinado ecosistema a partir de las medidas anuales de respiración del suelo (R_s), erosión del suelo, y de los aportes de C debidos a la caída de la hojarasca:

$$TBCA = R_s + Erosión - Aportes\ hojarasca \qquad\qquad Ec.2$$

2) Sin embargo, en el modelo no estacionario ("*non-steady-sate*") propuesto por Giardina y Ryan (2002) para aquellos ecosistemas en los que las condiciones de equilibrio no son aplicables, se tiene en cuenta cualquier cambio referente al reservorio de carbono en el suelo para un periodo de tiempo determinado, incluyendo el C almacenado en las raíces, la capa de hojarasca y el suelo mineral:

$$TBCA = R_s + Erosión - Aportes\ hojarasca + \Delta[C_{raíces} + C_{hojarasca} + C_{suelo}] \qquad Ec.3$$

El reservorio de C correspondiente a la biomasa aérea, así como la tasa anual de secuestro de carbono, se estimó a partir de la aplicación de ecuaciones alométricas específicas en función de los diámetros basales y los respectivos incrementos anuales de cada uno de los individuos presentes en las parcelas (5 x 5 m) previamente delimitadas para cada uno de los usos del suelo. El reservorio de C en el suelo y en la biomasa radicular se estimó mediante la extracción de 24 *cores* (10 cm de diámetro y 15 cm de longitud) distribuidos al azar según los tipos de cobertura vegetal más representativos de cada uso. Además, se estimaron las tasas anuales de CO_2 emitido por el suelo (o "respiración del suelo"), y de C exportado por erosión hídrica laminar, así como los aportes de C al suelo derivados del "desfronde" o caída de hojarasca, y el C acumulado anualmente en el suelo mineral, la capa de hojarasca y la biomasa radicular para cada uno de los usos del suelo.

El reservorio total de C a nivel de ecosistema (biomasa aérea y subterránea, y carbono orgánico en el suelo) disminuyó conforme aumentó el grado de intensificación del

uso del suelo, siendo el reservorio total de C en el uso forestal más del doble que en el olivar y en el campo agrícola abandonado (Tabla 2.1). En los tres usos del suelo se observó un patrón similar en cuanto al C almacenado en la parte subterránea (suelo y biomasa radicular), el cual supuso más del 60% del reservorio total de C a nivel de ecosistema. Este resultado fue consistente con los patrones de productividad primaria neta observados para cada uso (Tabla 2.2), y está en línea con los patrones globales de distribución de los reservorios de C observados para otros ecosistemas limitados por el agua, en los que el C almacenado en la parte subterránea constituye dos tercios del reservorio total del ecosistema (Grünzweig et al., 2007; Jackson et al., 2002; Lal, 2004b).

Tabla 2.1. Reservorios de carbono y nitrógeno total del suelo (0-15 cm), razón C:N, reservorios de C de la biomasa aérea y subterránea (0-15 cm) en cada uso del suelo.

	Uso forestal	Campo abandonado	Olivar secano
Carbono orgánico del suelo (g C m^{-2})	5189.3 ± 154.9	3060 ± 441	2658 ± 514.8
Nitrógeno total del suelo (g N m^{-2})	336.3 ± 5.2	279 ± 3.6	284.1 ± 5.2
Razón C:N	15.4 ± 0.4	11.0 ± 0.4	9.3 ± 0.5
Carbono biomasa aérea (g C m^{-2})	3293.8 ± 2072.6	$351,3 \pm 49.6$	830.3 ± 52.1
Carbono biomasa subterránea (g C m^{-2})	305.4 ± 42.9	252.9 ± 42.9	162.2 ± 43.8
Reservorio de C del ecosistema (g C m^{-2})	8780.7 ± 2270.4	3664.3 ± 533.5	3640.6 ± 611

La respiración del suelo resultó ser el componente más importante en el balance de C de los tres usos del suelo independientemente de la aproximación utilizada (Tabla 2.2). El C exportado por erosión hídrica laminar resultó insignificante en comparación con las pérdidas de C por respiración del suelo. Aunque las tasas de acumulación de C en el suelo ($\Delta C_R + \Delta C_H + \Delta C_S$) resultaron menores en comparación con las pérdidas de C por R_s, influyeron significativamente en las estimaciones del carbono total asignado a la parte subterránea (TBCA) de cada uso del suelo. Es importante señalar que si no consideramos estos componentes ($\Delta[C_S + C_L + C_R] = 0$) en la estimación de TBCA de estos ecosistemas estaremos subestimando la capacidad de secuestro de C en el suelo en un 23.5, 16.1 y 12.8% en el campo agrícola abandonado, el uso forestal y el olivar, respectivamente.

Los valores de productividad primaria neta total obtenidos a partir de la combinación de metodologías tales como la aplicación de ecuaciones alométricas (para estimar la

cantidad de C acumulado en la biomasa aérea) y la aproximación utilizada (TBCA *approach*) basada en la ley de conservación de la masa (para estimar la cantidad de C acumulado en la parte subterránea de cada uno de los usos del suelo) fueron similares a los valores de productividad primaria neta observados en otros ecosistemas mediterráneos mediante otras técnicas tales como las torres de *Eddy Covariance* (Valentini et al., 2000; Allard et al., 2008). No obstante, la asunción de equilibrio no es correcta para estos ecosistemas mediterráneos debido a que subestima la capacidad subterránea de secuestro de carbono, especialmente en el caso del campo agrícola abandonado que actualmente se encuentra en fase de recubrimiento vegetal. Los resultados de esta investigación sugieren, por tanto, que se debe considerar el modelo no estacionario propuesto por Giardina y Ryan (2002) para una estimación adecuada de la capacidad subterránea de secuestro de carbono de estos ecosistemas mediterráneos.

Tabla 2.2. Flujos anuales de C (g C m^{-2}) y C total asignado a la parte subterránea (TBCA) de cada uso del suelo.

	Uso forestal	Campo abandonado	Olivar de secano
Respiración del suelo (F_S)	766 ± 64.2	648 ± 64.3	427 ± 30.3
Aportes de C por desfronde (F_A)	128.4 ± 9.3	88.4 ± 11.4	26 ± 9.31
C exportado por erosión (F_E)	1.43 ± 0.38	2.21 ± 0.23	2.58 ± 0.66
Acumulación de C en el suelo (ΔC_S)	-	14.6	-
Acumulación de C en la capa de hojarasca (ΔC_L)	73.2 ± 4.1	49.5 ± 5	12 ± 4.1
Acumulación de C en la biomasa radicular (ΔC_R)	50.3 ± 8.7	106 ± 12.2	44.8 ± 14.7
TBCA estimado como F_S - F_A	649.8 ± 21.9	559.4 ± 26.7	401.8 ± 21.7
TBCA incluyendo F_E	651.3 ± 22.2	561.6 ± 26.9	404.4 ± 22.3
TBCA (F_S - F_A + F_E + ΔC_S + ΔC_L + ΔC_R)	774.8 ± 35	731.8 ± 44.1	461.2 ± 41.1
TBCA (F_S - F_A + F_E + ΔC_S)	651.3 ± 22.2	576.2 ± 26.9	404.4 ± 22.3
TBCA (F_S - F_A + F_E + ΔC_L)	724.4 ± 26.3	611.1 ± 31.9	416.4 ± 26.4
TBCA (F_S - F_A + F_E + ΔC_R)	701.6 ± 30.9	667.7 ± 39.1	449.3 ± 37
Productividad Primaria Neta Aérea	260.4 ± 20.5	174.9 ± 28.9	93.7 ± 11.4
Productividad Primaria Neta Subterránea	387.4 ± 17.5	365.9 ± 22	230.6 ± 20.5

Capítulo 3: Variabilidad temporal de la respiración del suelo: factores de control.

Resumen

Después de la fotosíntesis (Productividad Primaria Bruta, PPB), la respiración del suelo (R_s) es el flujo de carbono más importante entre los ecosistemas terrestres y la atmósfera y un componente clave en el ciclo global del carbono ya que regula la cantidad de carbono que se almacena en el suelo (Valentini et al., 2000).

La región mediterránea ha sido identificada como una de las regiones más sensibles al cambio climático global. Las proyecciones de los modelos de cambio climático, y las tendencias ya observadas durante las últimas décadas para esta región, apuntan a un incremento de la temperatura (4-5 ºC) y una menor disponibilidad de agua en el suelo (25-30%) para las próximas tres décadas (Sabaté et al., 2002; IPPC 2007). En particular, el cuadrante suroriental de la Península Ibérica, de clima mediterráneo seco-subhúmedo y semiárido, ha sido identificado como una de las zonas más vulnerables, ya que los modelos apuntan a un incremento en la frecuencia y duración de los periodos de sequía, así como en los eventos de lluvia de intensidades extremas durante el periodo estival para esta región (Giorgi y Lionello, 2008).

Dado que la respiración del suelo es muy sensible a las fluctuaciones de temperatura y humedad, resulta esencial investigar la importancia relativa de estas variables climáticas en la dinámica de R_s en ecosistemas mediterráneos, con la finalidad de conocer cómo responderá a los cambios previstos por el clima, mejorar nuestro entendimiento del ciclo del carbono, y formular medidas necesarias de mitigación y adaptación a los cambios futuros predichos para estas zonas. Sin embargo, para evaluar la respuesta de la respiración del suelo a las fluctuaciones climáticas en estos ecosistemas tan heterogéneos espacialmente, es fundamental entender la respuesta relativa de cada componente del ecosistema (micrositio): "zonas de suelo desnudo" y "zonas vegetadas".

Los objetivos de este capítulo son: i) analizar la variabilidad temporal de la respiración del suelo en tres usos del suelo representativos de un ecosistema mediterráneo; ii) evaluar la importancia relativa de la temperatura y la disponibilidad de agua en el suelo como factores que controlan dicha variabilidad; y iii) evaluar la influencia de la

distribución y estructura de la vegetación en la respuesta de la respiración del suelo a la temperatura y disponibilidad de agua en cada uso del suelo.

La respiración del suelo se ha medido *in situ* con un sistema portátil de fotosíntesis acoplado a una cámara de suelo modelo LICOR-6400-09. Para capturar la variabilidad espacial de este parámetro se instalaron 30 collares de PVC (80 cm^2) distribuidos en función de los tipos de cobertura vegetal predominantes en cada uso de suelo, y localizados en los espacios entre individuos ("zonas de suelo desnudo") y próximos a los pies de los mismos ("zonas vegetadas"). Las medidas de R_s se llevaron a cabo mensualmente durante un periodo de dos años (enero 2006-diciembre 2007) y siempre en la misma franja horaria (9:00-12:00 am), acompañándose de medidas de temperatura y humedad del suelo. Además, se desarrolló un índice de biomasa aérea (ABI, *Aboveground Biomass Index*) para evaluar la influencia de la estructura de la vegetación y su distribución espacial en la variabilidad temporal de R_s, y un índice de "humedecimiento" del suelo (RWI, *Rewetting Index*) para evaluar la influencia del volumen y la distribución de las precipitaciones en las emisiones de CO_2 procedentes del suelo.

La tasa anual de R_s fue de 2.06 ± 0.07, 1.71 ± 0.09, y 1.12 ± 0.12 µmoles m^{-2} s^{-1} para el uso forestal, el campo agrícola abandonado y el olivar de secano, respectivamente. Los modelos de análisis de varianza (ANOVA) con medidas repetidas mostraron diferencias temporales significativas en la respiración, temperatura y disponibilidad de agua en el suelo en los tres usos del suelo. Para todos los usos del suelo, R_s presentó los valores mínimos en invierno como consecuencia de las bajas temperaturas características de esta época del año, y aumentó gradualmente conforme aumentó la temperatura del suelo durante la primavera, hasta que alcanzó su valor máximo en abril, coincidiendo con la época de productividad máxima propia de ecosistemas mediterráneos. Después de abril, los valores de R_s comenzaron a descender durante los meses de verano debido a la disminución del contenido de humedad del suelo, hasta que el efecto de la sequía sobre la respiración del suelo se puso de manifiesto cuando los valores de humedad del suelo se situaron por debajo del 10%. En general, el efecto limitante de la humedad del suelo sobre R_s fue evidente ya que ésta respondió rápida y abruptamente tras cada evento de lluvia.

La relación entre la respiración y la temperatura del suelo estuvo modulada por la disponibilidad de agua en el suelo. La respiración del suelo se correlacionó positivamente con la temperatura del suelo a partir de un umbral de disponibilidad de agua en el suelo (10% de humedad en el suelo para el caso del uso forestal y el olivar y 15% para el caso del campo agrícola abandonado). Sin embargo, por debajo de dicho umbral de humedad en

el suelo, la relación positiva entre la R_s y la temperatura del suelo se convirtió en negativa en los tres usos de suelo. De hecho, los valores de Q_{10} fueron significativamente mayores (P <0.001) durante el periodo de crecimiento (octubre-abril) (2.08, 2.20 y 1.86 para el uso forestal, campo agrícola abandonado y olivar, respectivamente) que para el periodo seco (mayo-septiembre) (0.40, 0.63 y 0.44 para el uso forestal, campo agrícola abandonado y olivar, respectivamente). Por otro lado, la R_s se correlacionó positivamente con el índice de humedecimiento en todos los usos de suelo, especialmente durante el periodo seco. Por último, las tasas de R_s en las "zonas vegetadas" fueron significativamente mayores que en las "zonas de suelo desnudo" en el uso forestal y el olivar. Sin embargo, en el campo agrícola abandonado no se encontraron diferencias significativas entre las manchas de vegetación y las zonas de suelo desnudo (Figura 3.1.).

Los modelos de regresión lineal y exponencial utilizados describieron de manera satisfactoria la respuesta de R_s frente a las variables ambientales durante los periodos húmedo y seco (Tabla 3.1). La combinación de factores abióticos (la temperatura y el índice de humedecimiento del suelo, RWI) y factores bióticos (la distancia al pie del individuo más próximo o el índice de biomasa aérea, ABI) explicaron una proporción considerable (entre un 39 y un 73%) de la variabilidad temporal de R_s en el uso forestal y el olivar. Sin embargo, en el campo agrícola abandonado la R_s no estuvo influenciada por el patrón de la vegetación, y bien la temperatura (durante el periodo húmedo) o el índice de humedecimiento (durante el periodo seco) resultaron suficientes para explicar entre un 51 y un 63% la variabilidad temporal de R_s.

En general, mientras que la temperatura del suelo resultó ser un buen indicador de la variabilidad temporal de R_s durante el periodo de crecimiento (octubre-abril), el índice de humedecimiento presentó un mejor ajuste que la humedad del suelo durante el periodo seco (mayo-septiembre) en este ecosistema mediterráneo (Tabla 3.1). Por otro lado, se observó que las variables ambientales explicaron una menor proporción de la varianza de R_s en las zonas vegetadas en comparación con las zonas de suelo desnudo, sugiriendo que la vegetación puede amortiguar la respuesta de R_s frente a las fluctuaciones de temperatura y humedad del suelo a través del sombreado, la interceptación de la precipitación y la actividad radicular (absorción y redistribución radicular del agua). Por el contrario, las zonas de suelo desnudo están directamente más expuestas y por lo tanto son más sensibles a las fluctuaciones ambientales. Por otro lado, el hecho de que el índice de humedecimiento haya resultado ser el mejor indicador de la variabilidad de R_s durante el periodo seco pone de relieve la importancia de considerar el efecto de los pulsos de

precipitación en las estimaciones anuales de las emisiones de CO_2 procedentes del suelo en estos ecosistemas mediterráneos.

Figura 3.1. Variabilidad temporal de R_s en los diferentes micrositios (zonas "vegetadas" y "de suelo desnudo" en el uso forestal (a), campo agrícola abandonado (b) y olivar (c).
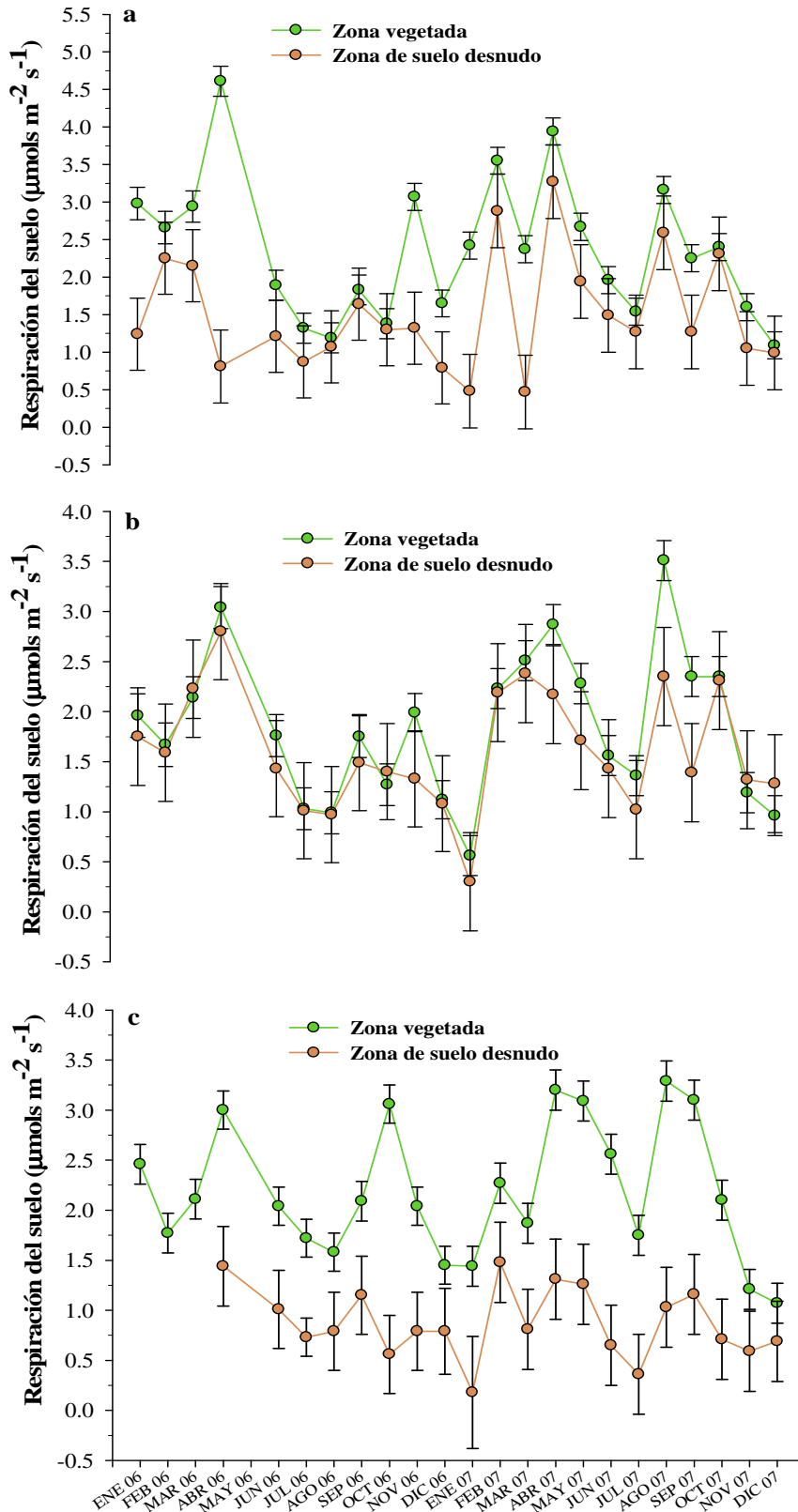
Tabla 3.1. Relaciones exponenciales y lineales entre Rs y factores abióticos y bióticos para los diferentes periodos y micro-sitios dentro de cada uso del suelo.

Periodo	Uso del suelo	Micrositio	Modelo	β_0	β_1	β_2	β_3	R^2	*P* valor	RMSE	n	AIC
Crecimiento (octubre-abril)	Forestal	Zona vegetada	$R_s=\beta_0\,e^{\beta_1 T}\,e^{(\beta_2 ABI)}$	-0.426 ± 0.12	0.109 ± 0.01	0.06 ± 0.01		0.39	<0.0001	3.84	216	12.05
		Zona desnuda	$R_s=\beta_0 e^{\beta_1 T}e^{(\beta_2 + RWI)\,+\,(\beta_3 + RWI2)}$	0.3 ± 0.13	0.194 ± 0.02	-0.366 ± 0.42	0.03 ± 0.05	0.76	<0.0001	4.66	40	8.29
	Campo abandonado		$R_s=\beta_0 e^{\beta_1 T}$	-1.21 ± 0.11	0.144 ± 0.01			0.51	<0.0001	8.03	224	8.65
		Zona vegetada	$R_s=\beta_0 e^{\beta_1 T}e^{(\beta_2 D)}$	1.266 ± 0.14	0.084 ± 0.00	-0.501 ± 0.05		0.55	<0.0001	18.32	192	8.69
	Olivar	Zona desnuda	$R_s=\beta_0 e^{\beta_1 T}$	-1.64 ± 0.27	0.121 ± 0.02			0.48	<0.0001	2.39	48	7.99
Seco (mayo-septiembre)	Forestal	Zona vegetada	$R_s = \beta_0 + \beta_1 RWI$	1.163 ± 0.01	0.77 ± 0.07			0.48	<0.0001	7.83	162	8.05
		Zona desnuda	$R_s = \beta_0 + \beta_1 RWI$	0.859 ± 0.13	0.64 ± 0.10			0.64	<0.0001	2.48	30	6.97
	Campo abandonado		$R_s = \beta_0 + \beta_1 RWI$	0.707 ± 0.11	0.952 ± 0.07			0.63	<0.0001	9.83	168	7.67
		Zona vegetada	$R_s = \beta_0\, e^{\beta_1 RWI}e^{(\beta_2 D)}$	0.672 ± 0.08	0.376 ± 0.05	-0.403 ± 0.06		0.45	<0.0001	2.99	144	11.74
	Olivar	Zona desnuda	$R_s = \beta_0 + \beta_1 RWI$	0.35 ± 0.08	0.307 ± 0.05			0.73	<0.0001	1.16	36	8.86

T: temperatura del suelo; ABI: índice de biomasa aérea; SWC: humedad volumétrica del suelo; RWI: índice de humedecimiento; D: distancia al pie del individuo más próximo. Se muestran los parámetros de los modelos que presentaron un mejor ajuste (β_0, β_1, β_2, y β_3), junto con los coeficientes de determinación ajustados (R^2), los errores cuadráticos medios (RSME), el número de observaciones (n), y el criterio de información de Akaike (AIC). Los parámetros de los modelos se estimaron utilizando el método de Levenberg-Marquardt.

Capítulo 4: Relación entre el patrón espacial de la vegetación, las propiedades del suelo y la respiración del suelo.

Resumen

En una escala anual, la variabilidad temporal de las tasas de respiración del suelo (R_s) es sensible a las fluctuaciones de temperatura y humedad del suelo. Sin embargo, la variabilidad espacial de la R_s a escala de sitio no suele explicarse únicamente a partir de variables microclimáticas, si no a partir de los atributos propios de cada ecosistema, que comprenden desde el tipo de vegetación, su estructura y distribución, hasta el contenido y calidad de la materia orgánica y las comunidades de micro- y macro-organismos presentes en el suelo.

Los objetivos del presente capítulo son: (i) explorar las relaciones entre la estructura de la vegetación y su distribución espacial, las propiedades del suelo y la R_s a escala de sitio; (ii) comprobar si los patrones de correlación difieren con el cambio de uso del suelo; e (iii) identificar los factores de control de la variabilidad espacial de R_s en cada uno de los usos del suelo.

Las medidas de R_s se llevaron a cabo en diciembre de 2006 y abril de 2007, coincidiendo con los valores mínimos (1.30 ± 0.1 μmol m^{-2} s^{-1}) y máximos (3.07 ± 0.1 μmol m^{-2} s^{-1}) de respiración del suelo observados durante un periodo de dos años para este ecosistema mediterráneo (Capítulo 3). Para ello, se instalaron 24 collares de PVC (80 cm^2) distribuidos en función de los tipos de cobertura vegetal predominantes en cada uso de suelo, y localizados en los espacios entre individuos ("claros" o "zonas desnudas") y próximos a los pies de los mismos ("zonas vegetadas" o manchas de vegetación"). Una vez realizadas las medidas de R_s, así como de temperatura y humedad del suelo, se llevó a cabo un muestreo destructivo (en los mismos puntos) mediante la extracción de 12 *cores* (10 cm de diámetro y 15 cm de longitud) con el fin de analizar las siguientes propiedades del suelo: contenido de carbono y nitrógeno de las fracciones ligera (lábil) y pesada (recalcitrante), C soluble en sulfato potásico, C orgánico de la biomasa microbiana y biomasa de raíces finas.

Para explorar las relaciones entre la distribución espacial y estructura de la vegetación, las propiedades del suelo consideradas y las tasas de respiración del suelo se utilizaron análisis de correlación de Pearson dado que las relaciones entre dichas variables fueron principalmente lineales (la covariación entre variables se exploró previamente mediante diagramas de dispersión). Para evaluar la influencia de la vegetación en las propiedades del suelo se utilizaron modelos de

regresión lineal, en los cuales las diferentes fracciones de C y N del suelo fueron consideradas como variables dependientes y los atributos de la vegetación (índice de biomasa aérea y biomasa radicular) como variables independientes. Por último y con el objetivo de identificar los factores de control de la variación espacial de R_s en cada uso del suelo se utilizaron modelos de regresión linear múltiple para cada uno de los usos del suelo.

Los Análisis de la Varianza (ANOVA) realizados mostraron diferencias entre los dos periodos de estudio para los contenidos en C y N de la fracción ligera pero no para los contenidos en C y N de la fracción pesada. Un patrón consistente en los tres usos del suelo fue que los contenidos en C y N de la fracción ligera de la materia orgánica del suelo estuvieron altamente correlacionados entre sí, y en una menor medida con el contenido en C y N de la fracción pesada en ambos periodos de muestreo.

Los coeficientes de determinación observados para ambos periodos mostraron evidencias de la relación existente entre la estructura y distribución espacial de la vegetación, las propiedades del suelo y las tasas de R_s en el uso forestal y el olivar. Sin embargo, en el campo agrícola abandonado no hubo relación entre los atributos de la vegetación (índice de biomasa aérea y biomasa radicular) y las propiedades del suelo o las tasas de R_s (Tabla 4.1).

Los modelos de regresión lineal utilizados explicaron una proporción considerable (entre un 41 y un 91%) de la variabilidad espacial de R_s observada en el área de estudio (Tabla 4.2). En el uso forestal el índice de biomasa aérea (84%) y la biomasa radicular (7%) explicaron un 91% de la variabilidad espacial de R_s en diciembre, mientras que el contenido en C de la fracción pesada explicó un 42% de la variabilidad espacial de R_s en abril. En el campo agrícola abandonado el contenido en C de la fracción pesada explicó un 70% de la variabilidad espacial de R_s en diciembre, mientras que la combinación de la biomasa microbiana (55%) y la humedad del suelo (15%) explicaron un 70% de la variabilidad espacial de R_s en abril. En el olivar de secano el contenido en C de la fracción ligera explicó entre un 67% (en diciembre) y un 41% (en abril) de la variabilidad espacial de R_s.

Los patrones de correlación observados han puesto de manifiesto la extrema importancia de la distribución espacial y estructura de la vegetación en la distribución de las diferentes fracciones de C y N del suelo así como en la respiración del suelo en el uso forestal y el olivar. Sin embargo, la falta de correlación entre el patrón espacial de la vegetación, la distribución de las diferentes fracciones de C y N del suelo y la respiración del suelo observada en el campo agrícola abandonado (a pesar de que han pasado 30 años desde que se produjo su abandono) sugiere la existencia de un umbral mínimo de densidad de vegetación necesario para que ésta ejerza una influencia en los patrones de distribución de las propiedades del suelo. Estos resultados ponen así mismo de

manifiesto el papel tan relevante que juega la "historia del sitio" en la dinámica de carbono en el suelo y la dificultad que presentan estos ecosistemas mediterráneos para recuperar el reservorio original de carbono en el suelo después de haber sido alterados.

Tabla 4.1. Coeficientes de regresión lineal y nivel de significancia (- no significativa; *P<0.05; **P< 0.001) de las relaciones existentes entre los atributos de la vegetación (biomasa aérea y radicular) y las fracciones de carbono (C) y nitrógeno (N) del suelo en cada uso del suelo y para cada periodo de muestreo.

	Uso forestal		**Campo abandonado**		**Olivar de secano**	
	Diciembre	Abril	Diciembre	Abril	Diciembre	Abril
MBC (mg kg^{-1} soil)	0.71*	0.51*	-	-	0.87**	0.89**
EDOC (mg kg^{-1} soil)	0.91**	0.46*	-	-	0.87**	0.73*
LFC (g kg^{-1} soil)	0.68*	-	-	-	0.61*	0.87**
LFN (g kg^{-1} soil)	0.74*	-	-	-	0.68*	0.92**
HFC (g kg^{-1} soil)	-	-	-	-	-	-
HFN (g kg^{-1} soil)	-	-	-	-	0.67*	0.67*
SOC (g kg^{-1} soil)	0.83**	-	-	-	0.81*	0.89**
TN (g kg^{-1} soil)	0.76*	-	-	-	0.74*	0.48*

MBC, C de la biomasa microbiana del suelo; EDOC, C orgánico disuelto-extraíble; LFC, contenido en carbono de la fracción ligera; LFN, contenido en nitrógeno de la fracción ligera; HFC, contenido en carbono de la fracción pesada; HFN, contenido en nitrógeno de la fracción pesada; SOC, carbono orgánico del suelo; TN, nitrógeno total del suelo.

Tabla 4.2. Relación lineal entre la respiración del suelo (R_s) y los factores abióticos y bióticos estudiados en cada uso del suelo y periodo de muestreo.

Sitio	Periodo	Variables independientes	Coeficientes de regresión parcial no estandarizados	Coeficientes de regresión parcial estandarizados	Adj. R^2	*F*	*P* valor
Uso forestal	Diciembre	Intercepto	1.006 ± 0.060				
		Ln(ABI) (g cm^{-1})	0.088 ± 0.012	0.775			
		Biomasa radicular (<2 mm) (g kg^{-1} suelo)	0.015 ± 0.005	0.304	0.908	55.04	<0.0001
	Abril	Intercepto	0.642 ± 0.899				
		C- Fracción pesada (g kg^{-1} suelo)	0.086 ± 0.029	0.689	0.422	9.022	0.013
Campo abandonado	Diciembre	Intercepto	$- 0.656 \pm 0.412$				
		C- Fracción pesada (g kg^{-1} suelo)	0.088 ± 0.018	0.856	0.703	24.69	0.001
	Abril	Intercepto	$- 0.842 \pm 0.931$				
		C- Biomasa microbiana (mg kg^{-1} suelo)	0.003 ± 0.001	0.792			
		Humedad del suelo (%)	0.106 ± 0.044	0.410	0.706	13.00	0.003
Olivar	Diciembre	Intercepto	0.122 ± 0.131				
		C- Fracción ligera (g kg^{-1} suelo)	0.098 ± 0.021	0.840	0.672	21.48	0.001
	Abril	Intercepto	1.557 ± 0.418				
		C- Fracción ligera (g kg^{-1} suelo)	0.272 ± 0.101	0.690	0.410	7.26	0.027

ABI: índice de biomasa aérea

Capítulo 5: Factores de control en la dinámica de descomposición de la hojarasca de dos especies predominantes de ecosistemas mediterráneos: dependencia del sitio y del tipo de hojarasca.

Resumen

La descomposición de la hojarasca es un proceso clave en el ciclo de carbono de los ecosistemas terrestres que determina la disponibilidad de nutrientes y el almacenamiento de carbono en el suelo (Schlesinger y Lichter, 2001). Entender qué factores y/o procesos controlan la dinámica de descomposición de la hojarasca y el consiguiente almacenamiento de carbono en el suelo es particularmente importante en estos ecosistemas limitados por el agua, caracterizados por unos contenidos bajos de materia orgánica en el suelo y una escasa disponibilidad de nutrientes, así como por unas condiciones climáticas (altas temperaturas, distribución irregular de las precipitaciones) que limitan la capacidad de secuestro de carbono de estas zonas (UNEP-UNDP-UNCCD, 2008).

A escala global, los modelos de descomposición de hojarasca han utilizado la temperatura, la humedad del suelo y la composición química del material vegetal como variables predictoras (Aerts, 1997; Coûteaux et al., 1995), ya que ejercen una fuerte influencia sobre la actividad de los microorganismos descomponedores. Sin embargo, estos modelos subestiman las tasas de descomposición observadas en ecosistemas áridos y semiáridos (Parton et al., 2007), sugiriendo que además de la descomposición biológica por parte de los microorganismos, otros factores abióticos contribuyen de manera significativa en los patrones de la descomposición de la hojarasca en estos ecosistemas. Procesos tales como la fotodegradación y la fragmentación física de la hojarasca causada por los procesos erosivos han sido identificados recientemente como principales factores de control de la de la descomposición de la hojarasca en otros ecosistemas limitados por el agua (Austin y Vivanco, 2006; Throop y Archer, 2007).

Los objetivos de este capítulo son: (i) determinar las tasas de descomposición de dos tipos de hojarasca que difieren en su composición química (*Pinus halepensis* Miller y *Rosmarinus officinalis* L.) y que son predominantes de ecosistemas mediterráneos; y (ii) evaluar si los factores de control de la dinámica de descomposición de la hojarasca difieren con el tipo de hojarasca. Dadas las diferencias que los usos del suelo considerados presentan en cuanto a cobertura y densidad de vegetación así como en determinadas propiedades del suelo (biomasa microbiana, densidad de C y N en el suelo), esperamos que el factor "sitio" influya en las tasas y en los patrones de descomposición de la hojarasca de las distintas especies consideradas.

Para cuantificar las tasas de descomposición de la hojarasca se ha utilizado el método de la bolsa de mantillo. Éste consiste en confinar hojarasca fresca en unas bolsas de malla (10 x 10 cm; 1,4 mm de haz de luz) que se colocan sobre el suelo y se recogen cada tres meses para estimar la pérdida de peso durante dicho periodo. Para estudiar la dinámica de la descomposición se ha asumido el patrón de pérdida exponencial propuesto por Olson (1963). En cada uso del suelo se delimitaron cuatro parcelas, dos próximas a individuos de pino carrasco y dos próximas a individuos de romero, y se depositaron en el suelo un total de 144 bolsas de hojarasca (2 especies x 2 individuos x 2 usos del suelo x 6 periodos de muestreo x 3 réplicas) durante un periodo de 20 meses. En cada periodo de muestreo se determinó la pérdida de peso, el contenido en C, N, y ceniza para cada una de las muestras recogidas. El contenido en ceniza se utilizó como indicador de la deposición del suelo sobre la hojarasca debida a los procesos de erosión. Además, se llevaron a cabo medidas de temperatura (0-2 cm) y humedad (0-15 cm) del suelo con una periodicidad horaria y quincenal respectivamente, y el volumen, duración e intensidad de cada evento de precipitación se registró mediante un pluviógrafo conectado a un *data-logger*.

Las tasas de descomposición (*k*) variaron en función de la especie y del sitio. En general, la hojarasca de *Pinus halepensis* se descompuso más lentamente ($k = 0.17 \pm 0.03$) que la hojarasca de *Rosmarinus officinalis* (k= 0.51 ± 0.02) ($R^2 = 0.742$; F= 132.18; P<0.0001). Después de 20 meses, la fracción de hojarasca restante constituyó aproximadamente un 70% y un 45% de su peso original para el pino carrasco y el romero, respectivamente. Por otro lado, se observaron diferencias en la dinámica del nitrógeno (N) durante las primeras fases de la descomposición: mineralización del N en el caso de *Pinus halepensis* e inmovilización del N en el caso de *Rosmarinus officinalis.* Así mismo, el patrón de la razón C:N mostrado en ambas especies durante el proceso de descomposición fue muy diferente.

A pesar de que se observó un efecto significativo del factor "sitio" en la dinámica de descomposición de las dos especies consideradas, el patrón no fue similar para ambos tipos de hojarasca. A lo largo del periodo de incubación, las tasas de descomposición correspondientes a la hojarasca de romero (más lábil) fueron más altas en el uso forestal que en el campo agrícola abandonado ($R^2 = 0.64$; F= 41.51; P <0.0001). Sin embargo, las pérdidas de peso correspondientes a la hojarasca del pino (más recalcitrante) no variaron entre sitios durante las primeras fases del periodo de incubación, aunque sí resultaron ser superiores en el campo agrícola abandonado que en el uso forestal durante las últimas fases del mismo ($R^2 = 0.68$; F= 45.93; P <0.0001).

A lo largo del periodo de incubación, las variaciones observadas en cuanto a la pérdida de peso y el contenido en carbono o nitrógeno de la hojarasca (independientemente de la especie y del uso del suelo) no estuvieron relacionadas con variables ambientales tales como la temperatura y

humedad del suelo, la intensidad, la duración o el volumen acumulado de las precipitaciones correspondiente a cada periodo de incubación. Por otro lado, los modelos de regresión linear múltiple empleados para relacionar la variación en el patrón (espacial) de la descomposición de la hojarasca de cada especie con parámetros de composición química de la hojarasca (contenido en carbono, nitrógeno o razón C:N) o con características inherentes al sitio (condiciones de temperatura y humedad del suelo, y contenido en ceniza) indicaron que los factores de control varían en función de la especie. Así, mientras que la variación de los patrones de descomposición de la hojarasca de *Rosmarinus officinalis* estuvo relacionada con su contenido en nitrógeno o su razón C:N (explicando entre un 33 y un 37% de la varianza), en el caso de *Pinus halepensis* ésta estuvo relacionada con el contenido en ceniza, que explicó un 44% de la varianza durante las últimas fases del periodo de incubación (Tabla 5.1).

Estos resultados, junto a los patrones observados en la dinámica del nitrógeno de cada especie (mineralización vs. inmovilización), sugieren que mientras que la descomposición de hojarascas más lábiles (romero) podría estar modulada principalmente por factores bióticos (actividad de los microorganismos del suelo), en la descomposición de hojarascas más recalcitrantes (pino) intervienen además otros factores abióticos como la erosión del suelo y la fotodegradación.

Tabla 5.1. Factores de control de los patrones de descomposición de cada especie en cada periodo de muestreo.

Periodo (días acumulados)	*Pinus halepensis*					*Rosmarinus officinalis*				
	variable	R^2	β_0	β_1	*F*	variable	R^2	β_0	β_1	*F*
120	n.s.					n.s.				
240	Nitrógeno (%)	0.34	-0.252	-0.211[*]	5.69	n.s.				
330	n.s.					n.s.				
420	n.s.					Nitrógeno (%)	0.33	-0.43	-0.81[*]	6.46
490	Ceniza (%)	0.44	0.067	-0.138[**]	9.65	Razón C:N	0.37	-3.77	0.97[*]	6.92
580	Ceniza (%)	0.44	0.283	-0.251[**]	9.78	n.s.				

Nota: n.s., regresión no significativa; * $P < 0.05$; ** $P < 0.01$.

Referencias

Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79, 439- 449.

Allard, V., Ourcival, J.M., Rambal, S., Joffre, R., Rocheteau, A., 2008. Seasonal and annual variation of carbon exchange in an evergreen Mediterranean forest in southern France. Global Change Biology 14, 714-725.

Austin, A.T., Vivanco, L., 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nature 442, 555-558.

Coûteaux, M.M., Bottner, P., Berg, B., 1995. Litter decomposition, climate and litter quality. Tree 10 (2), 63-66.

Giardina, C.P., Ryan, M.G., 2002. Total belowground carbon allocation in a fast-growing *Eucalyptus* plantation estimated using a carbon balance approach. Ecosystems 5, 487-499.

Giorgi, F., Lionello, P., 2008. Climate change projections for the Mediterranean region Global and Planetary Change 63, 90-104.

Grünzweig, J.M., Gelfand, I., Fried, Y., Yakir, D., 2007. Biogeochemical factors contributing to enhanced carbon storage following afforestation of semi-arid shrubland. Biogeosciences 4, 891-904.

IPPC, 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M and Miller HL, eds. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press, 1-996.

Jackson, R.B., Banner, J.L., Jobbágy, E.G., Pockman, W.T., Wall, D.H., 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418, 623-626.

Lal, R., 2003. Soil erosion and the global carbon budget. Environment International 29 (4), pp. 437-450.

Lal, R., 2004b. Carbon sequestration in dryland ecosystems. Environmental Management 33, 528-544.

Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44, 322-331.

Parton, W., Silver, W.L., Burke, I.C., Grassens, L., *et al*., 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. Science 315, 361-364.

Raich, J.W., Nadelhoffer, K.J., 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology 70 (5), 1346-1354.

Sabaté, S., Gracia, C., Sánchez, A., 2002. Likely effects of climate change on growth of *Quercus ilex*, *Pinus halepensis*, and *Fagus sylvatica* forest in the Mediterranean region. Forest Ecology and Management 162, 23-37.

Schlesinger W.,H., Litchter, J., 2001. Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO_2. Nature 411, 466-469.

Throop, H.L., Archer, S.R., 2007. Interrelationships among shrub encroachment, land management, and litter decomposition in a semidesert grassland. Ecol. Appl. 17 (6), 1809-1823.

UNEP-UNDP-UNCCD, 2008. Carbon in Drylands: Desertification, Climate Change and Carbon Finance. Technical Note for Discussions at CIC 7, Istanbul, Turkey -03-14.

Valentini, R., Matteucci, G.R., Dolman, A.J., Schulze, E.D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404, 861-863.

Conclusiones generales

1. Los patrones de distribución de los reservorios de carbono a nivel de ecosistema (biomasa aérea y subterránea, y carbono orgánico en el suelo) han sido consistentes con los patrones de productividad primaria neta observados en los tres usos del suelo estudiados. En general, más del 60% del carbono absorbido por estos ecosistemas se asigna a la parte subterránea (suelo y biomasa radicular), señalando la importancia de incluir el carbono total acumulado en la parte subterránea para estimar la productividad primaria neta de estos ecosistemas mediterráneos.

2. Los valores de productividad primaria neta obtenidos en este estudio a partir de la combinación de metodologías tales como la aplicación de ecuaciones alométricas (para estimar la cantidad de C almacenado en la biomasa aérea) y la aproximación basada en la ley de conservación de la masa TBCA (para estimar la cantidad de C almacenado en la parte subterránea del ecosistema) fueron similares a los valores de productividad primaria neta observados en otros ecosistemas mediterráneos mediante otras técnicas tales como las torres de *Eddy Covariance.*

3. En estos ecosistemas mediterráneos se debe considerar el modelo no estacionario para una estimación adecuada de la capacidad de secuestro de carbono en el suelo puesto que se ha comprobado que la asunción de equilibrio subestima la capacidad de secuestro de C en estos ecosistemas, especialmente en el campo agrícola abandonado.

4. Se ha puesto de manifiesto la gran importancia de la respiración del suelo en el balance de carbono en suelos mediterráneos con independencia del nivel de intensificación, así como la necesidad de considerar su respuesta frente a los pulsos de precipitación (volumen y distribución) en las estimaciones anuales de las emisiones de CO_2 procedentes del suelo.

5. Se ha demostrado que los valores anuales medios de Q_{10} por sí solos no son un buen indicador de la respuesta de la respiración del suelo frente a la temperatura en estos ecosistemas mediterráneos secos, en los que la baja disponibilidad de agua en el suelo limita la respuesta de la actividad microbiana y radicular frente a la temperatura.

6. Se ha demostrado la efectividad de los índices propuestos en esta memoria para explicar la variabilidad de la respiración en el suelo debida a los patrones de precipitación (índice de humedecimiento, *RWI*) y a la estructura de la vegetación (índice de biomasa aérea, *ABI*). El índice de humedecimiento ha sido un buen predictor, especialmente en el periodo seco, explicando entre un 45 y un 73% de la varianza en la respiración del suelo en los tres usos considerados.

7. Se ha puesto de relieve la extrema importancia del patrón espacial de la vegetación en la distribución de las diferentes fracciones de carbono y nitrógeno del suelo, así como en modular la respuesta de la respiración del suelo frente a las fluctuaciones microclimáticas en el uso forestal y el olivar. La ausencia de estas relaciones observada en el campo agrícola abandonado pone de manifiesto el papel potencial de la "historia del sitio" en el ciclo de C del suelo, así como la dificultad que presentan estos ecosistemas tan frágiles para recuperar el reservorio original de carbono en el suelo después de haber sido alterados.

8. Los resultados de este estudio sugieren que la reducción de la vegetación en estos ecosistemas puede incrementar la vulnerabilidad de los mismos al cambio climático dada la mayor sensibilidad a las fluctuaciones ambientales (temperatura y humedad del suelo) observada en las zonas de suelo desnudo en comparación con las zonas vegetadas.

9. En ausencia de eventos de lluvia de magnitud extrema, las pérdidas de C por erosión hídrica resultaron insignificantes en comparación con las pérdidas de C debidas a la respiración del suelo, y tuvieron poca influencia en el balance neto de C de estos ecosistemas. Sin embargo, la relevancia de la erosión en el balance (neto) de C no debe ser obviada debido a:

i) el efecto directo de la erosión en los patrones de productividad primaria neta (pérdidas de nutrientes asociadas a las zonas fuente y ganancias a las zonas sumidero), y

ii) la interacción de la erosión con los procesos de descomposición de la hojarasca y de la materia orgánica del suelo.

10. Para evaluar el efecto neto de la erosión en el balance de C a escala de "sitio" en estos ecosistemas es necesario aumentar la escala de estudio, tanto temporal (décadas) como espacialmente (escala de cuenca o subcuenca), así como considerar el papel que

desempeñan las diferentes fases de la erosión (arranque, transporte y deposición) en la descomposición de la hojarasca y la materia orgánica del suelo.

11. La contribución de este trabajo al conocimiento de los reservorios y flujos (entradas y salidas) de C en diferentes usos del suelo de un ecosistema mediterráneo, así como de los factores de control de la dinámica de los principales flujos de C, puede ayudar a comprender los procesos de pérdida y acumulación de carbono en el suelo, así como a predecir la respuesta de dichos flujos de carbono frente a las condiciones climáticas futuras previstas por los modelos de cambio climático y al impacto de los cambios de uso de suelo que alteren la estructura y la distribución de la vegetación.

Así mismo, este conocimiento puede ser de utilidad para adoptar políticas de gestión territorial adecuadas orientadas a las medidas compensatorias (conservación de los reservorios de carbono) y de mitigación (reducción de las emisiones de CO_2 optimizando la capacidad de secuestro de carbono) ante la perspectiva del cambio climático, prestando atención a los campos de cultivo abandonados.

General Introduction

Introduction

Terrestrial ecosystems play an important role in the global carbon (C) balance (Cox et al., 2000). Soils are the largest carbon reservoir of the terrestrial carbon budget, containing 2157- 2296 Pg to a depth of 1 m (1462-1548 Pg in organic forms and 695-748 Pg as carbonate). Organic carbon in the top 30 cm of soils, which is the most prone to change as a result of land use or climatic change, is estimated to range from 684 to 724 Pg, which is about the quantity of C in vegetation (610 Pg) and somewhat higher than that present in the atmosphere (590 Pg C) (Batjes and Sombroek, 1997).

Carbon storage in terrestrial ecosystems is governed by the difference that exists between inputs from aboveground and belowground net primary production and outputs through erosion and decomposition of plant material and soil organic matter on both short and long term scales. At site level, the major C influx occurs through the assimilation of atmospheric CO_2 by plant photosynthesis (also called gross primary productivity, GPP). A fraction of total photosynthesis or GPP is allocated and stored aboveground for the production of foliage, stems and branches, and reproductive organs (Figure 1). Another fraction of the C assimilated by photosynthesis is allocated belowground (TBCA, *Total Belowground Carbon Allocation*) to the production of coarse and fine roots, for root respiration and exudation, and to maintain mycorrhizal activity (Raich and Nadelhoffer, 1989). The remainder is respired back to the atmosphere through soil respiration, which includes root respiration, as a sub-product of photosynthesis, and litter and soil organic matter decomposition (Edwards et al., 1970; Schlesinger, 1997; Wiant, 1967). Losses of carbon through the leaching of dissolved organic or inorganic C, or by soil erosion, while generally very low compared to soil respiration (Edwards and Harris, 1977; Forrester et al., 2006; Giardina and Ryan, 2002; Raich, 1983; Schlesinger 1977; 1984), may have a significant influence on the total soil carbon budget in dry Mediterranean ecosystems (Lal 2003; Smith et al., 2007).

On a worldwide scale, terrestrial ecosystems are a major net sink for atmospheric CO_2 (about 1 Gt C yr^{-1}), because they assimilate and accumulate more atmospheric CO_2 than that is released back to the atmosphere (Schimel, 1995). Thus, forest biomes are an important component of the global C budget, because they: i) allocate and store large amounts of C in live biomass, detritus and soil organic matter; ii) can be either net C sources or sinks, depending on their management and dynamics; and iii) play an important role in regulating atmospheric CO_2 concentration and climate (Fahey et al., 2010).
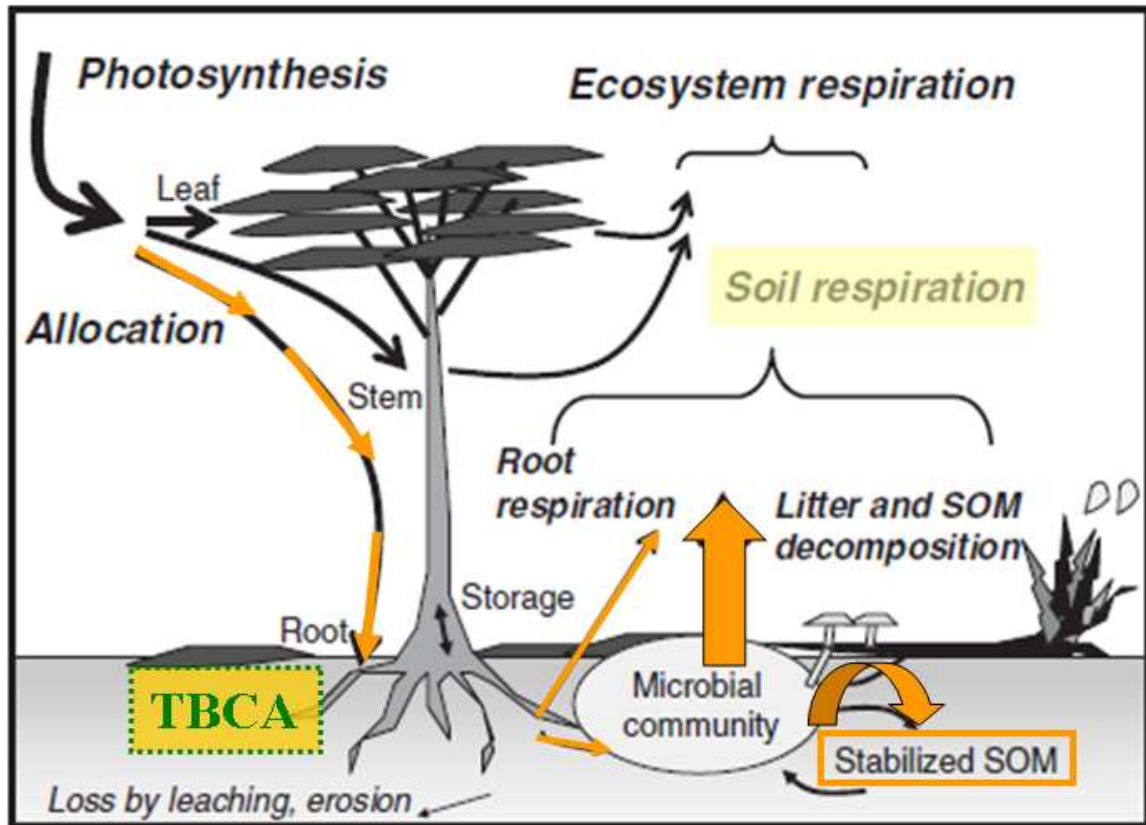
Fig.1. Pathways of carbon flow through ecosystems. Adapted from Trumbore (2006).

Among the most important global changes taking place are land use and climate change, increases in atmospheric CO_2 concentration and ultraviolet radiation (280-400 nm), land degradation and desertification, alterations in biogeochemical cycles of nitrogen and the introduction of exotic species (Millennium Ecosystem Assessment, 2005; Sala et al., 2000). Land use change is the main driver of soil organic carbon (SOC) losses and land degradation (Lal, 2004a; Post et al. 2000; Powlson et al., 2011), and is responsible for 20% of global anthropogenic CO_2 emissions to the atmosphere (Le Quéré et al., 2009; The Terrestrial Carbon Group, 2008). Thus, in addition to impacting local environmental conditions, land use changes have become a driving force behind the global carbon cycle and climate (Foley et al., 2005).

It is well known that either depletion of ecosystem carbon pools (that is, the sum of all organically derived C present in soils, roots and aboveground components) or increases in CO_2 atmospheric emissions caused by the conversion of native vegetation to agricultural lands may be partially offset by the recovery of woody vegetation in abandoned lands. However, uncertainties in the patterns of C loss following land use change and the rates of recolonization of old fields by native woody vegetation are critical data gaps that limit our understanding of the role of Mediterranean ecosystems as potential sinks of atmospheric C.

Thus, quantifying the size of C pools and the rates of C losses or accumulation caused by land use change is a first step towards an in depth understanding of the impacts of land management on C dynamics in the Mediterranean basin, and a key issue for successfully implementing strategies designed to offset C emissions through deforestation and forest degradation for this region under the Kyoto Protocol ("clean development mechanism"; UNFCCC, 2008) and from a climate change perspective (Millenium Ecosystem Assessment, 2005; UNEP-UNDP-UNCCD, 2008).

It has been suggested that the Mediterranean region is highly sensitive to global climate change (Sala et al., 2000; Schröter et al., 2005). Recent global and regional models predict a 4-5°C warming and 25-30% lower soil water availability over the next three decades in Mediterranean ecosystems as a result of lower rainfall and changes in rain distribution (Giorgi and Lionello, 2008; IPPC, 2007; Sabaté et al., 2002), which may alter soil C fluxes, and hence soil C storage. In particular, the southeast of the Iberian Peninsula, with its sub-humid and semi-dry Mediterranean climate, has been identified as an especially vulnerable area to global change, because of an increase in the frequency and duration of drought periods, and in the number of extreme-intensity rainfall events that occur during the summer period (Giorgi and Lionello, 2008). This scenario will inevitably affect the structure and dynamics of ecosystems and the services they provide, such as soil water retention or carbon sequestration (Foley et al., 2005; Millenium Ecosystem Assessment, 2005).

As a result of global climate change and alterations in land use, many ecosystems are currently experiencing changes in the primary abiotic and biotic factors that control soil C fluxes and storage (Álvaro-Fuentes and Paustian, 2011; Sala et al. 2000; Foley et al., 2005; Fahey et al., 2009; Quinton et al., 2010). After gross primary productivity, soil respiration is the second most important carbon flux in ecosystem-atmosphere interactions (Schimel, 1995), and plays a major role in determining the C sequestration potential in many ecosystems (Valentini et al., 2000). Given the large quantity of CO_2 that soils release annually, and the fact that soil respiration is very sensitive to changes in soil temperature and moisture (Davidson et al., 1998; Lloyd and Taylor, 1994), it is important to understand how alterations in vegetation and soil, resulting from land use intensification, may interact with predicted climate change to alter soil respiration and C storage. This is of interest for drought-affected regions, as drylands cover about 41-47% of the terrestrial surface, host more than 38% of the world's population, contain 27% of the global soil organic carbon (SOC) stock, and have a large potential for C sequestration (FAO, 2004; Grünzweig et al.,

2003, 2007; Lal, 2004b; Millenium Ecosystem Assessment, 2005; Reynolds et al., 2007; UNEP-UNDP-UNCCD, 2008; WRI, 2002). However, heterogeneous dry Mediterranean ecosystems are characterized by a set of features that constrain their resilience after the cessation of disturbance: i) low and episodic rainfall; ii) slow vegetation growth, iii) potentially high litter and soil organic matter mineralization rates; iv) slow recovery of soil C pools after degradation; and v) a long history of cultivation (Albaladejo et al., 1998; Asner et al., 2003; Austin and Vivanco, 2006; Martínez-Mena et al., 2002; Vallejo et al., 2006). These features, coupled with the intensity and duration of land use, will determine rates of soil C sequestration and the time periods required to attain maximum C-storage potential (Asner et al., 2003; Kauffman et al., 2009).

Therefore, understanding which environmental factors control soil C fluxes under different land uses is fundamental for our understanding of terrestrial ecosystem functioning in dry environments from a climate change perspective. Besides being controlled by soil temperature and water availability (Davidson et al., 1998; Lloyd and Taylor, 1994), soil C fluxes are modulated by biotic factors, such as vegetation (Ryan and Law, 2005; Vargas and Allen, 2008). Thus, in heterogeneous arid, semiarid and Mediterranean-type ecosystems the patchy distribution of vegetation is also an important factor to bear in mind, because shrub/tree canopies affect C inputs and outputs through multiple pathways: i) they provide the principal carbon source to decomposer microorganisms through dead plant material, thus determining both litter quantity and quality (Raich and Tufekcioglu, 2000; Swift et al., 1979); ii) they alter the soil moisture regime, through the interception of precipitation and the extraction of soil water through transpiration (McCulley et al., 2004; Rutter and Morton, 1977); iii) they influence soil structure, temperature and solar radiation conditions, and subsequent microbial activity (Austin and Vivanco 2006; Dirks et al. 2010; Gallo et al., 2006; McCulley et al. 2004; Raich and Tufekcioglu, 2000); iv) they lead to pronounced patterns of erosion and associated processes of soil transport and deposition (Bautista et al. 2007; Bochet et al. 2006; Martínez-Mena et al. 2001; Throop and Archer, 2007); and v) a considerable fraction of soil respiration stems directly from the vegetation via root or rhizosphere respiration (Högberg et al., 2001). Thus, to predict the responses of soil C fluxes to soil temperature and water availability fluctuations and ecosystem attributes under different land uses in such heterogeneous ecosystems, it is necessary to understand the relative responses of each ecosystem component (microsite): beneath-canopy and inter-canopy locations.

Therefore, identifying the factors controlling the main soil C fluxes within different land use types in a Mediterranean ecosystem is critical to better understand soil C cycling and storage capacity, and hence to improve their management for C emission offset schemes under the Kyoto Protocol. The relative importance of the different C components within the C balance of each land use type, the interactions between them, and their controlling factors, are the subject of ongoing debate (Grace and Rayment, 2000; Lal, 2003; Throop and Archer, 2007; Trumbore, 2006; Valentini et al., 2000; Van Oost et al., 2007).

General Hypothesis, objectives and structure of the thesis

The general hypothesis of the current study is that the conversion of native ecosystems to agricultural lands and subsequent land abandonment can lead to shifts in canopy structure and consequently influence soil C fluxes and storage through alterations in soil microclimatic (e.g., temperature, moisture and solar radiation exposure) and microsite conditions (e.g., soil resources and microbial communities, and runoff and soil erosion patterns).

According to this hypothesis, the general objectives of the present thesis are: i) to quantify C pools and fluxes (outputs and inputs) along a local land use intensification gradient (open forest, abandoned agricultural field, olive grove) in a dry Mediterranean ecosystem; ii) to assess the relative importance of the different C fluxes within the C balance of each land use type; and iii) to identify the factors controlling the main C fluxes within each land use/site. These land use types are representative of the land use changes that occurred throughout the 20th century in this and other Mediterranean landscapes as a result of agriculture intensification and subsequent land abandonment. We hope that the research we have carried out and which we describe here will help further understand the processes and factors that influence the capacity of different land uses to sequester and store carbon.

To achieve these general objectives, four specific objectives have been established:

- To describe C pools, fluxes, and allocation patterns along a land use intensification gradient in a dry Mediterranean ecosystem, and assess the

relative importance of the different C fluxes in the C balance of each land use type.

- To investigate temporal variability in soil respiration and identify the abiotic and biotic factors controlling it within each land use type.

- To explore the links between vegetation spatial patterns, soil carbon and nitrogen pools and respiration rates, and identify the abiotic and biotic factors controlling it within each land use type.

- To compare the mass loss rates and changes in nitrogen content of two predominant litter types (*Pinus halepensis* Miller and *Rosmarinus officinalis* L.), and to assess whether the factors controlling decomposition dynamics differ between litter types.

This thesis consists of an introduction, a chapter in which the study area is described (Chapter 1), four main chapters corresponding to each one of the above mentioned specific objectives (Chapters from 2 to 5), which are written as independent publications, general conclusions, references and appendixes.

Chapter 1. **Study site and experimental design**

This chapter focuses on describing the climate, geology, relief, soils and the most frequent vegetation types in the study area. The experimental set-up is also described.

Chapter 2. **Carbon pools, fluxes, and allocation patterns**

The main goal of this chapter is to describe C pools and allocation patterns along a local land use intensification gradient (open forest, abandoned agricultural field, rain-fed olive grove). In addition, soil C influxes (litterfall) and effluxes (soil respiration and erosion) are estimated, along with the annual changes in soil C, root biomass and litter-layer, within each land use type. The specific objective of this chapter is to compare two C balance approaches based on steady-state or non-steady-state conditions in order to assess how C fluxes (outputs and inputs) affect the estimates of total C allocated belowground.

This chapter corresponds to the published paper:

Almagro, M., López, J., Boix-Fayos, C., Albaladejo, J., Martínez-Mena, M. (2010). Belowground carbon allocation patterns in a dry Mediterranean ecosystem: A comparison of two models. *Soil Biology and Biochemistry* 42 (9), 1549-1557.

Chapter 3. **Factors controlling temporal variations of soil respiration**

This chapter focuses on investigating seasonal variations in soil respiration, soil temperature and soil water content under three representative land uses in a dry Mediterranean ecosystem. Likewise, the relative importance of temperature and soil moisture as predictors of soil respiration is evaluated. Finally, we assess whether the response of soil respiration to soil temperature and water content differs between different micro-sites (beneath- and inter-canopy locations) within each land use type.

This chapter corresponds to the published paper:

Almagro, M., López, J., Querejeta, J.I., Martínez-Mena, M. (2009). Temperature dependence of soil CO_2 efflux is strongly modulated by seasonal patterns of moisture availability in a Mediterranean ecosystem. *Soil Biology and Biochemistry* 41 (3), 594-605.

Chapter 4. **Links between vegetation patterns, soil carbon and nitrogen pools, and respiration rate**

This chapter focuses on exploring links between vegetation patterns, soil carbon and nitrogen pools and respiration rates within each land use type. Moreover, we aim at identifying the factors controlling spatial variability in soil respiration within each land use/site.

This chapter corresponds to the manuscript:

Almagro, M., Querejeta, J.I., Boix-Fayos, C., Martínez-Mena, M. Soil carbon pools and respiration rates are decoupled from current vegetation patterns in a 30 yr old abandoned agricultural field in a Mediterranean ecosystem. *Soil Biology and Biochemistry* (under review).

Chapter 5. **Factors controlling leaf-litter decomposition dynamics: dependence on litter type and site conditions**

The main goal of this chapter is to investigate the decomposition dynamics of two predominant leaf litter types (*Pinus halepensis* Miller and *Rosmarinus officinalis* L.) in Mediterranean ecosystems. More specifically, the objectives are: (1) to compare the mass loss rates and changes in nitrogen content of these two predominant litter types; and (2) to assess whether the factors controlling decomposition dynamics differ between litter types.

This chapter corresponds to the manuscript:

Almagro, M., Martínez-Mena, M. Exploring the factors controlling leaf-litter decomposition dynamics in a Mediterranean ecosystem: dependence on litter type and site conditions. *Plant and Soil* (under review).

References

Albaladejo, J., Martínez-Mena, M., Roldan, A., Castillo, V., 1998. Soil degradation and desertification induced by vegetation removal in a semiarid environment. Soil Use and Management 14, 1-5.

Álvaro-Fuentes, J., Paustian, K., 2011. Potential soil carbon sequestration in a semiarid Mediterranean agroecosystem under climate change: Quantifying management and climate effects. Plant and Soil 338, 261-272.

Asner, G.P., Archer, S., Hughes, R.F., Ansley, R.J., Wessman, C.A., 2003. Net changes in regional woody vegetation cover and carbon storage in Texas Dryland 1937-1999. Global Change Biology 9, 316-335.

Batjes, N.H., Sombroek, W.G., 1997. Possibilities for carbon sequestration in tropical and subtropical soils. Global Change Biology 3, 161–173.

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408, 184-187.

Edwards, C.A., Reichle, D.E., Crossley, D.A.Jr., 1970. The role of soil invertebrates in turnover of organic matter and nutrients. In: Reichle, D.E. (Eds) Analysis of temperate forest ecosystems, Springer-Verlag, New York, 12-172 pp.

Edwards, N.T., Harris, W.F., 1977. Carbon cycling in a mixed deciduous forest floor. Ecology 58, 431-437.

Fahey, T.J., Woodbury, P.B., Battles, J.J., Goodale, C.L., Hamburg, S., Ollinger, S., Woodall, C.W., 2010. Forest carbon storage: ecology, management, and policy. Frontiers in Ecology and the Environment 8 (5), pp. 245-25.

Foley, J.A., De Fries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Zinder, P.K., 2005. Global consequences of land use. Science 309 (5734), pp. 570-574.

Forrester, D.I., Bauhus, J., Cowie, A.L., 2006. Carbon allocation in mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. Forest Ecology and Management 233, 275-284.

Giardina, C.P., Ryan, M.G., 2002. Total belowground carbon allocation in a fast-growing *Eucalyptus* plantation estimated using a carbon balance approach. Ecosystems 5, 487-499.

Giorgi, F., Lionello, P., 2008. Climate change projections for the Mediterranean region Global and Planetary Change 63, 90-104.

Grace, J., Rayment, M., 2000. Respiration in the balance. Nature 404 (6780), pp. 819-820.

Grünzweig, J.M., Lin, T., Rotenberg, E., Schwartz, A., Yakir, D., 2003. Carbon sequestration in arid-land forest. Global Change Biology 9, 791-799.

Grünzweig, J.M., Gelfand, I., Fried, Y., Yakir, D., 2007. Biogeochemical factors contributing to enhanced carbon storage following afforestation of semi-arid shrubland. Biogeosciences 4, 891-904.

IPPC, 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M and Miller HL, eds. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press, 1-996.

Kauffman, J.B., Hughes, R.F., Heider, C., 2009. Carbon pool and biomass dynamics associated with deforestation, land use, and agricultural abandonment in the neotropics. Ecological Applications 19 (5), 1211-1222.

Lal, R., 2003. Soil erosion and the global carbon budget. Environment International 29 (4), pp. 437-450

Lal, R., 2004a. Soil carbon sequestration impacts on global climate change and food security. Science 304 (5677), 1623-1627.

Lal, R., 2004b. Carbon sequestration in dryland ecosystems. Environmental Management 33, 528-544.

Le Quéré, C., Raupach, M.R., Canadell, J.G., Marland, G., *et al.*, 2009. Trends in the sources and sinks of carbon dioxide. Nature Geosciences 2 (12), pp. 831-836.

Martínez-Mena, M., Álvarez Rogel, J., Castillo, V., Albaladejo, J., 2002. Organic carbon and nitrogen losses influenced by vegetation removal in a semi-arid soil. Biogeochemistry 61 (3), 309-321.

Middleton, N.J., Thomas, D.S.G., eds., 1997. World Atlas of Desertification. U.N. Environment Programme, Edward Arnold, New York.

Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Desertification Synthesis. World Resources Institute, Washington, DC.

Noy-Meir, I, 1973. Desert ecosystems: environment and producers. Annual Review of Ecoloy and Systematics 4, 25-51.

Post, W.M., Kwon, K.C., 2000. Soil carbon sequestration and land use change: processes and potential. Global Change Biology 6: 317-327.

Powlson, D.S., Gregory, P.J., Whalley, W.R., Quinton, J.N., Hopkins, D.W., Whitmore, A.P., Hirsch, P.R., Goulding, K.W.T., 2011. Soil management in relation to sustainable agriculture and ecosystem services. Food Policy 36, 572-587.

Quinton, J.N., Govers, G., Van Oost, K., Bardgett, R.D., 2010. The impact of agricultural soil erosion on biogeochemical cycling. Nature Geoscience 3, pp. 311-313.

Raich, J.W., 1983. Effects of forest conversion on the carbon budget of a tropical soil. Biotropica 15, 177-184.

Raich, J.W., Nadelhoffer, K.J., 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology 70 (5), 1346-1354.

Sabaté, S., Gracia, C., Sánchez, A., 2002. Likely effects of climate change on growth of *Quercus ilex*, *Pinus halepensis*, and *Fagus sylvatica* forest in the Mediterranean region. Forest Ecology and Management 162, 23-37.

Sala, O.E., Chapin, F.S., Arnesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., *et al.*, 2000. Biodiversity: Global biodiversity scenarios for the year 2100. Science 287, pp. 1770-1774.

Schimel, D.S., 1995. Terrestrial ecosystems and the carbon cycle. Global Change Biology 1 (1), 77-91.

Schlesinger, 1997. An analysis of global change, 2nd edition, Academic Press, San Diego, U.S.A., pp.150.

Schlesinger, W.H., 1984. Soil organic matter: a source of atmospheric CO_2, in: Woodwell, G.M. (Ed.), The role of terrestrial vegetation in the global carbon cycle: measurement by remote sensing. John Wiley & Sons, Chichester, England, 111-127 pp.

Schlesinger, W.H., Litchter, J., 2001. Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO_2. Nature 411, pp. 466-469.

Schröter, D., Cramer, W., Leemans, R., Prentice, I.C., Araújo, M.B., Arnell, N.W., Bondeau, A., et al., 2005. Ecosystem service suplí and vulnerability to global change in Europe. Science 310 (25): 1333-1337.

Smith, S.V., Bullock, S.H., Hinojosa-Corona, A., Franco-Vizcaíno, E., Escoto-Rodriguez, M., Kretzschmar, T.G., Farfán, L.M., Salazar-Ceseña, J.M., 2007. Soil erosion and significance for carbon fluxes in a mountainous mediterranean-climate watershed. Ecological Applications 17 (5), 1379-1387.

The Terrestrial Carbon Group, 2008. How to include terrestrial carbon in developing nations in the overall climate change solution, http://www.terrestrialcarbon.org

Throop, H.L., Archer, S.R., 2007. Interrelationships among shrub encroachment, land management, and litter decomposition in a semidesert grassland. Ecological Applications 17 (6), pp. 1809-1823.

Trumbore, S., 2006. Carbon respired by terrestrial ecosystems – recent progress and challenges. Global Change Biology 12, 141-153.

UNEP-UNDP-UNCCD, 2008. Carbon in Drylands: Desertification, Climate Change and Carbon Finance. Technical Note for Discussions at CIC 7, Istanbul, Turkey -03-14.

UNFCCC (United Nations Framework Convention on Climate Change). 2008. Kyoto Protocol reference manual. Climate Change Secretariat (UNFCCC), Bonn, Germany.

Valentini, R., Matteucci, G.R., Dolman, A.J., Schulze, E.D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404, 861-863.

Vallejo, R., Aronson, J., Pausas, J.G., Cortina, J., 2005. Restoration of Mediterranean woodlands, in: van Andel, J., Aronson, J. (Eds.), Restoration Ecology. The new frontier. Blackwell Science Ltd., pp. 193-207.

Van Oost, K., Quine, T. A., Govers, G., *et al.*, 2007. The impact of agricultural soil erosion on the global carbon cycle. *Science* 318, 326-329.

Wiant, H.V., 1967. Has the contribution of litter decay to forest soil respiration been overestimated? Journal of Forestry 65, 408-409.

1. Study site and experimental design

1.1. Location of the study site

The study area is located in Cehegín in the northwest of the province of Murcia in southeastern Spain. The present work was conducted in the Burete experimental area (38º3´N, 1º46´W), situated between the Quípar and Burete mountain ranges. Elevation in the experimental area ranges from 600 to 800 m above sea level.
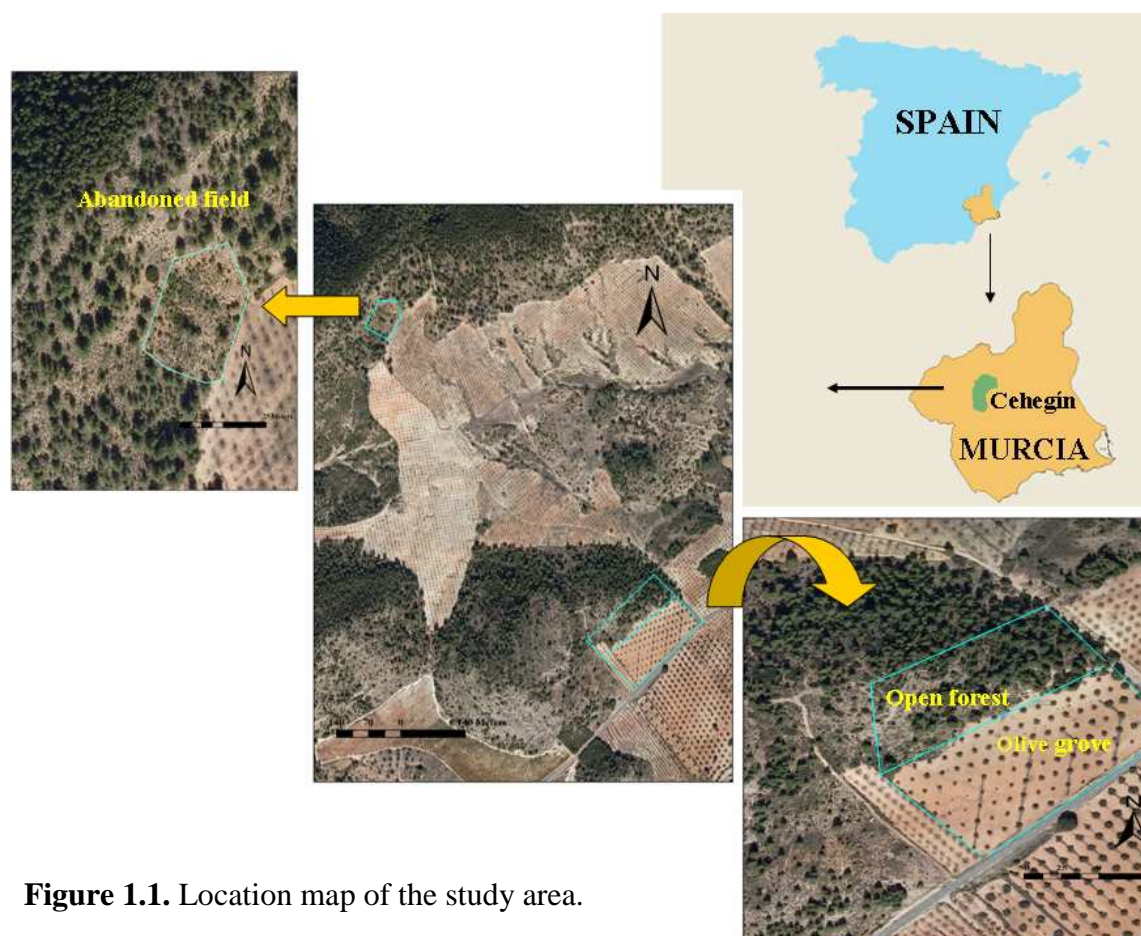
Figure 1.1. Location map of the study area.

This area is representative of the agricultural, socioeconomic and environmental situation of many dry-land farming areas in the Mediterranean region, where the main limitation to agriculture is water shortage. The landscape represents a heterogeneous mosaic of agricultural practices (rain-fed and irrigated orchards and olive groves (25%), dry-land farming (7.7 %) and, to a lesser extent, vineyards (1.8%)). Forests and shrublands occupy 60% (Ministerio de Medio Ambiente, Agua y Medio Rural, 2001).

1.2. Geology, relief and soils

The experimental area is located in the Betic Cordilleras, within the Subbetic zone. The dominant lithology consists mainly of marine carbonate rocks (e.g., dolomitized limestone, limestone with silex nodules, and red nodular limestones) of the Jurassic, marls and marly limestone of the Cretacic, and marls, sandstones and limestones of the Trassic (IGME, 1978).

The soils in the study area are mainly Leptosols (in the mountain ranges), Regosols, Kastanozems and Calcisols (in the agricultural lands), and Fluvisols (in both Quipar and Argos valleys) (Alías et al., 1987). Overall, soils in the study area are shallow, with a low soil organic matter content and high percentage of carbonates.

1.3. Climate

The climate is dry subhumid Mediterranean, with mean annual precipitation ranging from 300 to 400 mm and a mean annual temperature of 15 to 16 ºC (Cehegín Meteorological Station, 1953-1986 period). Mean monthly rainfall ranges from 8 mm (July) to 50 mm (October), following a bimodal distribution with two rainy seasons (autumn and spring), and a dry period in summer. High rainfall variability between and within years is very common in the area.
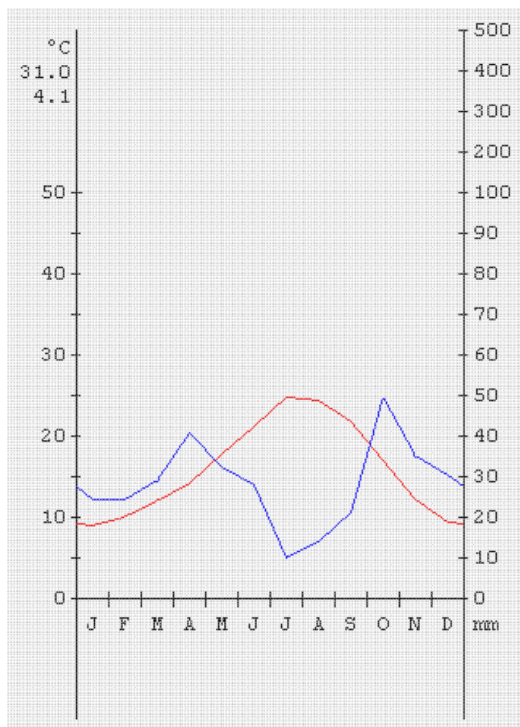
Figure 1.2. Monthly rainfall (blue line) and mean monthly temperatures (red line) between January 1953 and December 1986. Data from Cehegín weather station (38º 5´ N, 1º 47´ W; 572 m.a.s.l.).

Monthly temperatures oscillate from 0 ºC or below 0 ºC (December and January) to 40 ºC (July and August). The mean annual potential evapotranspiration (calculated by the Thornthwaite method; Thornthwaite, 1948) reaches 800 mm yr^{-1}, so the annual water deficit is 430 mm. July and August are the driest months, when the maxima in monthly temperature and potential evapotranspiration occur.

1.4. Vegetation

The potential vegetation in the study area is characterized by a mixed forest dominated by *Quercus faginea* and *Quercus Ilex* in higher mountain areas, and by *Quercus Ilex* and *Quercus coccifera* with scattered *Pinus halepensis* in lower mountain areas and valleys (Rivas-Martínez, 2008). However, as a result of land use intensification and subsequent land abandonment, together with selective logging practices and reforestation works that took place in the 1970s, current forest patches in the study area are a mixture of *Pinus halepensis* with *Quercus coccifera*, *Rosmarinus officinalis*, *Juniperus oxycedrus*, *Rhamnus lycioides*, *Cistus clusii*, *Cistus albidus*, *Pistacia lentiscus,* and *Daphne gnidium* (Abellán and Sánchez, 2010).

1.5. Experimental design

Three neighbouring sites (located within a radius of 2 km) representative of each land use type were selected to carry out the study: 1) a circa 150-yr-old mixed Aleppo pine-kermes oak open forest, 2) an abandoned agricultural field, which was cultivated with cereal for several years until abandonment in 1980, when establishment of typical Mediterranean vegetation started, and 3) a rain-fed olive grove without terraces, regularly ploughed along the contour lines, and planted with a 10 x 10 m spacing (107 olive trees/ha), which has been cultivated for 100 years. These land use types are representative of the land use changes that occurred throughout the 20th century in this and other Mediterranean landscapes as a result of agriculture intensification and subsequent land abandonment (Padilla et al., 2010 and references herein). The open forest and abandoned field sites are covered by a typical Mediterranean shrubland with scattered Aleppo pines (*Pinus halepensis*). Although both sites show the same dominant plant species (*Rosmarinus officinalis, Quercus coccifera,* and *Juniperus oxycedrus*), the open forest site

has a more developed vegetation structure, with a total vegetation cover of about 65% compared with 35% of the abandoned agricultural field site.

Figure 1.3. View of the sites representative of each land use type: open forest (A and C), abandoned agricultural field (B and D) and olive grove (E and F).

The three sites are located on a glacis hillslope with a mean slope of 10-12%, good drainage and a high percentage of stones on the surface. The open forest, abandoned agricultural field and olive grove sites occupy around 1.2, 0.15 and 1.8 ha, respectively. The three sites have the same microclimatic and soil texture conditions, but differ in the

degree (and type) of vegetation cover and belowground properties, as a result of land use history (Table 1.1).

The soils in the study sites, with a loamy texture, derived from limestone colluvia (open forest and olive grove sites) and Triasic marl colluvia (abandoned agricultural field site), are classified as Petrocalcic Calcisol (open forest site), Hypercalcid Calcisol (olive grove site), and Haplic Regosol (Calcaric) (abandoned agricultural field site) (IUSS-WRB, 2006). Because the forest and olive grove sites are located on soils developed from the same parent materials and are exposed to the same climatic conditions, the difference in soil properties were assumed to be primarily attributed to soil use and cultivation which is responsible for breaking limestone crust. The soil profile characteristics in the three areas are displayed in the Appendixes I, II and III. Overall, the soils in the study site are shallow, with an underlying caliche layer at 17-19 cm depth, and with low soil organic matter content and high percentage of carbonates (Table 1.1; Martínez-Mena et al., 2008).

Rather than comparing C pools and fluxes among different land uses, this study focuses on understanding below-ground C cycling and the factors controlling the main C balance components within representative land uses/sites. Moreover, we felt it was important to explore the links between vegetation, climatic parameters, and soil C pools and fluxes within representative land use types. Hence, we chose to intensively study one site in each land use type rather than attempting to replicate sites across the ecosystem. Thus, although the experimental design of this study may be considered a case of "simple pseudoreplication" (Hurlbert, 1984) for the purpose of comparing soil C pools and fluxes betwen different land uses, we feel that the approach is suitable for: i) characterizing C pools, fluxes and allocation patterns; ii) testing the suitability of different C-budgeting models to estimate total belowground C allocation; iii) assessing the main C components of soil carbon balance; and iv) identifying the factors controlling the main soil C fluxes along a land use intensification gradient in a Mediterranean ecosystem. Previous studies have used a similar experimental design to describe soil C pools and fluxes and identify the major ecological controls on them in other ecosystem types (Allen and Vargas, 2008 Conant et al., 1998; Gulledge and Schimel, 2000; Maestre and Cortina, 2003; McCulley et al., 2004; Rey et al., 2002; 2010).

Table 1.1. Main characteristics of the experimental area.

Variable	Open forest	Abandoned agricultural field	Olive grove
Vegetation characteristics	Open Aleppo pine woodland	Shrubland with scattered Aleppo pines	Olive trees
Standing biomass (g m^{-2})	6862 ± 4318	735 ± 103	2487 ± 114
Mean tree stem diameter (cm)	8.37 ± 0.4	3.97 ± 0.48	30.8 ± 0.4
Mean shrub stem diameter (cm)	1.72 ± 0.07	1.86 ± 0.09	-
Plant cover (%)	64.77± 3.95	35.17 ± 3.51	12 ± 0.1
Mean annual litterfall (g m^{-2})	267.5 ± 17.85	184.1 ± 17.8	54.1 ± 19.3
Mean annual aboveground NPP (g m^{-2})	542.5 ± 47.7	365.2 ± 60.4	195.2 ± 23.7
Mean annual belowground NPP (g m^{-2})	807 ± 36.5	762.5 ± 45.8	480.1 ± 47.7
Soil characteristics			
Clay (%)	20.9 ± 0.5	19.3 ± 0.8	24.8 ± 0.7
Silt (%)	59.3 ± 0.6	54.8 ± 0.8	59.7 ± 1.1
Sand (%)	19.7 ± 0.8	25.8 ± 1.4	15.5 ± 1.1
Bulk density	0.91 ± 0.02	1.25 ± 0.03	1.44 ± 0.02
pH H$_2$0	8.02	8.30	8.13
CO$_3$Ca (%) (0-19 cm)	38.2	32.3	61.9
Maximum soil depth (cm)	17	17	20
Mean annual soil temperature (ºC)	16.93 ± 0.27	16.80 ± 0.27	16.72 ± 0.26
Mean annual soil water content (%)	10.28 ± 0.24	14.86 ± 0.24	15.01 ± 0.28

NPP: Net Primary Productivity

References

Abellán, P., Sánchez, D., 2010. Guía de la naturaleza de Cehegín. Excmo. Ayuntamiento de Cehegín. ISBN: 978-84-693-4005-9, Murcia, España.

Alías, L.J., Ortíz, R., Martínez, J., Alcaraz, F., López, B., 1987. Proyecto LUCDEME. Mapa de suelos 1:100000. Cehegín 911: 26-36.

Conant, R.T., Klopatek, J.M., Malin, R.C., Klopatek, C.C., 1998. Carbon pools and fluxes along an environmental gradient in northern Arizona. Biogeochemistry 43, 43-61.

Gulledge, J., Schimel, J.P., 2000. Controls on soil carbon dioxide and methane fluxes in a veriety of taiga forest stands in interior Alaska. Ecosystems (3), 269-282.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54(2), 187-211.

Instituto Geológico Minero de España (IGME), 1978. Mapa geológico de España 1:50000, Cehegín 911: 25-36.

IUSS Working Group WRB, 2006. World reference base for soil resources. World Soil Resources reports 103. FAO, Rome.

Maestre, F.T., Cortina, J., 2003. Small-scale spatial variation in soil CO_2 efflux in a Mediterranean semiarid steppe. Applied Soil Ecology 23, 199-209.

McCulley, R.L., Archer, S.R., Boutton, T.W., Hons, F.M., Zuberer, D.A., 2004. Soil respiration and nutrient cycling in wooded communities developing in grassland. Ecology 85(10), 2804-2817.

Martínez-Mena, M., López, J., Almagro, M., Boix-Fayos, C., Albaladejo, J., 2008. Effect of water erosion and cultivation on the soil carbon stock in a semiarid area of South-East Spain. Soil and Tillage Research 99, 119-129.

Ministerio de Medio Ambiente, Agua y Medio Rural, 2000-2009. Mapa de cultivos y aprovechamientos de España 1:50000, Cehegín 911: 25-36.

Padilla, F.M., Vidal, B., Sánchez, J., Pugnaire, F.I., 2010. Land use changes and carbon sequestration through the twentieth century in a Mediterranean mountain ecosystem: Implications for land management. Journal of Environmental Management 91, 2688-2695.

Rey, A., Pegoraro, E., Oyonarte, C., Were, A., Escribano, P., Raimundo, J., 2010. Impact of land degradation on soil respiration in a steppe (*Stipa tenacissima* L.) semi-arid ecosystem in the SE of Spain. Soil Biology and Biochemistry 43(2), 393-403.

Rey, A., Pegoraro, E., Tedeschi, V., De Parri, I., Jarvis, P.G., Valentini, R., 2002. Annual variation in soil respiration and its components in a coppice oak forest in Central Ital. Global Change Biology 8, 851- 866.

Rivas-Martínez, S., 2008. Globalbioclimatics, http://www.globalbioclimatics.org

Thornthwaite, C.W., 1948. An approach toward a rational classification of climate. The geographical review, 38.

USDA Natural Resources Conservation Service. Soil Survey Staff 2006. Keys of Soil Taxonomy. Tenth Edition. Washington.

Vargas, R., Allen , M.F., 2008. Environmental controls and the influence of vegetation type, fine roots and rhizomorphs on diel and seasonal variation in soil respiration. New Phytologist 179: 460-471.

2. Carbon pools, fluxes, and allocation patterns

Abstract

Total belowground C allocation (TBCA) accounts for a large fraction of gross primary production, it may overtake aboveground net primary production, and contributes to the primary source of detrital C in the mineral soil. Here, we measure soil respiration, water erosion, litterfall and estimate annual changes in C stored in mineral soil, litter and roots, in three representative land uses in a Mediterranean ecosystem (open forest, abandoned agricultural field, rain-fed olive grove), and use two C balance approaches (steady-state and non-steady-state) to estimate TBCA. Both TBCA approaches are compared to assess how different C fluxes (outputs and inputs) affect our estimates of TBCA within each land use. In addition, annual net primary productivity is determined and C allocation patterns are examined for each land use. We hypothesized that changes in C stored in mineral soil, litter and roots will be slight compared to soil respiration, but will still have a significant effect on the estimates of TBCA. Annual net primary productivity was 648 ± 31.5, 541 ± 42.3 and 324 ± 22.3 g C m^{-2} yr^{-1} for forest, abandoned agricultural field and olive grove, respectively. Across land uses, more than 60 % of the C was allocated belowground. Soil respiration (F_S) was the largest component in the TBCA approaches across all land uses. Annual C losses through water erosion were negligible compared to F_S (less than 1%) and had little effect on the estimates of TBCA. Annual changes in C stored in the soil, litter layer and roots were low compared to F_S (16, 24 and 10 % for forest, abandoned agricultural field and olive grove, respectively), but had a significant effect on the estimates of TBCA. In our sites, an assumption that $\Delta[C_S + C_R + C_L]/\Delta t = 0$ will underestimate TBCA, particularly in the abandoned agricultural field, where soil C storage may be increasing more rapidly. Therefore, the steady-state model is unsuited to these Mediterranean ecosystems and the full model is recommended.

2.1. Introduction

Carbon storage in terrestrial ecosystems is governed by the difference that exists between inputs from aboveground and belowground net primary production and outputs through erosion and decomposition of plant material and soil organic matter on both short and long term scales. Dry and semiarid lands, which are characterized by patches of vegetation and bare soil, are the dominant ecosystems in Mediterranean climates. Slow growth rates, difficult land recovery after degradation and potentially high mineralization rates make them especially sensitive to perturbations resulting from climate change, drought and land use changes (Asner et al., 2003; Domingo et al., 1999; Giorgi, 2006; Smith et al., 2000).

Vegetation allocates carbon (C) belowground to the production of coarse and fine roots, for root respiration and exudation, and to maintain mycorrhizal activity (Raich and Nadelhoffer, 1989). Total belowground C allocation (TBCA) accounts for a large fraction of gross primary production, it may overtake aboveground net primary production, and contributes to the primary source of detrital C in the mineral soil (Gower et al., 1996; Law et al., 1999; Ryan et al., 1994; 1997). Because of the lack of direct measurements of TBCA, Raich and Nadelhoffer (1989) proposed a conservation of mass approach to estimate TBCA (g C m^{-2} yr^{-1}) in ecosystems where the stocks of soil organic matter, roots, and litter were assumed to be nearly steady:

$$\text{TBCA} = F_S - F_A \qquad \text{Eqn. 1}$$

where F_S is the soil-surface CO_2 efflux (soil respiration) and F_A is the aboveground litterfall.

As the near-steady-state assumption is sometimes uncertain and problematic (for example, disturbed forests, forests established on agricultural land, croplands; Nadelhoffer et al., 1998), Giardina and Ryan (2002) proposed a similar approach, whereby C outputs from the soil equal C inputs minus any change in the C stored in soil per unit of time (Δt):

$$F_S + F_E = \text{TBCA} + F_A - \Delta\,[C_S + C_R + C_L]/\Delta t \qquad \text{Eqn. 2}$$

Soil-surface CO_2 efflux (F_S) is the largest output of C in forest soils. Although poorly quantified, the export of C through erosion and leaching (F_E) is very low compared with the other fluxes, and so has relatively little influence on the total soil carbon budget (Edwards and Harris, 1977; Forrester et al., 2006; Giardina and Ryan, 2002; Raich, 1983; Schlesinger 1977; 1984). At our study-site, the loss of C through leaching is probably negligible because of low soil water-extractable organic carbon concentrations (Martínez-Mena et al., 2008). However, we include the carbon mobilized by water erosion in our TBCA approach because of the importance of this process in the organic C balance of Mediterranean ecosystems (Smith et al., 2007). Soil C inputs include the C allocated belowground by plants for root production and respiration, exudation, and for the maintenance of mycorrhizal activity (TBCA), together with aboveground litterfall (F_A). The major components affecting C storage in soils are mineral soil organic matter (C_S), fine and coarse roots (C_R), and the litter layer (C_L).

Thus, through conservation of mass, TBCA can be estimated:

$$\text{TBCA} = F_S + F_E - F_A + \Delta\,[C_S + C_R + C_L]/\Delta t \qquad \text{Eqn. 3}$$

Both TBCA approaches have previously been used for different purposes in mature temperate or tropical forests, and in plantations with high stem density, a considerable litter layer thickness and medium to high mean annual precipitation (Davidson et al., 2002; Forrester et al., 2006; Giardina and Ryan, 2002; Newman et al., 2006; Raich and Nadelhoffer, 1989). However, the steady-state assumption has not been directly tested for dry Mediterranean woodlands or tree-crop fields.

This chapter focuses on characterizing C pools and allocation patterns along a land use intensification gradient in a Mediterranean ecosystem (open forest, abandoned agricultural field, rain-fed olive grove). The specific objective of the present work was to compare both C balance approaches to assess how different C fluxes (outputs and inputs) affect our estimates of TBCA within each land use. We hypothesized that changes in mineral C soil, litter and roots would be slight compared to soil respiration, but would have a significant influence on the estimates of TBCA.

2.2. Materials and methods

2.2.1. Measurements and calculations

2.2.1.1. Organic carbon pools

For each land use, 24 sampling points at 15 cm depth were distributed in a stratified manner, depending on the number of plant cover types within each land use. A composite sample from each point included a non-disturbed sample (core of 100 cm^3 volume) for bulk density measurements and a disturbed sample for C and N analysis. Soil samples for analyses were air-dried, ground and sieved through a 2 mm sieve. Before soil organic carbon (SOC) and total nitrogen (TN) were analysed, using a N/C Analyzer (Flash 1112 EA, Thermo-Finnigan, Bremen, Germany), soil carbonates were eliminated using 1 M HCl. Soil organic carbon stock (g m^{-2}) was computed as a product of the organic C concentration, bulk density and depth for each sampling point.

Figure 2.1. Some of the selected vegetation plots (5x5 m) in order to estimate aboveground biomass from species-specific allometric relationships in the forest and abandoned field sites. Dotted red lines indicate vegetation plots.

Aboveground biomass (AGB) was estimated from plot-based measurements of shrub and tree stem basal diameters (Fig. 2.1). Twenty-four 5x5 m plots were located in the forest (N=16) and abandoned agricultural field (N=8), and every single stem basal diameter was measured at the end of the growing season (2006) in order to estimate AGB from species-specific allometric relationships (Baeza et al., 2006; Baeza et al., 2011; Barberá et al., unpublished data). In the olive grove, AGB was estimated from trunk basal area measurements (N=30) using an allometric relationship developed using 18 *Olea europaea* L. trees growing in a cropland from southern Spain (Villalobos et al., 2006). Representative biomass samples (stems, twigs, and needles) were dried at 50 ºC for seven days, weighed and ground. The C content of AGB was estimated to be 48 % of dry weight, hereinafter referred to as ABG-C (g C m^{-2}).

Belowground biomass (BGB) was estimated using the core method (Vogt et al., 1998). Twelve soil cores were collected according to a stratified sampling design at each land use site in late December 2006. The sampling was repeated in late April 2007. Plant roots were sampled at a mean depth of 15 cm by collecting soil cores 8 cm in diameter (Fig. 2.2). The soil cores were gently rinsed through a series of three successively smaller sieves (5.0, 2.0, 1.0 mm). Roots were hand-picked from the sieves and placed in a tray. The remaining soil (< 1 mm) was mixed with tap water and the floating roots were decanted into a 0.1-mm mesh sieve. The flotation procedure was repeated until no more visible roots floated to the

Figure 2.2. Sampling auger (A) and soil from an individual core before being processed for root biomass estimates (B). Soil was rinsed through a series of sieves (C) while roots were hand-picked (D) and placed in a tray.

surface. The material collected in the 0.1 mm sieve was placed in the tray, and any material not derived from roots was removed. Roots were mixed with sodium hexametaphosphate for 24 h to disperse clay particles, rinsed with tap water, dried at 55º C for 4 days, and weighed. Roots were ground, and the C and N content were determined by using the same procedure as for the ABG-C samples. We calculated belowground biomass C values (BGB-C in g C m^{-2}) by multiplying the % C values by the total root sample weight and core size. Statistical analyses showed no significant differences in values between the two sampling periods, so we pooled the measurements from the two periods to obtain average C storage values for fine and coarse roots in each land use.

2.2.1.2. Components of the belowground C budget

2.2.1.2.1. Soil respiration

Soil CO_2 efflux was measured in situ with a portable soil respiration gauge (LI-6400, LI-COR, Lincoln, NB, USA) fitted with a soil respiration chamber (6400- 09, LI-COR, NB, USA). Measurements of soil CO_2 efflux were taken according to a stratified sampling design to capture the vegetation-based variation in each land use. In the olive grove, a relatively homogeneous ecosystem, six trees were randomly selected and a total of 24 PVC circular collars (5 cm depth, 10 cm diameter) were inserted at different distances from the stems. Areas closer to the tree stem were more intensively sampled because preliminary studies had shown higher variability in soil respiration at those locations (Saiz et al., 2006). In the inter-tree locations, six randomly distributed collars were considered enough to reliably estimate the mean soil respiration at the 90 % probability level, according to variance estimation procedures described by Snedecor and Cochran (1967). In the forest and abandoned field, a total of 30 collars were proportionally distributed among the most frequent soil cover types (*Pinus halepensis*, *Rosmarinus officinalis*, *Juniperus oxycedrus*, *Quercus coccifera*, *Rhamnus lycioides* and bare soil), and were also placed at different distances from the stems. Thirty sampling points were considered sufficient to estimate mean soil respiration at the 90 % probability level. To minimize the effects of chamber installation, the above-mentioned permanent soil collars were inserted into the soil to a depth of about 2 cm, to limit root severing (Wang et al., 2005) and care was taken not to disturb the soil structure. Soil collar heights were checked monthly to correct for possible changes in collar volume from one month to the next.

Figure 2.3. Soil respiration collars and/or litter traps beneath the most frequent plant cover types at each site: bare soil (A), *Rosmarinus officinalis* (B and D), *Pinus halepensis* (C and H), *Quercus coccifera* (E), *Rhamnus lycioides* (F), *Juniperus oxycedrus* (G), and *Olea europaea* (I).

Soil respiration measurements were performed monthly between January 2006 (two months after the collars were inserted to avoid soil alterations biases) and December 2007. Soil respiration measurements were always performed between 9:00 and 12:00 (solar time), because it has been shown that midday values of CO_2 efflux are representative of daily averages (Davidson et al., 1998; Larionova et al., 1989; Xu and Qi, 2001a).

2.2.1.2.2. C outputs by water erosion

To estimate the organic C exported in runoff and sediment by water erosion, two closed erosion plots (8 m long $\times$ 2 m wide) were installed in the forest and olive grove, respectively. In the abandoned agricultural field, three sediment traps (Gerlach type) were set up in different locations at the bottom of the slope. Precipitation depth after each event was obtained from two recording rain gauges installed in the experimental area. The runoff

and sediments were collected in a tank located at the bottom of the closed plots in the forest and olive grove, and in the sediment traps in the abandoned agricultural field. Sampling of the sediments from the tanks was carried out after thorough stirring. Five aliquots of 1 L were taken from different depths. The sediment was filtered, oven-dried at 60 °C, weighed to determine the suspended sediment concentration, ground and analyzed for organic C content. The sediment concentrations were averaged and multiplied by the total runoff to calculate total soil loss. From each tank and bottle (in abandoned agricultural field) an aliquot (20 ml) of runoff sample was filtered through a Fisherbrand glass fiber filter (0.45 μm) and the filtrate was used for dissolved organic C (DOC) determinations. Total OC export during a rainfall event was computed as the sum of OC in sediments plus OC in runoff.

Annual organic carbon losses by erosion (F_E in g C m^{-2} yr^{-1}) were calculated as the sum of the net carbon exported after every erosion event during one year, divided by the surface of the closed plots in the forest and olive grove, and by the drainage area of each sediment trap (calculated from a Digital Terrain Model with a resolution of 0.25 m) in the abandoned agricultural field. Water erosion was measured over a three-year period (2006-2009).

Figure 2.4. Recording rain instrument in the experimental area and closed water erosion plots in the forest (A) and olive grove (B), deposits (C), and sediment traps connected to a plastic bottle (D and E).

2.2.1.2.3. Aboveground litter inputs

Above-ground litter (F_A) was trapped in six trays (0.25 m^2 each) in the olive grove. In the forest and abandoned agricultural field, ten trays were distributed among the most common plant cover types. In the forest and abandoned agricultural field, some of these litter traps were installed on bare soil, but in the olive grove this would have been impractical because of occasional tillage. However, aboveground litter inputs at inter-tree locations may be assumed to be negligible in this land use. Each tray was set on the floor and collected monthly over a 3-year period (2006-2009). Once collected from the field, litter from each trap was dried at 55º C for four days and weighed. Because litter quality may differ between seasons, we analysed the C and N content of the trapped litter in February, May, August and November 2007, and assumed that the litter biomass averaged 48 % C. We estimated aboveground C-litter production (in g C m^{-2} yr^{-1}) by multiplying the sample weight by the averaged % C values.

2.2.1.2.4. Annual changes in the organic C stored

In the open forest and olive grove, we assumed that annual changes in soil C (ΔC_S) were negligible because both sites have been used in the same way since at least 1900, and previous research in forest (Nadelhoffer et al., 1998; Raich and Nadelhoffer, 1989) and agricultural (Burke et al., 1995; Lal, 2008) ecosystems suggests that soil C pool sizes reach a near-steady-state after 50 years of the same forest or agricultural management. However, in the abandoned agricultural field the strength of this assumption is presumably compromised. Therefore, we estimated ΔC_S for the abandoned agricultural field, assuming that soil C sequestration within the surface soil began after abandonment (30 years ago), and taking the soil C pool in the olive grove as a reference starting value.

We obtained estimates of annual increases in fine roots by using a modified root in-growth core technique (Fabião et al., 1985; Oliveira et al., 2000; McCulley et al., 2005). In early February 2007, we excavated 15-19 cm-deep cylindrical holes with a bucket auger (8 cm internal diameter) in each land use (N=12 root in-growth holes per site), distributed in a stratified manner, depending on the number of different plant cover types within each land use. The study-site is located on relatively shallow soils with underlying limestone crust at 17-19 cm depth (Martínez-Mena et al., 2008); therefore, we installed root in-growth bags (15 cm depth, 8 cm diameter) constructed of fibreglass-nylon mesh with 4.5 mm^2 openings

as deeply as possible at each root in-growth hole (between 4 and 19 cm) and refilled them with a root-free soil collected from each land use site of the study area (Fig. 2.5). We collected the root in-growth mesh bags the following February (2008). The root in-growth mesh bags were kept in a refrigerator to minimize decomposition during the time between collection and processing (at most, one month). We followed the same flotation-decantation procedure described above to obtain below-ground biomass and determined C and N concentrations by using the same C-N analyzer as for the BGB-C samples. The annual fine root production (in g C m^{-2} yr^{-1}) was calculated by multiplying the root % C by the root production values obtained from the total root sample weight and core size.

Figure 2.5. Root in-growth mesh bag (A) before being refilled with root-free soil and installed at one root in-growth hole, buried root in-growth mesh bags beneath different plant cover types (B, C and D), and one of the root in-growth mesh bags which were collected the following year (E and F).

Coarse root production was estimated from a simple allometric equation which assumes that coarse root production is proportional to aboveground NPP (Johnson and Risser, 1974):

$$NPP_{cr} = (ANPP/AGB) \times B_{cr} \hspace{4cm} \text{Eqn. 4}$$

where NPP_{cr} is coarse root net primary production, ANPP is aboveground net primary production, AGB is aboveground biomass, and B_{cr} is coarse root biomass. Likewise, annual coarse root C production was estimated by multiplying the % C by the coarse root production values obtained from the allometric equation. The ΔC_R was computed as the sum of fine and coarse root annual production.

The annual accumulation rates of litter layer C (ΔC_L) were estimated as the difference between the annual aboveground litterfall input and the aboveground litter decomposition C loss estimates at each land use site. To measure aboveground litter decomposition rates (k_c) we selected the dominant types of litter for each land use: *Pinus halepensis* needles, fine stems and fruits, and *Rosmarinus officinalis* leaves, flowers and stems in the forest and abandoned agricultural field; and *Olea europaea* leaves, fruits and fine stems in the olive grove. In April 2007, litter was collected weekly from several sheets distributed in each land use site. Litter samples were air-dried at room temperature. Oven-dry weight was determined for five samples per litter type after drying at 55º C for 4 days. Samples were ground and analysed for % C and % N in order to assess the initial litter % C and % N data. Subsamples (0.3 g) were combusted in a muffle furnace at 500º C for 5 h to determine ash content (ranged from 3% to 11% of sample mass). We thoroughly mixed each litter type material separately before placing 3.0 g (*Rosmarinus officinalis* litter type) or 5.0 g (*Pinus halepensis* and *Olea europaea* litter type) of leaves and fine stems ($\pm$ 0.01 g) inside 10 x 10 cm litterbags constructed of fibreglass-nylon mesh with 1.4 mm^2 openings. The initial concentration of litter in the litterbags (500 g m^{-2} in olive and pine, and 300 g m^{-2} in rosemary) was equivalent to circa 2 years of accumulated litter inputs, which averaged 264, 280 and 146 g m^{-2} yr^{-1} for olive, Aleppo pine and rosemary, respectively, in the study area.

Two fenced plots were installed beneath two randomly selected pine trees and rosemary shrubs in both forest and abandoned agricultural field sites, and beneath two randomly selected olive trees in the olive grove. We placed litterbags with their corresponding litter types on the soil surface inside the above-mentioned fenced plots on 19 June 2007 and followed their evolution for 20 months (Fig. 2.6). In the forest and abandoned agricultural field, a total of 72 litterbags were placed (2 litter types x 2 individuals x 6 sampling dates x 3 replicates), and 36 (2 individuals x 6 sampling dates x 3 replicates) in the olive grove. Each litterbag was carried inside an individual envelope to quantify how much litter was lost from the bags during the transport. We collected 3 litterbags from each fence plot every three months.

Once harvested from the field, litterbags were processed in the laboratory. Any material not derived from litter (seedlings, stones, soil fauna or fungi) was hand-picked before the litterbags were dried at 55° C and sieved to remove mineral soil. We mixed dried litter samples with tap water and decanted floating litter into a 0.1 mm mesh sieve. After drying for 4 days at 55° C the litter of each litterbag was weighed to determine mass change. The samples were ground and then subsampled for ash content, and % C and N determination (methods as previously described).

Figure 2.6. Litter-bags (A) before placing the dominant types of litter for each land use, and fenced plots were litter-bags were placed in the open forest (B), olive grove (C) and abandoned agricultural field (D) sites.

The C decomposition constant (k_c, yr^{-1}) was determined for each litter type by land use combination using a single exponential decay model (Olson, 1963):

$$\ln (C_t/C_0) = - k_c t \qquad \text{Eqn. 5}$$

where C_t and C_0 are the ash-free C content of the litter at time t and time 0.

To compare the land use patterns of decomposition to those of net primary production, soil respiration and erosion, the decomposition of C had to be expressed on the same scale (g C m^{-2} yr^{-1}). To accomplish this, and following McCulley et al. (2005), we assumed that

all aboveground litterfall production for each land use for the year would eventually enter the litter pool and be decomposed at the rate measured (k_c). Therefore, we obtained an estimate of aboveground litter C lost through decomposition (g C m^{-2} yr^{-1}) by multiplying the F_A values by k_c.

2.2.1.3. Net Primary Production

Annual above-ground net primary productivity (ANPP) and plant C uptake were determined over a two-year period (2006-2008) using a combination of pruning, harvesting, litterfall collection, and allometric methods (as mentioned in section 2.2.1.1.) appropriate for the different land uses types, followed by drying (55 º C), grinding, and dry combustion analysis of C and N concentrations in plant tissues. While traditional ecosystem studies typically compare ANPP among systems using a constant methodology, our experimental design required a more complex approach that tailored ANPP methods to each land use type. In the open forest and abandoned agricultural field, annual ANPP was estimated using the equation ANPP = ΔAGB + F_A, where ΔAGB is the annual increase in above-ground biomass (calculated from stem basal diameter increments, by applying the abovementioned species-specific allometric relationships), and F_A is annual aboveground litterfall. However, we used a combination of litterfall collection, pruning residues and olive yield for annual ANPP measurements in the olive grove. This approach enabled us to obtain the best estimate for each land use type under real-world management conditions.

TBCA estimates were converted to production estimates (belowground NPP) by assuming that 50 % of the C efflux was root and mycorrhizal respiration (the other 50 % incorporated new tissue) (Binkley and Ryan, 1998; Giardina et al., 2003; 2005; Litton and Giardina, 2008; Newman et al., 2006; Ryan, 1991).

We summed aboveground and belowground net primary production values to estimate net primary production (NPP-C) in each of the land uses. Because the aboveground and belowground production measurements were not experimentally paired, we used the average ANPP-C and BNPP-C values per land use and year in the summation for NPP-C.

2.2.2. Statistical Analyses

Differences in F_S and F_A with time were assessed using repeated-measures analysis of variance (ANOVA) (month = repeated measure, and land use was the main effect).

Analysis of variance (ANOVA) was performed to detect differences in litter decomposition rates between species. A t-test was performed to compare aboveground and belowground net primary productivity within each land use. A Pearson correlation test was used to examine the relationships between monthly soil respiration and litterfall inputs within each land use. Analyses were computed with SPSS procedure GLM (SPSS 15.0, Chicago, IL, USA) at the $P = 0.05$ significance level.

2.3. Results

2.3.1. Carbon pools and dynamics within each land use

The whole ecosystem carbon pool ranged from 3640.6 to 8780.7 g C m^{-2} across land uses, (Table 2.1), with approximately 62, 90 and 77% of the C stored belowground (soil plus roots) in forest, abandoned agricultural field and olive grove, respectively. The major contributor to the total belowground C pool was the C stored in the mineral soil as SOC, which accounted for 94, 92 and 94 % in the forest, abandoned agricultural field and olive grove, respectively. Carbon stored in aboveground biomass accounted for 37.5 (forest), 9.5 (abandoned agricultural field) and 22.8 (olive grove) % of the total carbon. The root: shoot biomass ratio was 0.1, 0.72 and 0.18 for forest, abandoned agricultural field and olive grove, respectively.

Table 2.1. Soil organic C and total N pools (0-15 cm), soil C: N, above- and belowground biomass C (0-15 cm), whole ecosystem C, and root: shoot ratios for each land use.

	Open forest	Abandoned field	Olive grove
Soil organic carbon (g C m^{-2})	5189.3 ± 154.9	3060 ± 441	2658 ± 514.82
Soil total nitrogen (g N m^{-2})	336.3 ± 5.2	279 ± 3.6	284.1 ± 5.2
Soil C:N	15.4 ± 0.4	11.0 ± 0.4	9.3 ± 0.5
Aboveground biomass C (g C m^{-2})	3293.8 ± 2072.6	351.3 ± 49,64	830.3 ± 52.1
Belowground biomass C (g C m^{-2})	305.4 ± 42.9	252.9 ± 42.9	162.2 ± 43.8
Total Ecosystem C (g C m^{-2})	8780.7 ± 2270.4	3664.3 ± 533.5	3640.6 ± 610.7
Root: shoot biomass	0.10	0.84	0.21

Lower aboveground litter C decomposition rates (k_c) were found for Aleppo pine litter (0.15 ± 0.02 and 0.29 ± 0.02 yr^{-1}) than for rosemary litter (0.71 ± 0.02 and 0.59 ± 0.02 yr^{-1}) in both forest and abandoned agricultural field, respectively (F=132.18; P<0.0001) (Fig.2.7). This means longer mean residence times for Aleppo pine litter (6.6 and 3.4 yr) with respect to rosemary litter (1.4 and 1.69 yr) in both forest and abandoned agricultural field, respectively. The average k_c value for olive litter was 0.54 ± 0.02 yr^{-1}, and its mean residence time was estimated to be 1.85 yr.
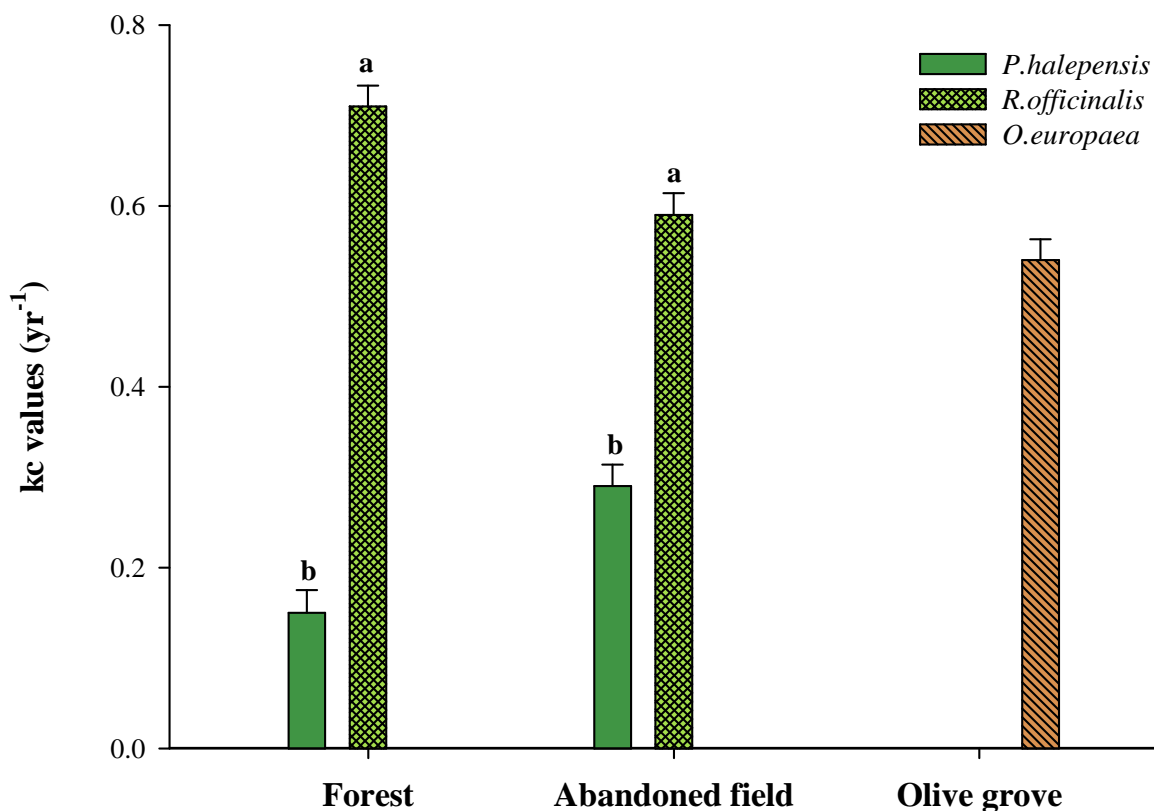
Figure 2.7. Aboveground litter decomposition rates (k_c) for the dominant types of litter for each land use. Within each land use, different letters indicate significant differences in decay constants between litter types ($P < 0.05$).

2.3.2. Components of the TBCA budget

Soil-surface CO_2 efflux across sites (F_S) was larger than any other component in the TBCA approach (Table 2.2). For more details about seasonal variations in soil respiration and differences between beneath- and inter-canopy locations within each land use, see Chapter 3. Greater litterfall inputs (F_A) were observed in the open forest and abandoned

agricultural field than in the olive grove. Monthly F_A and F_S were poorly correlated (r = 0.124, r = 0.242, and r = 0.232, P < 0.01 for forest, abandoned agricultural field and olive grove, respectively). Across sites, carbon losses by water erosion (F_E) were minor compared to F_S, averaging 1.43 ± 0.38, 2.21 ± 0.23, and 2.58 ± 0.66 g C m^{-2} yr^{-1} for forest, abandoned agricultural field and olive grove, respectively. The annual change in C in mineral soil (ΔC_S) associated to the recovery of the abandoned agricultural field averaged 14.6 g C m^{-2} yr^{-1}. Annual increases in coarse and fine roots (ΔC_R) were two-fold higher in the abandoned agricultural field than in open forest and olive grove. Greater litter accumulation rates (ΔC_L) occurred in the open forest (73.2 ± 4.1 g C m^{-2} yr^{-1}) and abandoned agricultural field (49.5 ± 5 g C m^{-2} yr^{-1}) than in the olive grove (12 ± 4.1 g C m^{-2} yr^{-1}), because of greater litterfall inputs and lower decomposition rates.

2.3.3. Total belowground carbon allocation

Using both TBCA approaches, we found that the open forest and abandoned agricultural field allocated much more C belowground annually than the olive grove (Table 2.2). We quantified the effect of changes in the C stored in soil, litter layer, and roots ($\Delta[C_S + C_R + C_L]/\Delta t$ in Eqn. 3) on TBCA by comparing TBCA estimated with the full model (Eqn. 3) with the TBCA estimated assuming zero change in C storage (Eqn. 1). Assuming that $\Delta[C_S + C_R + C_L]/\Delta t = 0$, estimates of TBCA were 17.5% lower than estimates calculated from the full model (Eqn. 3). The abandoned agricultural field had the largest bias (- 23.5%), followed by forest (- 16.1%) and olive grove (- 12.8%). Annual increases in roots were responsible for most of the increase in C storage in abandoned agricultural field and olive grove. Including only estimates of root biomass in the calculation of TBCA (that is, assuming that $\Delta[C_S + C_L]/\Delta t = 0$ and TBCA $= F_S + F_E - F_A + \Delta C_R/\Delta t$) reduced the bias in TBCA to an average underestimation of 8.7 and 2.6% in abandoned agricultural field and olive grove, respectively. However, annual increases in litter layer C mass were responsible for most of the increase in C storage in the open forest, reducing the bias in TBCA to an average 6.5 % underestimate.

Table 2.2. Annual carbon fluxes (g C m^{-2}) and total belowground carbon allocation within each land use.

	Open forest	Abandoned field	Olive grove
Annual C from soil-surface respiration (F_S)	766 ± 64.2	648 ± 64.3	427 ± 30.3
Annual litterfall C (F_A)	128.4 ± 9.3	88.4 ± 11.4	26 ± 9.31
Annual C loss by soil and water erosion (F_E)	1.43 ± 0.38	2.21 ± 0.23	2.58 ± 0.66
Annual change in soil C (ΔC_S)	*	14.6	*
Annual change in litter layer C (ΔC_L)	73.2 ± 4.1	49.5 ± 5	12 ± 4.1
Annual change in coarse and fine root C (ΔC_R)	50.3 ± 8.7	106 ± 12.2	44.8 ± 14.7
TBCA calculated as F_S - F_A	649.8 ± 21.9	559.4 ± 26.7	401.8 ± 21.7
TBCA including C exported from the site (F_E)	651.3 ± 22.2	561.6 ± 26.9	404.4 ± 22.3
TBCA (F_S - F_A + F_E + ΔC_S + ΔC_L + ΔC_R)	774.8 ± 35	731.8 ± 44.1	461.2 ± 41.1
TBCA (F_S - F_A + F_E + ΔC_S)	651.3 ± 22.2	576.2 ± 26.9	404.4 ± 22.3
TBCA (F_S - F_A + F_E + ΔC_L)	724.4 ± 26.3	611.1 ± 31.9	416.4 ± 26.4
TBCA (F_S - F_A + F_E + ΔC_R)	701.6 ± 30.9	667.7 ± 39.1	449.3 ± 37
Aboveground Net Primary Productivity (ANPP)	260.4 ± 20.5	174.9 ± 28.9	93.7 ± 11.4
Belowground Net Primary Productivity (BNPP)	387.4 ± 17.5	365.9 ± 22	230.6 ± 20.5
ANPP: BNPP	0.67	0.47	0.40
Aboveground production: biomass (ANPP: AGB)	0.08	0.49	0.11
Coarse and fine root production: biomass (ΔC_R: BGB)	0.16	0.42	0.27

* Negligible.
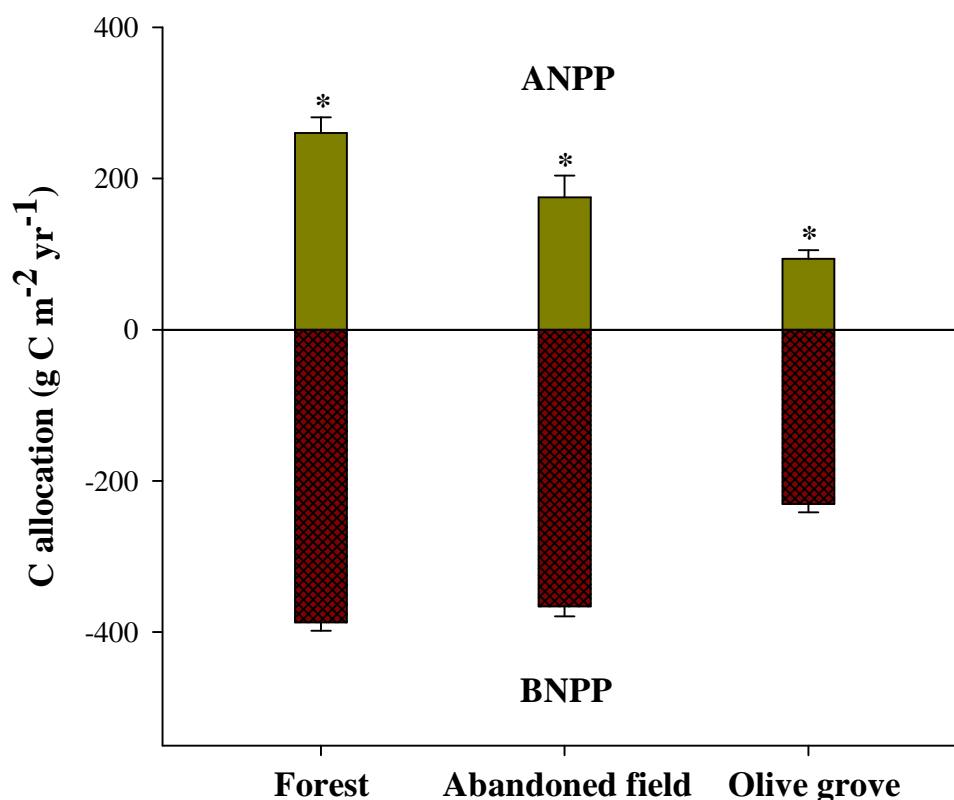
Figure 2.8. Net primary production and C allocation patterns within each land use. Within each land use type, asterisk symbols indicate significant differences between aboveground and belowground net primary production (*$P < 0.05$).

2.3.4. Net primary productivity and carbon allocation patterns within each land use

Annual aboveground net primary productivity (ANPP-C) calculated during two years of measurements averaged 260.4 ± 20.5, 174.9 ± 28.9 and 93.7 ± 11.4 g C m^{-2} yr^{-1} for forest, abandoned agricultural field and olive grove, respectively. Annual belowground net primary productivity (BNPP-C) estimated from TBCA values averaged 387.4 ± 11, 365.9 ± 13.4 and 230.6 ± 10.9 g C m^{-2} yr^{-1} for forest, abandoned agricultural field and olive grove, respectively (Fig. 2.8). Therefore, annual net primary productivity (ANPP-C plus BNPP-C) was 648 ± 31.5, 541 ± 42.3 and 324 ± 22.3 g C m^{-2} yr^{-1} for forest, abandoned agricultural field and olive grove, respectively. Across land uses, more than 60 % of the C was allocated belowground (Fig.2.8). The abandoned agricultural field was more productive than forest and olive grove, as shown by the higher *annual production: biomass* relationships in both aboveground and belowground C components (Table 2.2).

2.4. Discussion

2.4.1. Carbon pools and allocation patterns

Carbon pools in the mineral soil (0-15 cm), aboveground and belowground (0-15 cm) biomass in all three land uses (Table 2.1) fell within the range of values reported for similar Mediterranean land use types (Álvarez et al., 2007; Beier et al., 2009; Boix-Fayos et al., 2009; Grünzweig et al., 2003; 2007; Peñuelas et al., 2007). Across land uses, approximately one-third of the whole ecosystem C was stored belowground, which is consistent with the observed C allocation patterns within each land use type (Fig. 2.8). In water-limited ecosystems, more than 50 % of the C is allocated belowground (Grünzweig et al., 2007; Jackson et al., 2002; Nosetto et al., 2006; Vargas et al., 2008; this chapter), highlighting the importance of including total belowground C accumulation to estimate net primary productivity in these Mediterranean ecosystems.

The root: shoot ratio found for the abandoned agricultural field (Table 2.1) fell within the range reported for different forests and woodlands around the world (reviewed by Mokany et al., 2006). However, our root: shoot ratios for both forest and olive grove were extremely low. Although the core method has been widely used to estimate root biomass, permitting comparisons with existing data, there are some methodological difficulties associated with measuring root biomass by this method (Mokany et al., 2006; Vogt et al., 1996). In our study, the sampling depth (0-15 cm) and the failure to sample the root crown and coarse structural roots of woody plants likely led to an underestimated root biomass, and hence provided lower root: shoot ratios, especially in the forest and olive grove. However, although our estimations of belowground biomass and production may be somewhat underestimated for all land uses, and therefore net primary productivity at the ecosystem scale, we do not expect these root production underestimations to have strongly biased the TBCA values in this Mediterranean ecosystem for the following reasons. First, because of root distribution decreases exponentially with soil depth, greatest root biomass concentrations have been found near the surface across different ecosystems around the world (Jackson et al., 1996). Between 50 and 90% of roots were found in the first 10 or 20 cm of the soil in different Mediterranean woodlands and shrublands or Aleppo pine stands (Ares and Peinemann, 1992; Kummerow et al., 1977; Kummerow et al., 1981; Rambal and Leuterne, 1987; Rey et al., 2002; Schenk and Jackson, 2002; Silva and Rego, 2003).

Second, our experimental area is located on relatively shallow soils with an underlying limestone crust at 17-19 cm depth (Alías et al., 1987; Martínez-Mena et al., 2008). Although roots can penetrate through cracks in the underlying petrocalcic horizon (caliche layer) to reduce the effects of summer drought by absorbing water from deeper soil layer (Kummerow et al., 1990; Vargas et al., 2008), greatest root biomass was concentrated in the first 17-19 cm of the soil of all land uses. Given the nature of our soils and the distribution of roots with depth found by several authors in similar ecosystems, we expect our estimates of belowground biomass and production to be robust.

Overall, annual net productivity values provided by this study combining both TBCA (full model; Eqn. 3) and biomass-inventory approaches were in reasonable agreement with the estimates for other Mediterranean ecosystems provided by several studies using the eddy-covariance approach (Allard et al., 2008; Falge et al., 2002; Pereira et al., 2007; Valentini et al., 2000).

2.4.2. Components of the TBCA budget

Soil-surface CO_2 efflux in the study area (F_S) was the largest component in the TBCA approach (more than 93% across land uses). Several authors have highlighted the importance of soil respiration as the major flux in the TBCA of different ecosystems around the world (Giardina and Ryan, 2002; Kaye et al., 2005; Litton et al., 2003; McDowell et al., 2001). However, it is difficult to completely understand the soil respiration component since measurement of this parameter would involve both autotrophic root and mycorrhizae respiration (R_A) and heterotrophic respiration (R_H) stemming from SOM and root exudate decomposition by soil microorganisms and fungi (Hanson et al., 2000; Kuzyakov & Cheng, 2001, 2004). Root respiration has been suggested to account for at least 50 % of total soil respiration in many ecosystems (Haynes and Gower, 1995; Högberg et al., 2001; Keith et al., 1997; Misson et al., 2006). However, in low-productivity ecosystems, the relative contribution of roots to soil respiration decreases (reviewed by Hanson et al., 2000; Subke et al., 2006; Unger et al., 2009), because less C is allocated to the roots, which results in lower autotrophic respiration fluxes. Several studies have noted the importance of heterotrophic respiration as a major component of soil respiration in Mediterranean ecosystems, where it may account for up to 59% (Tang and Baldocchi, 2005), 67% (Beier et al., 2009), 77% (Rey et al., 2002), 85% (Unger et al., 2009) or 88% (Tedeschi et al., 2006) of the total soil respiration flux.

However, we could not quantify the contribution of R_H and R_A to soil respiration in this study, and therefore we cannot determine whether soil respiration along this land use intensification gradient was driven by root respiration and exudation or soil organic matter and root exudate decomposition.

Annual C losses by water erosion were negligible compared to F_S (less than 1% across land uses) and had little influence on the estimates of TBCA. When estimates of C losses by erosion were included in the calculation of TBCA, the TBCA values were 0.22% (in open forest), 0.39% (in abandoned agricultural field), and 0.64% (in olive grove) higher than when assuming $F_E=0$ (that is, assuming that TBCA = F_S - F_A + $\Delta[C_S + C_R + C_L]/\Delta t$). These results agree with the results of several authors who have suggested soil erosion plays an insignificant role in the annual carbon balance across different ecosystems (Forrester et al., 2006; Giardina and Ryan, 2002; Litton et al., 2004). But none of these studies assessed the effect of soil erosion on the carbon balance by direct estimations. Rates of soil C mobilized by water erosion for all land uses fell within the lower range of those directly quantified for similar Mediterranean ecosystems at the catchment scale (7 g C m^{-2} yr^{-1}; Smith et al., 2005; from 2 to 21.8 g C m^{-2} yr^{-1}; Albergel et al., 2006; from 0.4 to 19.9 g C m^{-2} yr^{-1}; average, 6 g C m^{-2} yr^{-1}, Boix-Fayos et al., 2009). Using the water erosion rates (F_E) of those subcatchments with a similar land use type reported by Boix-Fayos et al. (2009) at our site would increase TBCA by 0.3, 0.4 and 5% in forest, abandoned agricultural field and olive grove, respectively. Our low F_E rates would be explained because of the fact that few high-intensity rainfall events (maximum intensity in 30 min of more than 15 mm h^{-1}; Martínez-Mena et al., 2001) occurred in the experimental area over the three-year study period. However, in a previous study we observed higher water erosion rates, and how only two events were the main contributors to the total C export in the experimental area over 15 months (Martínez-Mena et al., 2008). The role of water erosion in the carbon balance needs to be assessed over long time periods (Quinton et al., 2010; Trumbore, 2006). Furthermore, soil transport and deposition by water erosion may influence litter decomposition dynamics. Besides facilitate decomposer colonization, soil transport processes may cause fragmentation or abrasion to litter, increasing the surface area available for microbial attack (Throop and Archer, 2007; 2008). In contrast, soil deposition on litter (or the burial of litter) might block solar radiation, diminishing decomposition by photodegradation, an important driver in aboveground litter decomposition in semi-arid ecosystems (Austin and Vivanco, 2006). The net effect of soil

transport on litter decomposition dynamics will need to be clarified before we can fully understand the role of water erosion in the organic C balance in Mediterranean ecosystems.

The annual litterfall and decomposition rates estimated were comparable to values reported for other Mediterranean shrublands, Aleppo pine forests and agroecosystems (García Plé et al., 1995; García-Pausas et al., 2004; Rodríguez Pleguezuelo et al., 2009). Across land uses, lower litterfall inputs and higher litter decomposition rates were observed in olive grove than in open forest or abandoned agricultural field. Besides the biological and physical processes discussed above, litter quality also plays a critical role in litter decomposition dynamics. When subsamples of each litter type were analysed for % C and % N across seasons, significantly lower C:N ratios were observed in olive litter type (26.41 ± 0.98) than in pine (67.00 ± 0.71) or rosemary (35.00 ± 0.71) litter types (F= 744.85; P<0.0001). Smaller C:N ratios are indicative of a more easily decomposable substrate, which explains the higher aboveground litter decomposition rates measured in the olive grove despite lower microbial biomass in this site (see Table 3.2 in Chapter 3). In contrast, the recalcitrant pool of *P. halepensis* needles has been estimated to be 60% (Rovira and Vallejo, 2002), which limits decomposition and enhances the accumulation of a relatively high amount of recalcitrant SOM. Hence, higher litter accumulated C: decomposed C were observed in open forest (1.32) and abandoned agricultural field (1.27) than in olive grove (0.85).

Annual changes in C stored in the soil, litter layer and coarse and fine roots were slight in comparison with F_S (16.1, 26.2 and 13.3 % for forest, abandoned agricultural field and olive grove, respectively), but had a notable influence on the estimates of TBCA (an average difference of 17.5 % between the models across land uses). However, the major contributors to changes in soil C storage differed between land uses. Whereas annual increases in roots (ΔC_R) accounted for most of the increase in C storage in abandoned agricultural field and olive grove sites, annual increases in litter layer C mass (ΔC_L) were responsible for most of the increase in C storage in the forest site.

When our TBCA estimates were converted to production estimates according to assumptions previously made that belowground NPP is about 50% of TBCA (Table 2), we observed that the coarse and fine root production (ΔC_R) estimates only accounted for 12% (open forest), 29% (abandoned agricultural field) and 19% (olive grove) of the total BNPP. Besides coarse and fine root production, BNPP refers to root exudation, mortality, and losses to detritivores, and mycorrhizal growth (Litton and Giardina, 2008). Root exudates and mycorrhizae probably represent a large portion of BNPP in most ecosystems (Giardina

et al., 2004; Hobbie, 2006). Unfortunately, neither mycorrhizal production nor exudation was included in this study, the inclusion of which might have improved our estimates of ΔC_R and ΔC_R: BNPP.

2.5. Conclusions

Despite annual inputs of 903.2 ± 44.3 (open forest), 820.2 ± 55.5 (abandoned agricultural field) and 487.2 ± 50.4 (olive grove) g C m^2 yr^{-1} as F_A and TBCA, alterations in total C stored (litter, mineral soil and roots) were 16, 23 and 12 % of TBCA for forest, abandoned agricultural field and olive grove, respectively, suggesting that a large proportion of TBCA returned to the atmosphere through soil respiration, especially in the olive grove.

Since estimating BNPP is labour intensive and methodologically complicated, especially in soils with an underlying petrocalcic horizon, the TBCA approach described might be considered a more straightforward method for estimating belowground C sequestration in such ecosystems. However, an assumption that $\Delta[C_S + C_R + C_L]/\Delta t = 0$ will underestimate TBCA in our sites, particularly in the abandoned agricultural field, where storage may be increasing more rapidly. Therefore, the use of the steady-state model is unsuited to these Mediterranean ecosystems and the full model is recommended.

Likewise, water erosion should not be overlooked when estimating TBCA in these Mediterranean ecosystems. Besides including measurements of C mobilized by erosion over long time periods, the role of water erosion in the organic C balance in these Mediterranean ecosystems will not be properly understood until specific studies relating soil transport to decomposition dynamics are carried out.

Future studies of belowground C cycling should involve the direct measurement of mycorrhizal production and exudation.

References

Alberger, J., Mansouri, T., Zante, P., Mamou, B., Abdeljaoued, S., 2006. Organic carbon in the sediments of hill dams in a semiarid Mediterranean area. In: Roose, E.J., Lal, R., Feller, C., Barthes, B., Stewart, B.A. (Eds.), Soil Erosion and Carbon Dynamics. Advances in Soil Science, Taylor and Francis, Boca Raton, FL.

Alías, L.J., Ortíz, R., Martínez, J., Alcaraz, F., López, B., 1987. Proyecto LUCDEME. Mapa de suelos E 1:100000. Cehegín-911. Ministerio de Agricultura, Pesca y Alimentación, España.

Allard, V., Ourcival, J.M., Rambal, S., Joffre, R., Rocheteau, A., 2008. Seasonal and annual variation of carbon exchange in an evergreen Mediterranean forest in southern France. Global Change Biology 14, 714-725.

Álvarez, S., Soriano, M.A., Landa, B.B., Gómez, J.A., 2007. Soil properties in organic olive groves compared with that in natural areas in a mountainous landscape in southern Spain. Soil Use and Management 23, 404-416.

Ares, A., Peinemann, N., 1992. Fine-root distribution of coniferous plantations in relation to site in southern Buenos Aires, Argentina. Canadian Journal of Forest Research 22, 1575-1582.

Asner, G.P., Archer, S., Hughes, R.F., Ansley, R.J., Wessman, C.A., 2003. Net changes in regional woody vegetation cover and carbon storage in Texas Dryland 1937-1999. Global Change Biology 9, 316-335.

Austin, A.T., Vivanco, L., 2006. Plant litter decomposition in a semiarid ecosystem controlled by photodegradation. Nature 442, 555-558.

Baeza, M.J., Raventós, J., Escarré, A., Vallejo, V.R., 2006. Fire risk and vegetation structural dynamics in Mediterranean shrubland. Plant Ecology 187 (2), 189-201.

Baeza MJ, Santana VM, Pausas JG, Vallejo VR (2011) Successional trends in standing dead biomass in Mediterranean basin species. Journal of Vegetation Science 22(3): 467-474.

Beier, C., Emmett, B.A., Tietema, A., Schmidt, I.K., Peñuelas, J., Láng, E.K., Duce, P., De Angelis, P., Gorissen, A, 2009. Carbon and nitrogen balances for six shrublands across Europe. Global Biogeochemical Cycles 23, GB4008, doi: 10.1029/2008GB003381.

Binkley, D., Ryan, M.G., 1998. Net primary production and nutrient cycling in replicated stands of *Eucalyptus saligna* and *Albizia falcataria*. Forest Ecology and Management 112, 79-85.

Boix-Fayos, C., de Vente., J., Albaladejo, J., Martínez-Mena, M., 2009. Soil carbon erosion and stock as affected by land use changes at the catchment scale in Mediterranean ecosystems. Agriculture, Ecosystems and Environment 133, 75-85.

Burke, I.C., Lauenroth, W.K., Coffin, D.P., 1995. Soil organic matter recovery in semiarid grasslands: implications for the conservation reserve program. Ecological Applications 5(3), 793-801.

Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperature mixed hardwood forest. Global Change Biology 4, 217-227.

Davidson, E.A., Savage, K., Bolstad, P., Clark, D.A., Curtis, P.S., Ellsworth, D.S., Hanson, P.J., Law, B.E., Luo, Y., Pregitzer, K.S., Randolph, J.C., Zak, D., 2002. Belowground carbon allocation in forests estimated from litterfall and IRGA-based soil respiration measurements. Agricultural and Forest Meteorology 113, 39-51.

Domingo, F., Villagarcía, L., Brenner, A.J., Puigdefábregas, J., 1999. Evapotranspiration model for semi-arid shrub-lands tested against data from SE Spain. Agricultural and Forest Meteorology 95, 67-84.

Edwards, N.T., Harris, W.F., 1977. Carbon cycling in a mixed deciduous forest floor. Ecology 58, 431-437.

Fabião, A., 1985. Growth dynamics of superficial roots in Portuguese plantations of *Eucalyptus globulus* Labill. Studied with a mesh bag technique. Plant and Soil 83, 233-242.

Falge, E., Baldocchi, D., Tenhunen, J., Aubinet, M., Bakwin, P., Berbigier, P., Bernhofer, C., Burba, G., Clement, R., Davis, K.J., Elbers, J.A., Goldstein, A.H., Grelle, A., Granier, A., Guðmundsson, J., Hollinger, D., Kowalski, A.S., Katul, G., Law, B.E., Malhi, Y., Meyers, T., Monson, R.K., Munger, J.W., Oechel, W., Tha Paw, K., Pilegaard, K., Rannik, U., Rebmann, C., Suyker, A., Valentini, R., Wilson, K., Wofsy, S., 2002. Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. Agricultural and Forest Meteorology 113, 53–74.

Forrester, D.I., Bauhus, J., Cowie, A.L., 2006. Carbon allocation in mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. Forest Ecology and Management 233, 275-284.

García-Pausas, J., Casals, P., Romanyà, J., 2004. Litter decomposition and faunal activity in Mediterranean forest soils: effects of N content and the moss layer. Soil Biology and Biochemistry 36, 989-997.

García-Plé, C., Vanrell, P., Morey, M., 1995. Litter fall and decomposition in a *Pinus halepensis* forest on Mallorca. Journal of Vegetation Science 6, 17-22.

Giardina, C.P., Coleman, M.D., Hancock, J.E., King, J.S., Lilleskov, E.A., Loya, W.M., Pregitzer, K.S., Ryan, M.G., Trettin, C.C., 2005. The response of belowground carbon allocation in forests to global change. In: Binkley, D., Menyailo, O. (Eds.), Tree species effects on soils: implications for global change, NATO Science Series, Kluwer Academic Publishers, Dordrecht, pp. 119-154.

Giardina, C.P., Binkley, D., Ryan, M.G., Fownes, J.H., Senock, R.S., 2004. Belowground carbon cycling in a humid tropical forest decreases with fertilization. Oecologia 139, 545-550.

Giardina, C.P., Ryan, M.G., 2002. Total belowground carbon allocation in a fast-growing *Eucalyptus* plantation estimated using a carbon balance approach. Ecosystems 5, 487-499.

Giardina, C.P., Ryan, M.G., Binkley, D., Fownes, J.H., 2003. Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest. Global Change Biology 9, 1438-1450.

Giorgi, F., 2006. Climate change hot-spots. Geophysical Research Letters 33, L08707.

Gower, S.T., Songracic, S., Landsberg, J.J., 1996. A global trend in belowground carbon allocation: can we use the relationship at smaller scales. Ecology 77, 1750-1755.

Grünzweig, J.M., Lin, T., Rotenberg, E., Schwartz, A., Yakir, D., 2003. Carbon sequestration in arid-land forest. Global Change Biology 9, 791-799.

Grünzweig, J.M., Gelfand, I., Fried, Y., Yakir, D., 2007. Biogeochemical factors contributing to enhanced carbon storage following afforestation of semi-arid shrubland. Biogeosciences 4, 891-904.

Hanson, P.J., Edwards, N.T., Garten, C.T., Andrews, J.A., 2000. Separating root and soil microbial contributions to soil respiration: A review of methods and observations. Biogeochemistry 48, 115-146.

Haynes, B.E., Gower, S.T., 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. Tree Physiology 15, 317-325.

Hobbie, E.A., 2006. Carbon allocation to ectomycorrhizal fungi correlates with belowground allocation in culture studies. Ecology 87, 563-569.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A.F., Ekblad, A., Högberg, M.N., Nyberg, G., Ottosson-Löfvenius, M., Read, D.J., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411, 789-792.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108, 389-411.

Jackson, R.B., Banner, J.L., Jobbágy, E.G., Pockman, W.T., Wall, D.H., 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418, 623-626.

Johnson, F.L., Risser, P.G., 1974. Biomass, annual net primary production, and dynamics of six mineral elements in a post oak-blackjack oak forest. Ecology 55, 1246-1258.

Kaye, J.P., McCulley, R.L., Burke, C., 2005. Carbon fluxes, nitrogen cycling, and soil microbial communities adjacent urban, native and agricultural ecosystems. Global Change Biology 11, 575-587.

Keith, H., Raison, R.J., Jacobsen, K.L., 1997. Allocation of carbon in a mature eucalypt forest and some effects of soil phosphorus availability. Plant and Soil 196, 81-99.

Kummerow, J., Krause, D., Jow, W., 1977. Root system of chaparral shrubs. Oecologia 29, 163-177.

Kummerow, J., Kummerow, M., Trabaud, L., 1990. Root biomass, root distribution and the fine-root growth dynamics of *Quercus coccifera* L. in the garrigue of southern France. Vegetatio 87, 37-44.

Kummerow, J., Montenegro, G., Krause, D., 1981. Biomass, phenology and growth. In: Miller, P. (Ed.), Resource use by chaparral and matorral, Springer-Verlag, Berlin, 1981, pp. 69-96.

Kuzyakov, Y., Cheng, W., 2001. Photosynthesis controls of rhizosphere respiration and organic matter decomposition. Soil Biology and Biochemistry 33, 1915-1925.

Kuzyakov, Y., Cheng, W., 2004. Photosynthesis controls of CO_2 efflux from maize Rhizosphere. Plant and Soil 263, 85-99.

Lal, R., 2008. Soil carbon stocks under present and future climate with specific reference to European ecoregions. Nutr. Cycl. Agroecosyst. 81, 113-127.

Law, B.E., Ryan, M.G., Anthoni, P.M., 1999. Seasonal and annual respiration of a ponderosa pine ecosystem. Global Change Biology 5, 169-182.

Litton, C.M., Giardina, C.P., 2008. Below-ground carbon flux and portioning: global patterns and response to temperature. Functional Ecology 22, 941-954.

Litton, C.M., Ryan, M.G., Knight, D.H., Stahl, P.D., 2003. Soil-surface CO_2 efflux and microbial biomass in relation to tree density 13 years after a stand replacing fire in a lodgepole pine ecosystem. Global Change Biology 9 (5), 680-696.

Litton, C.M., Ryan, M.G., Knight, D.H., 2004. Effects of tree density and stand age on carbon allocation patterns in postfire lodgepole pine. Ecological Applications 14 (2), 460-475.

Martínez-Mena, M., Castillo, V., Albaladejo, J., 2001. Hydrological and erosional response to natural rainfall in a degraded semi-arid area of Southeast Spain. Hydrological Processes 15, 557-571.

Martínez-Mena, M., López, J., Almagro, M., Boix-Fayos, C., Albaladejo, J., 2008. Effect of water erosion and cultivation on the soil carbon stock in a semiarid area of South-East Spain. Soil and Tillage Research 99, 119-129.

McCulley, R.L., Burke, I.C., Nelson, J.A., Lauenroth, W.K., Knapp, A.K., Kelly, E.F., 2005. Regional patterns in carbon cycling across the Great Plains of North America. Ecosystems 8, 106-121.

McDowell, N.G., Balster, N.J., Marshall, J.D., 2001. Belowground carbon allocation of Rocky Mountain Douglas-fir. Canadian Journal of Forest Research 31, 1425-1436.

Mielnick P.C., Dugas, W.A., 2000. Soil CO_2 efflux in a tallgrass prairie. Soil Biology and Biochemistry 32 (2), 221-228.

Misson, L., Gershenson, A., Tang, J., McKay, M., Cheng, W., Golstein, A., 2006. Influences of canopy photosynthesis and summer rain pulses on root dynamics and soil respiration in a young ponderosa pine forest. Tree Physiology 26, 833-844.

Mokany, K., Raison, R.J., Prokushkin, A.S., 2006. A critical analysis of root: shoot ratios in terrestrial biomes. Global Change Biology 12, 84-96.

Nadelhoffer, K.J., Raich, J.W., Aber, J.D., 1998. A global trend in belowground carbon allocation: comment. Ecology 79(5), 1822-1825.

Newman, G.S., Arthur, M.A., Muller, R.N., 2006. Above- and belowground net primary production in a temperate mixed deciduous forest. Ecosystems 9, 317-329.

Nosseto, M.D., Jobbágy, E.G., Paruelo, J.M., 2006. Carbon sequestration in semi-arid rangelands: Comparison of *Pinus ponderosa* plantations and grazing exclusion in NW Patagonia. Journal of Arid Environments 67, 142-156.

Oliveira, M.R.G., van Noordwijk, M., Gaze, S.R., Brouwer, G., Bona, S., Mosca, G., Hairiah, K., 2000. Auger sampling, ingrowth cores and pinboard methods. In: Smith, A.L., Bengough, A.G., Engels, C., van Noordwijk, M., Pellerin, S., van de Geijn, C.S. (Eds.), Roots methods. A Hanbook. Springer-Verlag, Berlin, Heidelberg, Germany, 175-210 pp.

Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44, 322-331.

Peñuelas, J., Prieto, P., Beier, C., Cesaraccio, C., De Angelis, P., De Datos, G., Emmett, B.A., Estiarte, M., Garadnai, J., Gorissen, A., Kovács, E., György, K.D., Llorens, L., Pellizzaro, G., Riis-Nielsen, T., Schmidt, I.K., Sirca, C., Sowerby, A., Spano, D., Tietema, A., 2007. Response of plant species richness and primary productivity in shrublands along a north-south gradient in Europe to seven years of experimental warming and drought: reductions in primary productivity in the heat and drought year of 2003. Global Change Biology 13, 2563-2581,

Pereira, J.S., Mateus, J.A., Aires, L.M., Pita, G., Pio, C., David, J.S., Andrade, V., Banza, J., David, T.S., Paço, T.A., Rodrigues, A., 2007. Net ecosystem carbon exchange in three contrasting Mediterranean ecosystems- the effect of drought. Biogeosciences 4, 791-802.

Quinton, J.N., Govers, G., Van Oost, K., Bardgett, R.D., 2010. The impact of agricultural soil erosion on biogeochemical cycling. Nature Geoscience 3, 311-313.

Raich, J.W., 1983. Effects of forest conversion on the carbon budget of a tropical soil. Biotropica 15, 177-184.

Raich, J.W., Nadelhoffer, K.J., 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology 70 (5), 1346-1354.

Rambal, S., Leuterne J., 1987. Changes in aboveground structure and resistances to water uptake in *Quercus coccifera* along a rainfall gradient. In: Tehnunen, J.D. (Ed.), Plant response to stress, Springer-Verlag, Berlin, 191-200, pp.

Rey, A., Pegoraro, E., Tedeschi, V., De Parri, I., Jarvis, P.G., Valentini, R., 2002. Annual variation in soil respiration and its components in a coppice oak forest in Central Ital. Global Change Biology 8, 851- 866.

Rodríguez-Pleguezuelo, C.R., Durán Zuazo, V.H., Muriel Fernández, J.L., Martín Peinado, F.J., Franco Tarifa, D., 2009. Litter decomposition and nitrogen release in a sloping Mediterranean subtropical agroecosystem on the coast of Granada (SE, Spain): Effects of floristic and topographic alteration on the slope. Agriculture, Ecosystems and Environment 134, 79-88.

Rovira, P., Vallejo, V.R., 2002. Labile and recalcitrant pools of carbon and nitrogen in organic matter decomposing at different depths in soil: an acid hydrolysis approach. Geoderma 107, 109-141.

Ryan, M.G., 1991. A simple method for estimating gross carbon budgets for vegetation in forest ecosystems. Tree Physiology 9, 255-266.

Ryan, M.G., Lavigne, M.B., Gower, S.T., 1997. Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. Journal of Geophysical Research 102 (D24), 28871-84.

Ryan, M.G., Linder, S., Vose, J.M., Hubbard, R.M., 1994. Dark respiration in pines, in: Gholz, H.L., Linder, S., McMurtie, R.E. (Eds.), Ecological Buletin 43, Environmental constraints on the structure and productivity of pine forest ecosystems: a comparative analysis. Uppsala, Sweden, Munksgaard, 50-63 pp.

Saiz, G, Green, C., Butterbach-Bahl, K., Kiese, R., Avitabile, V., Farrel, E.P., 2006. Seasonal and spatial variability of soil respiration in four Sitka spruce stands. Plant Soil 287 (1-2), 161-176.

Schenk, J.H., Jackson, R.B., 2002. The global biogeography of roots. Ecological Monographs, 72(3), 311-328.

Schlesinger, W.H., 1977. Carbon balance in terrestrial detritus. Annual Review of Ecology and Systematics 8, 51-81.

Schlesinger, W.H., 1984. Soil organic matter: a source of atmospheric CO_2, in: Woodwell, G.M. (Ed.), The role of terrestrial vegetation in the global carbon cycle: measurement by remote sensing. John Wiley & Sons, Chichester, England, 111-127 pp.

Silva, J.S., Rego, F.C., 2003. Root distribution of a Mediterranean shrubland in Portugal. Plant and Soil 255, 529-540.

Smith, S.D., Huxman, T.E., Zitzer, S.F., Charlet, T.N., Housman, D.C., Coleman, J.S., Fenstermakerk, L.K., Seemann, J.R., Nowak, R.S., 2000. Elevated CO_2 increases productivity and invasive species success in an arid ecosystem. Nature 408, 79-82.

Smith, S.V., Bullock, S.H., Hinojosa-Corona, A., Franco-Vizcaíno, E., Escoto-Rodriguez, M., Kretzschmar, T.G., Farfán, L.M., Salazar-Ceseña, J.M., 2007. Soil erosion and significance for carbon fluxes in a mountainous mediterranean-climate watershed. Ecological Applications 17 (5), 1379-1387.

Smith, S.V., Sleezer, R.O., Renwick, W.H., Buddemeier, R., 2005. Fates of eroded soil organic carbon: Mississippi basin case study. Ecological Applications 15, 1929-1940.

Snedecor, G.W., Cochran, W.G., 1967. Statistical methods. Iowa state University Press, Ames, Iowa. USA, pp. 274.

Subke, J.A., Inglima, I., Cotrufo, M.F., 2006. Trends and methodological impacts in soil CO_2 efflux partitioning: a metaanalytical review. Global Change Biology 12, 921–943.

Tang, J., Baldocchi, D.D., 2005. Spatial-temporal variation in soil respiration in an oak-grass savanna ecosystem in California and its partitioning into autotrophic and heterotrophic components. Biogeochemistry 73, 183-207.

Tedeschi, V., Rey, A., Manca, G., Valentini, R., Jarvis, P.G., Borghetti, M., 2006. Soil respiration in a Mediterranean oak forest at different developmental stages after coppicing. Global Change Biology 12, 110-121.

Throop, H.L., Archer, S.R., 2007. Interrelationships among shrub encroachment, land management, and litter decomposition in a semidesert grassland. Ecological Applications 17 (6), 1809-1823.

Throop, H.L., Archer, S.R., 2008. Resolving the dryland decomposition conundrum: Some new perspectives on potential drivers. In: Lüttge, U., Beyschlag, W., Büdel, B., Francis, D. (Eds.), Progress in Botany 70. Springer-Verlag Berlin Heidelberg.

Trumbore, S., 2006. Carbon respired by terrestrial ecosystems – recent progress and challenges. Global Change Biology 12, 141-153.

Unger, S., Máguas, C., Pereira, J.S., Aires, L.M., David, T.S., Werner, C., 2009. Partitioning carbon fluxes in a Mediterranean oak forest to disentangle changes in ecosystem sink strength during drought. Agricultural and Forest Meteorology 149 (6-7), 949-961.

Valentini, R., Matteucci, G.R., Dolman, A.J., Schulze, E.D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404, 861-863.

Vargas, R., Allen, M.F., Allen, E.B., 2008. Biomass and carbon accumulation in a fire chronosequence of a seasonally dry tropical forest. Global Change Biology 14 (1), 109-124.

Villalobos, F.J., Testi, L., Hidalgo, J., Pastor, M., Orgaz, F., 2006. Modelling potential growth and yield of olive (*Olea europaea* L.) canopies. European Journal of Agronomy 24, 296-303.

Vogt, K.A., Vogt, D.J., Bloomfield, J., 1998. Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. Plant and Soil 200, 71-89.

Vogt, K.A., Vogt, D.J., Palmiotto, P.A., Boon, P., O´Hara, J., Asbjornsen, H., 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant and Soil 187 (2), 159-219.

Wang, W.J., Zu, Y.G., Wang, H.M., Hirano, T., Takagi, K., Sasa, K., Koike, T., 2005. Effect of collar insertion on soil respiration in a larch forest measured with a LI-6400 soil CO_2 flux system. Journal of Forest Research 10, 57–60.

Xu, M., Qi, Y, 2001. Spatial and seasonal variation of Q_{10} determined by soil respiration measurements at a Sierra Nevada Forest. Global Biogeochemistry Cycles 15, 687-696.

3. Factors controlling temporal variations of soil respiration

Abstract

Extensive research has focused on the temperature sensitivity of soil respiration. However, in dry Mediterranean ecosystems, soil respiration may have a pulsed response to precipitation events, especially during prolonged dry periods. Here, we investigate temporal variations in soil respiration (R_s), soil temperature (T) and soil water content (SWC) under three different land uses (a forest area, an abandoned agricultural field and a rain-fed olive grove) in a dry Mediterranean area of southeast Spain, and evaluate the relative importance of soil temperature and water availability as predictors of R_s. We hypothesize that soil moisture availability, rather than soil temperature, becomes the major factor controlling CO_2 efflux rates in this dry Mediterranean ecosystem during the summer dry season. Soil CO_2 efflux was measured monthly between January 2006 and December 2007 using a portable soil respiration gauge fitted with a soil respiration chamber (LI-6400- 09). Mean annual beneath canopy soil respiration rates were 2.35 $\pm$ 0.04, 1.87 $\pm$ 0.04, and 2.18 $\pm$ 0.04 μmol m^{-2} s^{-1} in the forest, abandoned field and olive grove, respectively. R_s was largely controlled by soil temperature above a soil water content threshold value of 10 % at 0-15 cm depth for forest and olive grove, and 15 % for abandoned field. However, below those thresholds R_s was controlled by soil moisture. Exponential and linear models adequately described R_s responses to environmental variables during the growing and dry seasons. Models combining abiotic (soil temperature and soil rewetting index) and biotic factors (aboveground biomass index and/or distance from the nearest tree) explained between 39 and 73% of the temporal variability of R_s in the forest and olive grove. However, in the abandoned field, a single variable – either soil temperature (growing season) or rewetting index (dry season) – was sufficient to explain between 51 and 63% of the soil CO_2 efflux. The fact that the rewetting index, rather than soil water content, became the major factor controlling soil CO_2 efflux rates during the prolonged summer drought emphasizes the need to quantify the effects of rain pulses in estimates of net carbon annual losses from soil in dry Mediterranean ecosystems.

3.1. Introduction

Soil respiration (R_s) results from plant litter and soil organic matter (SOM) decomposition and root respiration, and is proportional to the net primary productivity (NPP) of the ecosystem (Wang & Polglase, 1995). After gross primary productivity, soil respiration is the second most important carbon flux in ecosystems and is therefore an important component of the global carbon balance (Schimel, 1995). As a result of growing concern on climate change, and the increasingly recognized importance of the role of soils as potential carbon sinks, much effort is being devoted to obtaining better estimates of soil CO_2 efflux and to improve our understanding of the interactions between environmental variables and soil respiration.

The total global area of lands with a Mediterranean-type climate is about 2.75 million km^2 (Rambal 2001). Coupled General Circulation Models (GCMs) and ecophysiological models such as GOTILWA predict 1°C warming and 15-20% lower soil water availability for the next three decades in Mediterranean ecosystems as a result of smaller annual amounts of precipitation and also changes in rain distribution (IPPC, 2001; Sabaté et al., 2002), which may alter CO_2 fluxes from soils. Thus, it is important to understand which environmental factors control soil respiration and, moreover, how these factors affect CO_2 emissions from soils, especially in semiarid and dry ecosystems, where soil respiration is one of the main processes of C loss (Conant et al., 2000). However, soil processes in water-limited ecosystems, and in Mediterranean ecosystems in particular, have received relatively little attention (Raich & Schlesinger, 1992; Raich and Potter, 1995; Rey et al., 2002), and are currently under-represented in research networks (Reichstein et al., 2003; Valentini et al., 2003).

Extensive research has focused on the temperature sensitivity of soil respiration (Boone et al., 1998; Buchmann, 2000; Davidson et al., 1998; Lloyd and Taylor, 1994). In contrast to the continuous response of soil respiration to temperature typically found in mesic ecosystems, a growing number of studies have suggested that soil respiration in water-limited ecosystems has a pulsed response to precipitation events (Curiel-Yuste et al., 2003; Huxman et al., 2004; Jarvis et al., 2007; Noy-Meir, 1973). Understanding both continuous and discontinuous factors that govern CO_2 efflux dynamics and sources of variability is important for producing a predictive framework for understanding CO_2 efflux dynamics under varying meteorological conditions.

The spatial distribution of vegetation is also an important factor to bear in mind, because plants affect soil respiration through multiple pathways: i) by altering the soil moisture regime, through the interception of precipitation and the extraction of soil water via transpiration (Rutter and Morton, 1977); ii) by influencing soil microclimate and structure (Raich and Tufekcioglu, 2000); iii) by providing the principal carbon source to decomposer microorganisms through dead plant material, thus determining both litter quantity and quality (Swift et al., 1979); and iv) the fact that a considerable fraction of soil respiration stems directly from the vegetation via root or rhizosphere respiration (Högberg et al., 2001).

The objectives of this chapter were: (1) to investigate seasonal variations in soil respiration, soil temperature, and soil water content under three representative land uses in a semiarid Mediterranean ecosystem; (2) to evaluate the relative importance of temperature and soil moisture as predictors of soil respiration; and (3) to examine if the response of soil respiration to soil temperature and water availability differs at different locations (beneath- and inter-canopy) within each land use. We hypothesize that water availability, rather than temperature, becomes the major factor controlling CO_2 efflux rates in this Mediterranean ecosystem during the summer dry season. Here we ask two questions:

1. How do seasonal patterns of soil moisture availability modulate the response of soil respiration to changes in temperature?
2. Are different land uses similarly sensitive to differences in soil temperature and water availability?

3.2. Material and methods

3.2.1. Experimental design and field measurements

3.2.1.1. Soil respiration measurements

Soil CO_2 efflux was measured in situ with a portable soil respiration gauge (LI-6400, LI-COR, Lincoln, NB, USA) fitted with a soil respiration chamber (6400- 09, LI-COR, NB, USA). Measurements of soil CO_2 efflux were taken according to a stratified sampling design to capture the vegetation-based variation in each land use. The experimental design has been previously described in Chapter 2 (Section *2.2.1.2.1.,* page 31).

3.2.1.2. Temperature, moisture and precipitation measurements

Simultaneously with soil respiration measurements, soil temperature (T) and soil volumetric water content (SWC) were measured at 15 cm depth at each sampling point. Soil temperature was automatically recorded with a LI-6400 soil temperature probe, and soil water content was measured using a time domain reflectometry device (TDR). Precipitation depth, intensity and duration of each rainfall event were obtained from a recording rain instrument installed in the experimental area, which was connected to a data-logger (Hobbo, Onset Computer Corporation, Bourne, MA, USA). The data were stored at 1-min intervals.

3.2.1.3. Fine root biomass estimation

Plant roots were sampled to a mean depth of 10 cm by collecting soil cores 10 cm in diameter. Soil cores were collected in December 2006 and April 2007, beneath canopies (n=8) and in the inter-canopy sites (n=4) at each land use. Fine roots (< 2 mm diameter) were hand-picked, rinsed with tap water and decanted into a 0.1-mm mesh sieve. The flotation procedure was repeated until no more visible roots floated to the surface. The material collected in the 0.1-mm sieve was dried at 60 ℃ for 4 days. Any material not derived from roots was removed before weighing the final product.

3.2.1.4. Soil organic carbon estimation

Soil samples were collected in December 2006 and April 2007 from the top 15 cm at the same sampling points where plant roots were sampled. Soil samples for soil organic carbon (SOC) analyses were air-dried, and sieved through a 2 mm sieve. Before SOC in the mineral soil (<2 mm) was determined with a N/C analyzer (Flash 1112 EA, Thermo-Finnigan, Bremen, Germany), soil carbonates were eliminated using 1 M HCl.

3.2.2. Data analysis

3.2.2.1. Temperature response of soil respiration

The Q_{10} value, defined as the increment in soil respiration rate when temperature is increased by 10 ° C, was used to describe the sensitivity of soil respiration to temperature. For each land use, a Q_{10} value for the whole measurement period (January 2006 to December 2007) was computed on the basis of the monthly measurements of soil respiration rate and soil temperature. In addition, we estimated a specific Q_{10} value for the growing season (from October to April), and another one for the dry season (from May to September).

3.2.2.2. Rewetting index estimation

Relating monthly mean precipitation with soil respiration is difficult, because soil water availability also depends on soil water storage capacity, the water balance during previous weeks and months, and the rainfall distribution within the month. Therefore, a rewetting index was defined to quantify the rewetting potential of rain events. It was assumed that the rewetting capacity would be positively related with water input (amount of precipitation) and negatively related with water loss (evaporation, uptake by roots and percolation). Because percolation, evaporation and uptake by roots were impossible to estimate, time since the last rain event was used as a proxy for these water losses:

$$RWI = P / t$$

where RWI is the rewetting index, P is precipitation (mm), and t is time elapsed between rainfall event and R_s measurements (days).

3.2.2.3. Aboveground biomass index

Vegetation density and developmental stage (e.g. age, height) are important factors affecting soil respiration in forest stands. Because of the structural complexity of vegetation in the forest and abandoned field, an aboveground biomass index was defined in order to explain some of the spatial patterns of soil respiration observed in these land uses:

$$ABI = AB_1 / D_1 + AB_2 / D_2 + AB_3 / D_3 + AB_4 / D_4 + \ldots + AB_n / D_n$$

where AB represents the above-ground biomass (g) of the nearby trees and/or shrubs, and D is the distance (cm) from the soil collar to their stems. The aboveground biomass was calculated from stem basal diameter measurements, by applying species-specific allometric relationships (Baeza et al., 2006, 2011; G. Barberá, unpublished observations). However, in the olive grove the distance from the nearest tree trunk was used as an indicator of the effect of vegetation on soil respiration, because all the trees were the same age, size and shape.

3.2.2.4. Temporal and spatial upscaling

The annual soil CO_2 efflux for the period 1 January 2006 to 31 December 2007 was calculated using linear interpolation between measurement dates unless a measurement preceded or followed a climatic or management event known to have a large effect either on gas flux (e.g. snowmelt, pruning), in which case, the interpolation was truncated according to the timing of the event.

For each land use, soil respiration measurements at the beneath- and inter-canopy sites were upscaled. In the olive grove, we estimated mean canopy area by measuring the vertically projected crown area of 30 olive trees. Mean vegetation cover (%) was estimated by multiplying mean canopy area by the total number of olive trees, and dividing by the whole area. In the forest and abandoned area we estimated mean vegetation cover (%) based on measurements conducted on 16 and 10 plots (5 x 5 m) respectively. Averaged soil respiration was weighted by the % of beneath-canopy (BC) and inter-canopy (IC) area at each land use.

3.2.2.5. Modelling soil respiration and statistical analysis

Depending on the best statistical fit, we used either a model for R_s using soil temperature as an independent variable:

$$R_s = \beta_0 \, e^{\beta_1} \text{ or } \ln(R_s) = \ln(\beta_0) + \beta_1 T \qquad\qquad \text{Eqn. 1}$$

or the following models with soil temperature and other independent variables as drivers for Rs:

$$R_s = \beta_0 e^{\beta 1T} e^{\beta 2\theta} e^{\beta 3ABI} e^{\beta 3RWI} \quad \text{or} \quad \ln(R_s) = \ln(\beta_0) + \beta_1 T + \beta_2 \theta + \beta_3 ABI + \beta_4 RWI \quad \text{Eqn. 2}$$

$$R_s = \beta_0 e^{\beta 1T} e^{(\beta 2\theta)+(\beta 3\theta 2)} \quad \text{or} \quad \ln(R_s) = \ln(\beta_0) + \beta_1 T + \beta_2 \theta + \beta_3 \theta^2 \quad \text{Eqn. 3}$$

$$R_s = \beta_0 e^{\beta 1T} e^{(\beta 2RWI)+(\beta 3RWI2)} \quad \text{or} \quad \ln(R_s) = \ln(\beta_0) + \beta_1 T + \beta_2 RWI + \beta_3 RWI^2 \quad \text{Eqn. 4}$$

$$R_s = \beta_0 e^{\beta 1T} * (\beta_2 \theta) \qquad\qquad \text{Eqn. 5}$$

$$R_s = \beta_0 e^{\beta 1T} - (\theta - \beta_2)^2 \qquad\qquad \text{Eqn. 6}$$

$$R_s = \beta_0 e^{\beta 1T} * (\theta/(\theta + \beta_2)) \qquad\qquad \text{Eqn. 7}$$

where R_s (μmol m^{-2} s^{-1}) is soil CO_2 efflux, T (° C) is soil temperature, θ (%) is volumetric soil moisture, ABI is the above-ground biomass index, RWI is the rewetting index, and β_0, β_1, β_2, β_3 and β_4 are the model coefficients. Similar models have been used previously in other Mediterranean ecosystems (Allen and Vargas, 2008; Rey et al., 2002; Tang et al., 2005b; Xu et al., 2004). Equations (1), (2), (3) and (4), can be log-transformed to a linear model in order to conduct linear regression to estimate the parameters. To select the best model for predicting R_s, we used the root mean squared error (RMSE), and the Akaike information criterion (AIC), as a penalized likelihood criterion (Burnham & Anderson, 2002):

$$AIC = -2\ln(L) + 2p \qquad\qquad \text{Eqn. 8}$$

where L is the likelihood of the fitted model, and *p* is the total number of parameters in the model. The best statistical model minimizes the value of AIC.

In addition, to examine whether soil respiration rates measured for each land use differed consistently with time and whether the measurements were significantly affected by prevailing soil environmental conditions, soil respiration, soil temperature, and soil moisture data were analysed using a repeated measures ANOVA. The Tukey´s multicomparison test was used to detect differences between beneath-canopy and inter-canopy sites for each land use. Data were tested prior to analyses for assumptions of normality and homogeneity of variances. Before analysis, soil temperature, moisture, and respiration data were log-transformed.

Before examining the relationships between soil respiration and the environmental variables, we distinguished between growing season (from October to April) and dry season (from May to September), and between beneath-canopy and inter-canopy sites within each land use. A Pearson correlation test was used to examine the relationships between soil respiration and the environmental variables. All statistical analyses were performed with SSPS v15 (SPSS, Chicago, IL, USA).

3.3. Results

3.3.1. Seasonal variation in soil temperature and soil moisture

Both soil temperature and soil moisture content varied markedly with season. Maximum temperature coincided with minimum water contents in the summer, while minimum temperatures were recorded in winter when soil moisture was highest (Fig. 3.1).

Soil temperature showed a similar trend among the three land uses during the study period, increasing steadily until mid-summer to reach a mean maximum in July 2006 and 2007 (28.82 and 27.35 ºC, respectively), and then gradually falling through autumn and winter to reach the lowest values in January 2006 and 2007 (7.41 and 7.13 ºC, respectively). The annual mean daily temperature of soil was 16.83 º C, and there were no significant differences between years ($P > 0.05$).

The soil water content at 0-15 cm depth ranged from 23.14 (forest), 23.60 (abandoned) and 29.02% (olive grove) in winter (January 2006 and 2007) to 7.23 (forest), 10.14 (abandoned) and 9.66% (olive grove) in mid summer (July 2006 and 2007). Soil water content was below 10% from June until the end of September, except after occasional rainfall events, when it increased sharply. In addition, soil water content in the forest was consistently lower than in the other land uses throughout the two year study period (Fig. 3.1b), presumably because of: 1) greater canopy interception of rainfall; and 2) greater root water uptake (fine root biomass in the forest is 2 and 4 times greater than in the abandoned field and olive grove, respectively) (Table 3.1).
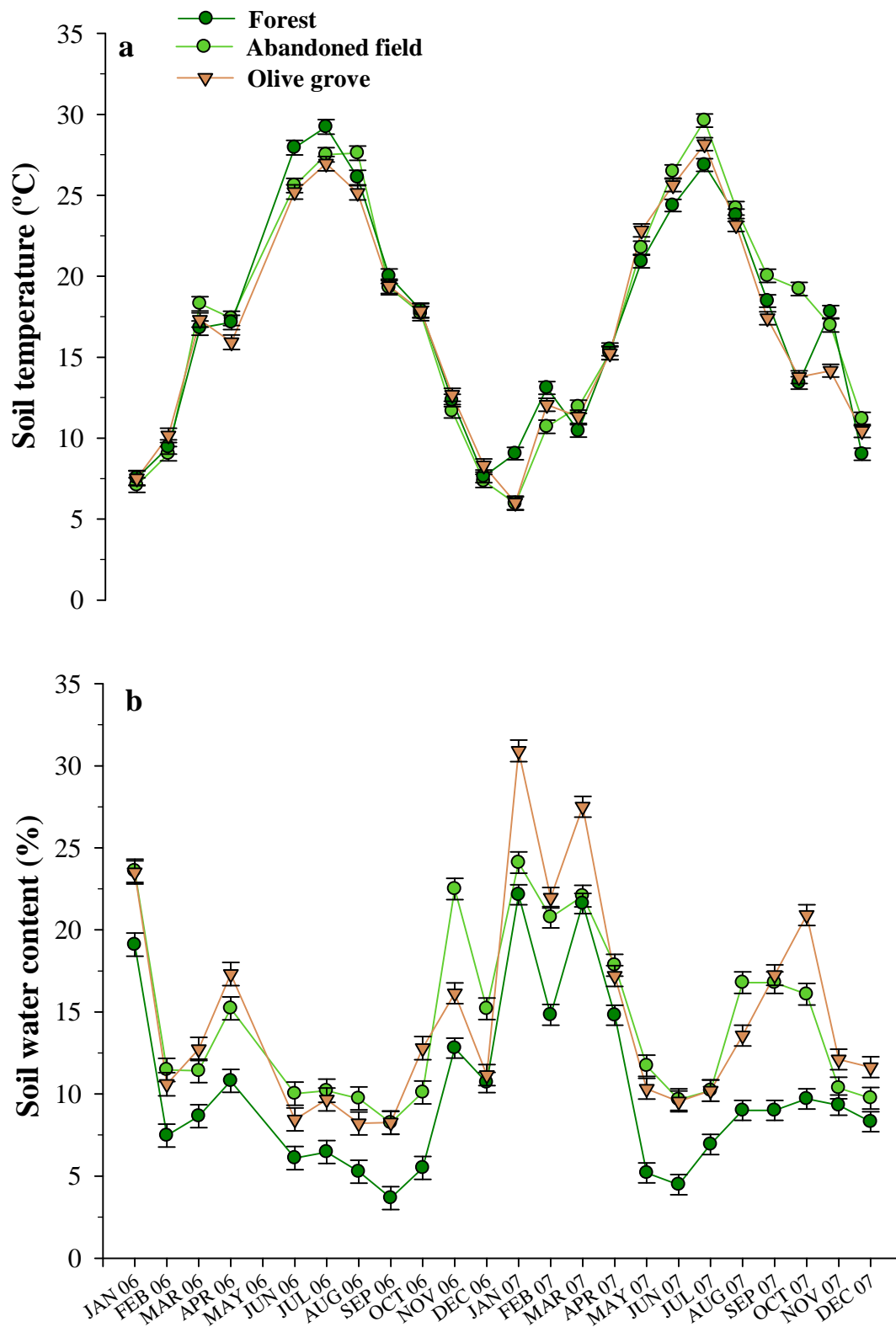
Figure 3.1. Seasonal variation of soil temperature (a) and water content (b) at 0-15 cm depth for each land use.

Table 3.1. Descriptive statistics (mean ± standard error) for soil respiration rate and environmental factors for the three land uses.

	Open forest		Abandoned field		Olive grove	
	Canopy (n=25)	**Inter-canopy** (n=5)	**Canopy** (n=25)	**Inter-canopy** (n=5)	**Canopy** (n=24)	**Inter-canopy** (n=6)
Soil respiration (μmol m^{-2}s^{-1})	2.36 ± 0.05a	1.50 ± 0.12b	1.87 ± 0.05a	1.63 ± 0.12a	2.18 ± 0.05a	0.87 ± 0.13b
Soil respiration (g C m^{-2} y^{-1})	892.08 ± 18.9a	567 ± 45.3b	706.86 ± 19a	616.14 ± 45.3a	824.04 ± 19a	328.86 ± 11.3b
Soil temperature (º C)	16.84 ± 0.28a	17.48 ± 0.72a	16.62 ± 0.31a	17.84 ± 0.74a	16.6 ± 0.29a	17.52 ± 0.77a
Soil water content (%)	10.02 ± 0.26b	11.93 ± 0.67a	15.06 ± 0.29a	13.76 ± 0.68a	15.17 ± 0.27a	13.92 ± 0.71a
SOC (g kg^{-1})*	36.01 ± 1.94a	23.06 ± 2.74b	17.27 ± 2.45a	18.80 ± 5.49a	15.44 ± 1.94a	9.22 ± 2.96b
Fine root biomass (<2mm) (g kg^{-1})*	13.53 ± 1.8a	5.55 ± 2.54b	4.74 ± 1.65a	4.79 ± 3.6a	3.67 ± 1.34a	1.39 ± 0.11b

For each land use, different letters (a-b) within the same row indicate statistically significant differences ($p < 0.05$) between beneath- and inter-canopy areas, according to Tukey´s test.

* The number of sampling points was 8 and 4 for beneath- and inter-canopy areas, respectively.

3.3.2. Seasonal variation in soil respiration

Soil respiration in all land uses varied markedly during the year, following changes in soil temperature during the autumn, winter and early spring, or changes in soil moisture during late spring and summer. Soil respiration increased steadily during spring following increases in temperature until April, when it reached a peak (3.58 ± 0.13 and 3.34 ± 0.12 μmol m^{-2} s^{-1} in April 2006 and 2007, respectively) (Fig. 3.2a). R_s then declined during the dry late spring and summer months, and the effect of summer drought became most apparent as the soil water content fell below 10%. The limiting effect of soil moisture on soil respiration was clear, as R_s responded quickly and sharply to each rainfall event that occurred during the summer. The overall mean soil respiration rate recorded in August 2006 across land uses (SWC= 7.68 ± 0.43 %; R_s= 1.23 ± 0.13 μmol m^{-2} s^{-1}) was much lower than that recorded in August 2007 (SWC= 13.30 ± 0.39 %; R_s= 3.32 ± 0.11 μmol m^{-2} s^{-1}), when a rainfall event of 22.4 mm occurred a few days before soil respiration rates were measured (Fig.3.2b). For all land uses, soil respiration rates were lowest in winter, when soil water content was highest and soil temperature lowest. Mean annual soil respiration rates beneath canopies were 2.35 ± 0.04, 1.87 ± 0.04, and 2.18 ± 0.04 μmol m^{-2} s^{-1} in the forest, abandoned agricultural field and rainfed olive orchard, respectively.

3.3.3. Response of soil respiration to soil temperature and soil moisture

Soil respiration was positively related ($p < 0.01$) with soil temperature for values of soil water content higher than 10% in the forest and olive grove, or higher than 15% in the abandoned field. However, the positive relationship between soil respiration and temperature found during the growing season shifted to negative during the dry season for all land uses (Table 3.2). On the other hand, a positive correlation ($p < 0.01$) was observed between soil water content and soil respiration for all land uses whenever soil temperature was above 16 ºC.

The mean annual Q_{10} values for forest, abandoned field and olive grove were 1.12, 1.35 and 1.36, respectively. The Q_{10} values were always significantly ($P<0.001$) greater for the growing season (2.08, 2.20 and 1.86 for forest, abandoned field and olive grove, respectively) than for the dry season (0.40, 0.63 and 0.44, respectively).

We also found a positive correlation (P<0.01) between rewetting index and soil respiration rate for all the land uses during the dry season, and in the forest (beneath canopies) and abandoned field during the growing season. The correlation values showed that the response of R_s to rainfall events was slightly higher in the forest and abandoned field than in the olive grove (Table 3.2).
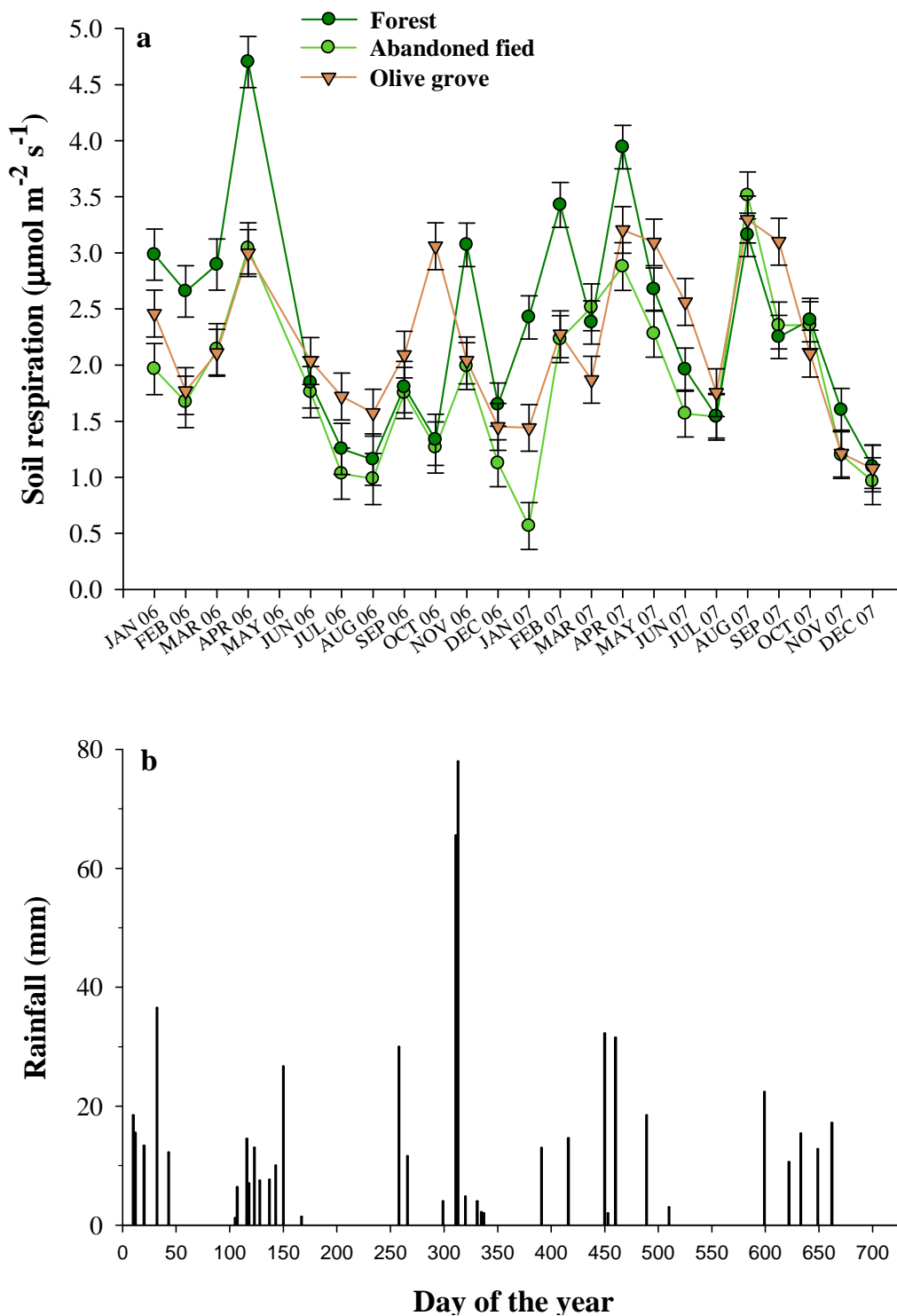
Figure 3.2. Seasonal variation of soil respiration rates for each land use (a) and rainfall events occurred during the study period (b).

3.3.4. Soil respiration variation at different locations within each land use

Soil respiration rates in the open forest and olive grove were significantly higher beneath canopies than in inter-canopy locations. However, in the abandoned field there were no significant differences in R_s between beneath- and inter-canopy sites (Table 3.1). This trend was consistent throughout the study period (Fig. 3.3). The greatest differences between locations were found in the olive grove. None of the land uses showed significant differences in soil temperature between beneath- and inter-canopy locations, and only for the open forest site was SWC beneath canopies significantly lower than in inter-canopy sites.

In order to better understand soil CO_2 efflux variation, and to identify the biotic and abiotic factors affecting it, multiple regression analyses were performed for each land use location and season. Since there were no significant differences in soil respiration between vegetated and bare soil areas in the abandoned agricultural field, we did not distinguish between beneath- and inter-canopy sites in either linear or nonlinear regression procedures for this land use.

The best models to explain soil respiration variation in the different seasons and locations at each land use are shown in Table 3.3. As mentioned above, during the growing season soil respiration correlated positively ($p < 0.01$) with soil temperature in all cases (Table 3.1). Soil temperature and above-ground biomass index explained 39% of soil respiration variation beneath canopies in the open forest (Table 3.3). Soil temperature and rewetting index explained 76% of the variation in R_s in the inter-canopy sites. In the abandoned field, soil temperature was the single best predictor of R_s, explaining 51.6% of variation in this parameter. In the olive grove, soil temperature was the best predictor of soil respiration rate beneath canopies, followed by the distance from the nearest tree stem. Together they accounted for 55% of the variation in soil respiration. Temperature as a sole variable explained 48% of soil respiration variability in the olive grove inter-canopy sites.

During the dry season, soil respiration was negatively correlated with soil temperature and positively correlated with the rewetting index in all the cases ($p < 0.01$). Interestingly, a very similar pattern was observed in the three land uses, as soil respiration was linearly controlled by the rewetting index as a single variable, except for the beneath-canopy site in the olive grove, where an exponential relationship best explained soil respiration variability, with both rewetting index and distance from the stem as predictors. In addition,

the rewetting index accounted for a larger proportion of the variation in R_s in the inter-canopy sites than beneath canopies for both the forest and the olive grove sites (Table 3.3).

Table 3.2. Pearson correlation coefficients between soil respiration (R_s), temperature (T_s), and water content (SWC), rewetting index (RWI), aboveground biomass index (ABI) and distance to the stem (D) for different seasons and locations at each land use.

			R_s	T_s	SWC	RWI	ABI	D
					Growing season			
Open forest	BC	R_s	1	0.56**		0.15**	0.25**	
		T_s		1	-0.262**			
		SWC			1			
	IC	R_s	1	0.45**				
		T_s		1				
		SWC			1			
Abandoned field		R_s	1	0.62**	-0.22**	0.41**		-0.25**
		T_s		1	-0.34**			
		SWC			1			
Olive grove	BC	R_s	1	0.54**			0.30**	-0.51**
		T_s		1	- 0.167*			
		SWC			1	0.22**		
	IC	R_s	1	0.67**				
		T_s		1				
		SWC			1			
					Dry season			
			R_s	T_s	SWC	RWI	ABI	D
Open forest	BC	R_s	1	-0.42**	0.40**	0.69**		
		T_s		1	-0.24**		-0.30**	
		SWC			1	0.38**		-0.47**
	IC	R_s	1	-0.60**		0.81**		
		T_s		1				
		SWC			1		-0.52*	
Abandoned field		R_s	1	-0.41**	0.69**	0.77**		- 0.177*
		T_s		1	-0.41**		-0.25**	
		SWC			1	0.78**		
Olive grove	BC	R_s	1	-0.41**		0.46**	0.23**	-0.40**
		T_s		1				
		SWC			1	0.47**		
	IC	R_s	1			0.80**	0.55**	
		T_s		1	-0.90**			
		SWC			1	0.98**		

* $P < 0.05$; ** $P < 0.001$; BC: beneath-canopy; IC: inter-canopy.
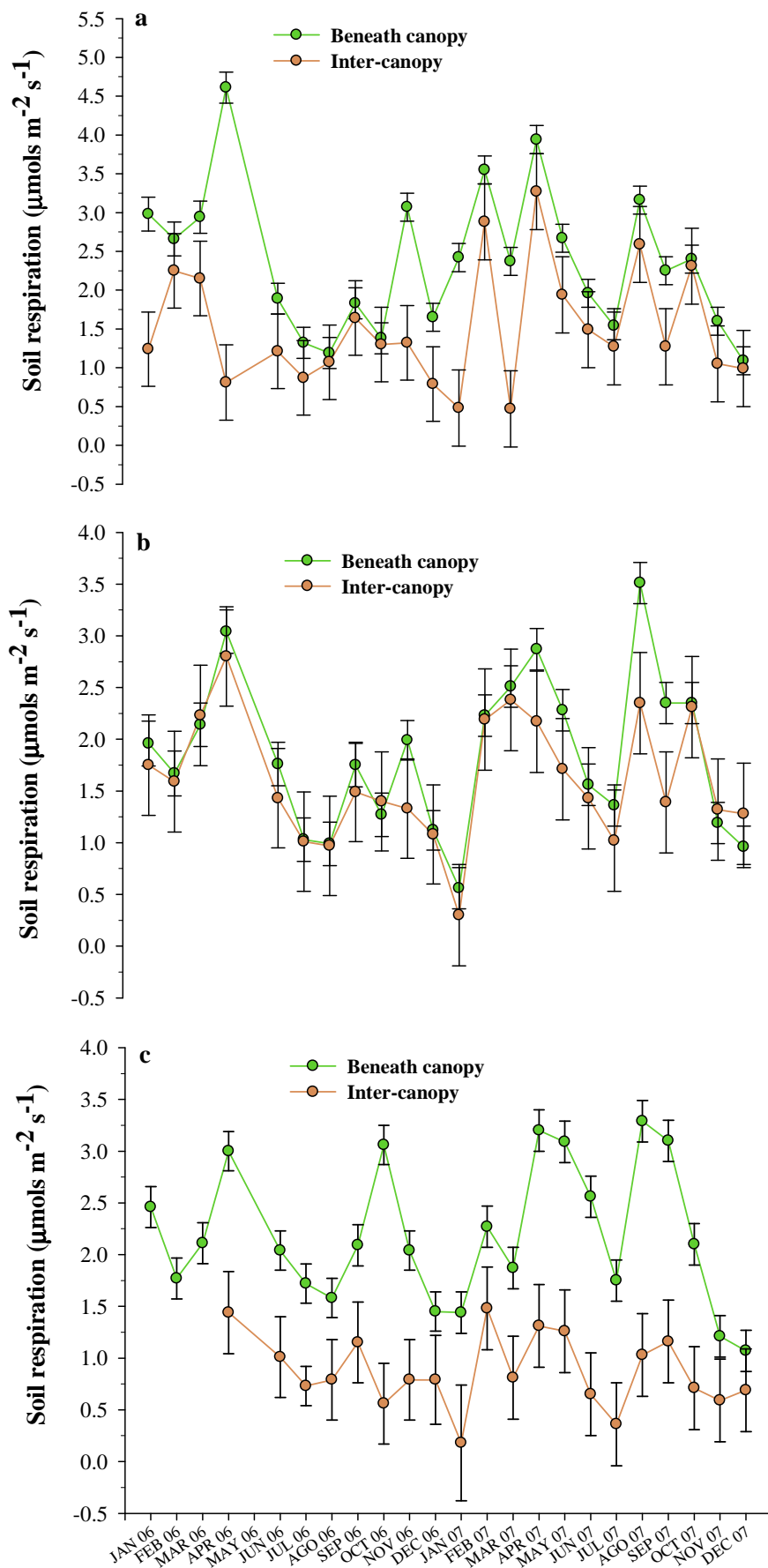
Figure 3.3. Seasonal variation of soil respiration at different sites for forest (a), abandoned field (b) and olive grove (c).

Table 3.3. Exponential and linear relationships between soil respiration rate and biotic and abiotic factors for different seasons and locations at each land use.

	Land use	Location	Model	β_0	β_1	β_2	β_3	R^2	*P* value	RMSE	n	AIC
Growing season	Open forest	**BC**	$R_s = \beta_0\, e^{\beta_1 T}\, e^{(\beta_2 ABI)}$	-0.43 ± 0.12	0.11 ± 0.01	0.06 ± 0.01		0.39	<0.0001	3.84	216	12.0
		IC	$R_s = \beta_0 e^{\beta_1 T} e^{(\beta_2 + RWI) + (\beta_3 + RWI2)}$	0.3 ± 0.13	0.20 ± 0.02	- 0.37 ± 0.42	0.03 ± 0 05	0.76	<0.0001	4.66	40	8.29
	Abandoned field		$R_s = \beta_0 e^{\beta_1 T}$	-1.21 ± 0.11	0.14 ± 0.01			0.51	<0.0001	8.03	224	8.65
	Olive grove	**BC**	$R_s = \beta_0 e^{\beta_1 T} e^{(\beta_2 D)}$	1.27 ± 0.14	0.08 ± 0.00	- 0.50 ± 0.05		0.55	<0.0001	18.32	192	8.69
		IC	$R_s = \beta_0 e^{\beta_1 T}$	-1.64 ± 0.27	0.12 ± 0.02			0.48	<0.0001	2.39	48	7.99
Dry season	Open forest	**BC**	$R_s = \beta_0 + \beta_1 RWI$	1.16 ± 0.01	0.77 ± 0.07			0.48	<0.0001	7.83	162	8.05
		IC	$R_s = \beta_0 + \beta_1 RWI$	0.86 ± 0.13	0.64 ± 0.10			0.64	<0.0001	2.48	30	6.97
	Abandoned field		$R_s = \beta_0 + \beta_1 RWI$	0.71 ± 0.11	0.95 ± 0.07			0.63	<0.0001	9.83	168	7.67
	Olive grove	**BC**	$R_s = \beta_0 e^{\beta_1 RWI} e^{(\beta_2 D)}$	0.67 ± 0.08	0.38 ± 0.05	- 0.40 ± 0.06		0.45	<0.0001	2.99	144	11.7
		IC	$R_s = \beta_0 + \beta_1 RWI$	0.35 ± 0.08	0.31 ± 0.05			0.73	<0.0001	1.16	36	8.86

BC: beneath-canopy; IC: inter-canopy; T: soil temperature; ABI: above-ground biomass index; SWC: soil water content; RWI: rewetting index; D: distance to the stem. The best-fit model parameters (β_0, $\beta_1 \beta_2$, and β_3) and standard error are reported for each model together with the squared coefficient of regression (R^2), the root mean squared error (RSME), the number of observations (n), and the Akaike information criterion (AIC). Model parameters were estimated using the Levenberg-Marquardt method.

3.4. Discussion

3.4.1. Effect of soil temperature on soil respiration

The seasonal pattern of soil respiration followed soil temperature for only part of the year (winter and part of spring and autumn), as previously reported for other drought-stressed Mediterranean ecosystems (Asensio et al., 2007b; Joffre et al., 2003; Matteuci et al., 2000; Rey et al., 2002). The Q_{10} values for soil respiration in these land uses ranged from 0.46 to 3.14, and thus fall within the range of values reported elsewhere (Jarvis et al., 2007; Kirschbaum, 1995; Raich & Schlesinger, 1992). But the mean annual Q_{10} values (1.12, 1.35 and 1.36 for forest, abandoned field and olive grove, respectively) showed low sensitivity to temperature compared with other studies reported in the literature (Chen et al, 2000; Davidson et al., 1998; Janssens and Pillegard, 2003). However, those other studies were carried out in more mesic forest ecosystems, where moisture was not limiting and where soil temperature was generally lower than at our site. A seasonal variation in Q_{10} values was observed, with the annual minimum occurring in summer and the annual maximum occurring during the fall-spring growing season. These data follow the same trend as other studies investigating soil respiration in laboratory incubations with semiarid soils under water limitation conditions (Conant et al., 2004), where Q_{10} values at lower temperatures (5-15 ° C) tended to be greater than those for warmer temperatures (25-35 ° C). This suggests, as Xu and Qi (2001a) also pointed out, that the average Q_{10} values alone may not be indicative of the sensitivity of soil respiration to temperature in an ecosystem. In any case, drawing conclusions from seasonal variations in Q_{10} is difficult because of our limited knowledge of how the responses of microbial communities and plant roots to changes in soil temperature differ (Boone et al., 1998; Giardina and Ryan, 2000).

3.4.2. Effect of soil moisture on soil respiration

Soil moisture is another major factor that may influence soil respiration in different ways. We know from laboratory studies and from theory that a high water content can impede the diffusion of CO_2 in soil (Doran and Linn, 1984; Doran et al., 1990; Skopp et al., 1990). On the other hand, a low soil water content can inhibit soil microbial activity and root respiration (Curiel-Yuste et al., 2003; Davidson et al., 1998; Xu and Qi, 2001a, b).

According to Luo & Zhou (2006), the optimum water content is usually somewhere near field capacity, when the macropore spaces are mostly air-filled, thus facilitating O_2 diffusion, and the micropore spaces are mostly water-filled, thus facilitating the diffusion of soluble substrates. In this study, soil moisture content seldom reached field capacity (field capacity between 20-26% and porosity between 40-45% for all land uses; data not shown), and never seemed to reach a high limiting value, but strongly limited soil respiration when the values dropped below 10 %. The results of this study show that low soil water content strongly limited the response of soil respiration to soil temperature. The relationship between soil CO_2 efflux and soil temperature was strongly modulated by soil moisture. At a low SWC, warmer temperatures actually caused soil respiration rates to decrease. We saw this effect in two ways. First, observing how the positive relationship between soil respiration and temperature during the growing season shifted to negative during the dry season. Second, Q_{10} values were 2.08, 2.20 and 1.86 for forest, abandoned field and olive grove, respectively, when soil moisture was > 10 %, but only 0.44, 0.63 and 0.44 when soil moisture was < 10 %. Other authors reported higher threshold values for soil moisture in Mediterranean ecosystems (Rey et al., 2002; Xu and Qi, 2001b), although the mean annual precipitation values of those ecosystems were higher than in our study area.

Soil respiration peaked sharply immediately after rainfall events, especially following prolonged drought periods (e.g. August 2007). The limiting effect of soil moisture on soil respiration is supported by the strong positive correlations found ($P<0.05$) between rewetting index and soil respiration across land uses during the dry season (Table 3.2). A rapid pulse of CO_2 production following precipitation and the rewetting of dry soils has been observed in a variety of ecosystems (Birch, 1958; Janerette et al., 2008; Law et al., 2001; Smith et al., 2004; Sponseller, 2007). It is known that soil microbial activity can be initiated within minutes of rewetting (García- Pichel & Belnap, 1996), but there is still an ongoing debate about the mechanistic basis for this initial flush of CO_2. Whereas some authors argue that pulses of CO_2 are derived from the microbial oxidation of labile soil organic matter (SOM), which becomes available as wetting and drying physically disrupt soil aggregates (Adu & Oades, 1978), others state that the CO_2 pulse comes from lysis of the soil microbial biomass caused by the osmotic shock induced by soil water potential, which releases a pool of labile organic matter that is used by the surviving microbes (Fierer and Schimel, 2003; Kieft et al., 1987). On the other hand, other studies have observed that a fraction of the pulse of CO_2 may be associated with a rapid enhancement in fine root and

mycorrhizal metabolic activity (Allen and Vargas, 2008; Heynemeyer et al., 2007). In addition to these biotic mechanisms, precipitation in semiarid and arid ecosystems has been shown to release the CO_2 bound to soil carbonates (Emmerich, 2003), and the infiltration of rainwater may displace CO_2 that accumulates in soil pore spaces during dry periods (Huxman et al., 2004). Both biotic and abiotic factors could explain the unusual CO_2 efflux peak observed during summer 2007 and some other CO_2 efflux peaks that occurred throughout the study period when soil respiration was measured shortly after a rainfall event.

Interestingly, soil respiration rate appeared to be less strongly affected by drought in the forest than in the other land uses (Fig. 3.1; Fig. 3.2). Deep rooting and root access to subsoil moisture reserves in late-successional Mediterranean forests and shrublands (Schenk and Jackson 2002) strongly favour the occurrence of hydraulic lift, defined as the passive movement of water from relatively wet, deep layers to drier, shallower layers using plant root systems as a conduit (Caldwell et al., 1998). Hydraulic lift has been shown to help maintain the activity of fine roots, mycorrhizal fungal mycelia and other soil microorganisms in the dry upper layers of soil during drought (Bauerle et al. 2007; Querejeta et al. 2007), which could explain the buffered response of R_s rates to soil moisture fluctuations in our late-successional forest.

3.4.3. Modelling soil respiration at the stand level

Soil temperature is the variable that has been most often used to explain changes in soil respiration (Janssens et al., 2000; Lloyd & Taylor, 1994; O´Connell, 1990), although soil moisture has also been used for this purpose (Davidson et al., 1998; Holt et al., 1990). However, soil temperature and soil moisture often co-vary in the field. In this study, high temperatures occurred when the soil water contents were low, and low temperatures coincided with high soil water contents. Thus, temperature effects on soil respiration can overshadow water content effects, and vice versa. To resolve this question we separated R_s into growing and dry seasons based on variations in soil temperature and SWC during the two-year study period.

Exponential and linear models adequately described soil respiration responses to environmental variables during both seasons. Soil temperature was a good predictor of soil respiration during the relatively wet growing season, explaining a large proportion of the

R_s variability observed in the experimental area. On the other hand, the rewetting index, rather than soil water content, was the most relevant parameter predicting soil respiration during the dry season, especially in the abandoned field and in the forest and olive grove inter-canopy sites, where it accounted for a significant proportion of the variability in CO_2 efflux. It is evident from the data for the three land uses that after a prolonged period of dryness, rainfall led to large CO_2 emissions, and those should be maintained for a few days before declining to a low basal rate. Jarvis et al. (2007) estimated that the time taken for CO_2 efflux to return to the pre-rainfall basal rate was about 30 days in a Mediterranean forest in Portugal.

To explain soil respiration rates beneath canopies in the forest and olive grove we needed to develop models combining abiotic and biotic factors (Table 3.3). Interestingly, abiotic factors explained a smaller proportion of the variability in CO_2 efflux beneath canopies than in the inter-canopy sites. Vegetation can buffer the response of R_s to soil temperature and moisture fluctuations through a wide array of mechanisms, including canopy shading, rainfall interception, and root activity (water uptake, hydraulic redistribution, etc). By contrast, inter-canopy sites are more directly exposed, and therefore are more sensitive, to environmental fluctuations.

In any case, our exponential and linear models could only explain part of the soil respiration variation. Because CO_2 efflux from soil does not only depend on soil temperature and water content, other biotic factors should be taken into consideration, such as changes in root and microbial activity, which may confound the response of R_s to abiotic factors (Trumbore et al., 1996). More than 50 % of the carbon assimilated by forest trees can be respired by roots and mycorrhizae (Högberg et al., 2001). In Mediterranean ecosystems, where there is no regular pattern of precipitation distribution, fine root growth and activity has a pulsed response to rainfall events. Whereas the temporal pattern of fine-root growth is strongly affected by soil temperature in many temperate ecosystems, López et al. (1998) showed that soil water availability was the main factor responsible for changes in root growth and activity in a Mediterranean forest exposed to drought, with peaks in spring and autumn. Likewise, microbial activity also increases sharply after a rainfall event (Curiel-Yuste et al., 2007). In two consecutive years, we observed peaks of R_s in April, coinciding with the period of peak net primary productivity in this Mediterranean ecosystem. Maximum photosynthetic activity occurs at the end of the growing season before the onset of severe drought stress (Varone and Gratani, 2004). Microbial activity increases at the same time because of the optimal conditions provided

by soil moisture and substrate supply, and R_s peaks can be observed as the roots exudates are consumed by the rhizosphere microbes (Christensen et al., 2007).

The fact that the highest soil respiration rates for all land uses were observed during the growing season, stresses the important roles of photosynthesis, net primary productivity and microbial activity, together with precipitation patterns, in determining soil respiration rates.

3.4.4. Implications for soil C cycle

The annual area-weighted average C losses through soil respiration from the forest, abandoned field and olive grove were estimated to be 766.12, 648.84 and 427.44 g C m^{-2} yr^{-1}, respectively. These C losses in the forest and abandoned field were similar to values reported for other ecosystems, such as the estimated 713 ± 88 g C m^{-2} yr^{-1} averaged across several Mediterranean woodlands (Raich and Schlesinger, 1992), and were in the higher range of those reported for the cross-site EUROFLUX study (760 ± 340 g C m^{-2} yr^{-1}) (Janssens et al., 2001). The estimated annual CO_2 efflux from soil in the olive grove was similar to that estimated for a savanna ecosystem in California by Tang et al. (2005a).

3.5. Conclusions

Soil respiration was largely controlled by soil temperature above a threshold value of 10% soil water content (0-15 cm depth) for forest and olive grove, or 15% for the abandoned field. Below those thresholds, R_s was primarily controlled by soil moisture.

Mean Q_{10} values alone may not be indicative of the sensitivity of soil respiration to temperature at ecosystem level, especially in drought-stressed regions, where a low soil water content strongly limits the response of root and microbial activity to temperature. In dry Mediterranean ecosystems, water is the main factor controlling above- and belowground processes, resulting in a moisture-dependent seasonal pattern for soil CO_2 emissions.

The results of this study stress the importance of soil water storage for soil respiration, and highlight the capacity of Mediterranean forest ecosystems to maintain relatively high biological activity even at low water supply.

The fact that the rewetting index, rather than soil water content, became the major factor controlling CO_2 efflux rates during the summer drought emphasizes the need to consider the response to rain pulses in estimates of net carbon annual losses in dry Mediterranean ecosystems.

References

Adu, J.K., Oades, J.M., 1978. Physical factors influencing decomposition of organic materials in soil aggregates. Soil Biology & Biochemistry 10, 109-115.

Asensio, D., Peñuelas, J., Llusià, J., Ogaya, R., Filella, I., 2007a. Interannual and interseasonal soil CO_2 efflux and VOC exchange rates in a Mediterranean holm oak forest in response to experimental drought. Soil Biology and Biochemistry 39, 2471-2484.

Asensio, D., Peñuelas, J., Ogaya, R., Llusià, J., 2007b. Seasonal soil and leaf CO_2 exchanges rates in a Mediterranean holm oak forest and their responses to drought conditions. Atmospheric Environment 41 (11), 2447-2455.

Baeza, M.J., Raventós, J., Escarré, A., Vallejo, V.R., 2006. Fire risk and vegetation structural dynamics in Mediterranean shrubland. Plant Ecology 187 (2), 189-201.

Baeza MJ, Santana VM, Pausas JG, Vallejo VR (2011) Successional trends in standing dead biomass in Mediterranean basin species. Journal of Vegetation Science 22(3): 467-474.

Bauerle, T.L., Richards, J.H., Smart, D.R., Eissenstat, D.M., 2008. Importance of internal hydraulic redistribution for prolonging the lifespan of roots in dry soil. Plant, Cell & Environment 31 (2), 177-186.

Birch, H.F., 1958. The effect of soil drying on humus decomposition and nitrogen availability. Plant and Soil 10, 9-31.

Boone, R.D., Nadelhoffer, K.J., Canary, J.D., Kaye, J.P., 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396, 570-572.

Buchmann, N., 2000. Biotic and abiotic factors regulating soil respiration rates in *Picea abies* stands. Soil Biology and Biochemistry 32, 1625-1635.

Burnham, K.P., Anderson, D.R., 2002. Model selection and inference. A practical information-theoretic approach. New York, NY, USA: Springer.

Caldwell, M.M., Dawson, T. E., Richards, J. H., 1998. Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113, 151-161.

Chen, H., Harmon, M.E., Griffiths, R.P., Hicks, W., 2000. Effects of temperature and moisture on carbon respired from decomposing woody roots. Forest Ecology and Management 138 (1-3), 51-64.

Conant, R.T., Klopatek, J.M., Klopatek, C.C., 2000. Environmental factors controlling soil respiration in three semiarid ecosystems. Soil Science of Society America Journal 64, 383-390.

Conant, R.T., Dalla-Betta, P., Klopatek, C.C., Klopatek, J.M., 2004. Controls on soil respiration in semiarid soils. Soil Biology and Biochemistry 36: 945-951.

Christensen, S., Bjørnlund, L., Vestergård, M., 2007. Decomposer biomass in the rhizosphere to assess rhizodeposition. Oikos 116, 65-74.

Curiel Yuste, J., Janssens, I.A., Carrara, A., Meiresonne, L., Ceulemans, R., 2003. Interactive effects of temperature and precipitation on soil respiration in a temperate maritime pine forest. Tree Physiology 23 (18), 1263-1270.

Curiel Yuste, J., Baldocchi, D.D., Gershenson, A., Goldstein, A., Misson, L., Wong, S., 2007. Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture. Global Change Biology (13), 2018-2035.

Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperature mixed hardwood forest. Global Change Biology 4, 217-227.

Doran, J.W., Mielke, L.N., Power, J.F., 1990. Microbial activity as regulated by soil water-filled pore space. In: Transactions of the 14th International Congress of Soil Science 3, 94-99.

Emmerich, W.E., 2003. Carbon dioxide fluxes in a semiarid environment with high carbonate soils. Agricultural and Forest Meteorology 116, 91-102.

Fierer, N. and Schimel, J.P., 2003. A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. Soil Sci. Soc. Am. J. 67, 798–805.

García-Pichel, F., Belnap, J., 1996. Microenvironments and microscale productivity of cyanobacterial desert crusts. Journal of Phycology 32, 774-782.

Giardina, C.P., Ryan, M G., 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. Nature 404, 858-861.

Gratani, L., Varone, L., 2004. Adaptive photosynthetic strategies of the Mediterranean maquis species according to their origin. Photosynthetica 42 (4), 551-558.

Heynemeyer, A., Hartley, I.P., Evans, S.P., De la Fuente, J.A.C., Ineson, P., 2007. Forest CO_2 efflux: uncovering the contribution and environmental responses of ectomycorrhizas. Global Change Biology 13, 1786-1797.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A.F., Ekblad, A., Högberg, M.N., Nyberg, G., Ottosson-Löfvenius, M., Read, D.J., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411, 789-792.

Holt, J.A., Hodgen, M.J., Lamb, D., 1990. Soil respiration in the seasonally dry tropics near Townville, North-Queensland. Australian Journal of Soil Research 28, 737-745.

Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., Ogle, K., Pockman, W.T., Sandquist, D.R., Potts. D.L., Schwinning, S., 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. Oecologia 141, 254-268.

IPCC, 2001. Climate Change 2001: The Physical Science Basis.

Janerette, G.D., Scott, R.L., Huxman, T.E., 2008. Whole ecosystem metabolic pulses following precipitation events. Functional Ecology, doi : 10.1111/j.1365-2435.2008.01450.x

Janssens, I.A., Meiresonne, L., Ceulemans, R., 2000. Mean soil CO_2 efflux from a mixed forest: temporal and spatial integration. In: Ceulemans, R., Veroustraete, V., Gond, V., Van Rensbergen, J. (Eds.), Forest Ecosystem Modelling, Upscaling and Remote Sensing. SPB Academic Publishing, The Hague, pp. 19-33.

Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Guðmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N.O., Vesala, T., Granier, A., Schulze, E.D. Lindroth, A., Dolman, A. J., Jarvis, P.G., Ceulemans, R., Valentini, R., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Global Change Biology 7 (3), 269-278.

Janssens, I.A., Pilegaard, K., 2003. Large seasonal changes in Q_{10} of soil respiration in a beech forest. Global Change Biology 9, 911-918.

Jarvis, P., Rey, A., Petsikos, C., Wingate, L., Rayment, M., Pereira, J., Banza, J., David, J.,Miglietta, F., Borghetti, M., Manca, G., Valentini, R., 2007. Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the "Birch effect". Tree Physiology 27, 929-940.

Joffre, R., Ourcival, J.M., Rambal, S., Rocheteau, A., 2003. The key-role of topsoil moisture on CO_2 efflux from a Mediterranean *Quercus ilex* forest. Annals of Forest Science 60 (6), 519-526.

Kieft, T.L., Soroker, E., Firestone, M.K., 1987. Microbial biomass response to a rapid increase in water potential when dry soil is wetted. Soil Biology and Biochemistry 19 (2), 119-126.

Kirschbaum, M.U., 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biology and Biochemistry 27, 753-760.

Law, B.E., Kelliher, F.M., Baldocchi, D.D., Anthoni, P.M., Irvine, J., Moore, D., Van Tuyl, S., 2001. Spatial and temporal variation in respiration in a young ponderosa pine forest during a summer drought. Agricultural and Forest Meteorology 110, 27- 43.

Linn, D.M., Doran, J.W., 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and non-tilled soils. Soil Science Society of America Journal 48 (6), 1267-1272.

Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. Functional Ecology 8, 315-323.

López, B., Sabaté, S., Gracia, C., 1998. Fine root dynamics in a Mediterranean forest: effects of drought and stem density. Tree Physiology 18, 601-606.

Luo, Y., Zhou, X., 2006. Soil Respiration. Elsevier, Amsterdam, 92 pp.

Matteucci, G., Dore, S., Stivanello, C., Rebmann, C., Buchmann, N., 2000. Soil respiration in beech and spruce forests in Europe : trends, controlling factors, annual budgets and implication for the ecosystem carbon balance. In: Schulze, E.D. (Ed.), Carbon and Nitrogen Cycling in European Forest Ecosystems. Springer-Verlag, Berlin, pp. 217-236.

Martínez-Mena, M., López, J., Almagro, M., Boix-Fayos, C., ALbaladejo, J., 2008. Effect of water erosion and cultivation on the soil carbon stock in a semiarid area of South-East Spain. Soil and Tillage Research 99, 119-129.

Noy-Meir, I., 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4, 25-52.

O´Connell, A.M., 1990. Microbial decomposition (respiration) of litter in eucalypt forests of south-western Australia: An empirical model based on laboratory incubations. Soil Biology and Biochemistry 22, 153-160.

Querejeta, J.I., Egerton-Warburton, L.M., Allen, M.F., 2007. Hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying in a California Oak savanna. Soil Biology and Biochemistry 39, 409-417.

Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and clima. Tellus Series B, 44: 81-99.

Raich, J. W., Potter, C.S., 1995. Global patterns of carbon dioxide emissions from soils. Global Biogeochemistry Cycles 9, 23-36.

Raich, J.W., Tufekcioglu, A., 2000. Vegetation and soil respiration: correlations and controls. Biogeochemistry 48, 71-90.

Rambal, S. 2001. Hierarchy and productivity of Mediterranean-type ecosystems. *In* Terrestrial Global Productivity. Eds J. Roy, B. Saugier and H. A. Mooney. Academic Press, San Diego, pp 315–344.

Rey, A., Pegoraro, E., Tedeschi, V., De Parri, I., Jarvis, P.G., Valentini, R., 2002. Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. Global Change Biology 8: 851- 866.

Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentini, R., Banza, J., Casals, P., Cheng, Y., Grünzweig, J.M., Irving, J., Joffre, R., Law, B.E., Loustau, D., Miglietta, F., Oechel, W., Ourcival, J.M., Pereira, J.S., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M., Romanya, J., Rossi, F., Tedeschi, V., Tirone, G., Xu, M., Yakir, D., 2003. Modelling spatiotemporal variability of soil respiration. Global Biogeochemical Cycles 17 (4), 15-1-15-17.

Rutter, A.J., Morton, A.J., 1977. A predictive model of rainfall interception in forests. III. Sensitivity of the model to stand parameters and meteorological variables. Journal of Applied Ecology 14 (2), 567-588.

Sabaté, S., Gracia, C., Sánchez, A., 2002. Likely effects of climate change on growth of *Quercus ilex*, *Pinus halepensis*, and *Fagus sylvatica* forest in the Mediterranean region. Forest Ecology and Management 162, 23-37.

Schenk, H.J., Jackson, R.B., 2002. The global biogeography of roots. Ecological Monographs 72 (3), 311-328.

Schimel, D. S. 1995. Terrestrial ecosystems and the carbon cycle. Global Change Biology 1 (1), 77-91.

Skopp, J., Jawson, M.D., Doran, J.W., 1990. Steady-state aerobic microbial activity as a function of soil Water content. Soil Science Society of America Journal 54 (6), 1619-1625.

Smith, D.L., Johnson, L., 2004. Vegetation-mediated changes in microclimate reduce soil respiration as woodlands expand into grasslands. Ecology 85 (12), 3348-3361.

Sponseller, R.A., 2007. Precipitation pulses and soil CO_2 flux in a Sonoran Desert. Global Change Biology 13, 426-436.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in terrestrial ecosystems, 5. Stud. Ecol., Blackwell Sci., Malden, Mass.

Tang, J., Baldocchi, D.D., 2005a. Spatial-temporal variation in soil respiration in an oak-grass savanna ecosystem in California and its partitioning into autotrophic and heterotrophic components. Biogeochemistry 73, 183-207.

Tang, J., Misson, L., Gershenson, A., Cheng, W.X., Goldstein, A.H., 2005b. Continuous measurements of soil respiration with and without roots in a ponderosa pine plantation in the Sierra Nevada mountains. Agricultural and Forest Meteorology 132: 212-227.

Trumbore, S., Chadwick, O.A., Amundson, R., 1996. Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. Science 272, 393-396.

Vargas, R., Allen , M.F., 2008. Environmental controls and the influence of vegetation type, fine roots and rhizomorphs on diel and seasonal variation in soil respiration. New Phytologist 179: 460-471.

Valentini, R. 2003. Fluxes of carbon, water and energy of European forests. Ecological Studies 163. Springer-Verlag, Berlin, Heidelberg, 270 p.

Wang, Y.P., Polglase, P.J., 1995. Carbon balance in the tundra, boreal forest and humid tropical forest during climate change: scaling up from leaf physiology and soil carbon dynamics. Plant, Cell and Environment 18 (10), 1226-1244.

Xu, M., Qi, Y, 2001a. Spatial and seasonal variation of Q_{10} determined by soil respiration measurements at a Sierra Nevada Forest. Global Biogeochemistry Cycles 15, 687-696.

Xu, M. y Qi, Y. 2001b. Soil-surface CO_2 efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. Global Change Biology 7: 667-677.

Xu, L.K., Baldocchi, D.D., Tang, J.W., 2004. How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. Global Biogeochemical Cycles 18: Art. No. GB4002, doi: 10.1029/2004GB002281.

4. Links between vegetation patterns, soil C and N pools, and respiration rate

Abstract

Soil respiration (R_s) is controlled by abiotic soil parameters interacting with characteristics of the vegetation and the soil microbial community. Few studies have attempted a comprehensive approach that simultaneously addresses the roles of all the major factors known to influence R_s. Here, we measured soil respiration, temperature, moisture, carbon (C) and nitrogen (N) contents in both light and heavy soil organic matter fractions, extractable dissolved organic C (DOC), as well as microbial and fine root biomass, in three representative land use types (open forest, abandoned agricultural field, rain-fed olive grove) in a Mediterranean ecosystem. Measurements were conducted in two contrasting seasons coinciding with the annual minimum (December) and maximum (April) R_s rates in this ecosystem. Our goal was to explore the links between heterogeneity in R_s, aboveground plant biomass and belowground properties within each land use type. Across sites, R_s rates were significantly higher in April (3.07 ± 0.1 µmol m^{-2} s^{-1}) than in December (1.30 ± 0.1 µmol m^{-2} s^{-1}). The labile soil organic matter fractions (light fraction C and N contents, microbial biomass C, and extractable DOC) were consistently and strongly related to one another, and to a lesser extent, to the C and N contents in the heavy fraction across sites and seasons. Linear models adequately explained a large proportion of the within-site variability in R_s (R^2 values ranged from 41 to 91% depending on land use and season), but major controls on R_s differed considerably between sites and seasons. In the open forest and olive grove sites, above- and belowground vegetation are the primary controls on spatial variability in labile soil C pools and R_s. In contrast, a complete lack of influence of current vegetation patterns on soil C pools and respiration rates in the abandoned agricultural field site highlights how site history can have lasting impacts on soil C cycling, and the difficulty that these Mediterranean ecosystems have in recovering their original C pools and cycling patterns after disturbance (i.e., clearing of native woody vegetation for cereal cultivation). Our results suggest that long old-field recovery times (>30 yrs) are needed before soil C and N pools and respiration rates start reflecting the typical patchy distribution of woody vegetation in dry Mediterranean ecosystems.

4.1. Introduction

Soil respiration (R_s) is estimated to be about 98 Pg C year^{-1} globally, making it the largest contributor to C fluxes from terrestrial ecosystems to the atmosphere (Bond-Lamberty and Thomson, 2010). Despite its importance to the global carbon budget, our understanding of soil respiration is still limited because of its high complexity and variability, which are controlled by many abiotic and biotic factors. Soil respiration is a combination of root respiration (including the respiration of living root tissue, symbiotic mycorrhizal fungi and associated microorganisms, and the decomposer organisms operating on root exudates and recently dead root tissues in the rhizosphere), respiration of heterotrophic bacteria and fungi active in the organic and mineral soil horizons, and soil faunal activity (Edwards et al., 1970; Wiant, 1967). Hence, soil respiration has been proposed as an indicator of soil carbon storage, soil biological activity, overall soil quality and site productivity (Golchin et al., 2008; Janssens et al., 2001).

Temporal patterns of soil respiration have been modelled by using the continuous records of temperature, moisture, photosynthesis and root activity (Davidson et al., 1998; Janssens et al., 2001; Tang et al., 2005; Vargas and Allen, 2008; Xu and Qi, 2001). However, the spatial variability of soil respiration within a site is often not explained by soil microclimatic variables, but is instead modulated by a complex set of interactions between plant and soil activity and differences in soil texture and chemistry. Different factors have been reported to act as controls on soil respiration at the site level: soil moisture (Adachi et al., 2006), aboveground plant biomass (Arevalo et al., 2010), fine root and microbial biomass (Scott-Denton et al., 2003; Søe and Buchmann, 2005), soil organic matter quantity and quality (Alvarez and Alvarez, 2000; McCulley et al., 2004), litter-layer thickness (Saiz et al., 2006), soil texture (Dilustro et al., 2005), surface stoniness or soil fauna (Romanyà et al., 2000). In addition to the complex set of abiotic and biotic factors that modulate soil respiration spatial patterns, the major drivers of soil respiration may change seasonally in response to plant inputs, root growth peaks, heterogeneous moisture withdrawal and microbial processes such as decomposition of labile substrates (Bahn et al., 2010; Casals et al., 2009; Curiel-Yuste et al., 2007; Fontaine et al., 2007; reviewed by Kuzyakov and Gavrichkova, 2010; Law et al., 1999; Stoyan et al., 2000). Besides, the patchy distribution of soil resources, roots and microorganisms in water-limited ecosystems hampers the study of the interactions between soil respiration, vegetation

characteristics and belowground properties (Maestre and Cortina, 2003; Merbold et al., 2011; Qi et al., 2010; Rey et al., 2010).

As a result of global climate change and alterations in land use, many ecosystems are currently experiencing changes in the primary abiotic and biotic factors that control R_s (Sala et al., 2000). Given the large quantity of CO_2 that soils release annually, it is important to understand how alterations in vegetation and soil, resulting from land use intensification, may interact with predicted climate change to alter soil respiration and C storage. In chapter 3, we reported consistent seasonal trends of R_s along this local land use intensification gradient, and showed how R_s rates were similarly sensitive to temporal fluctuations in soil temperature and precipitation pulses across land uses. The influence of vegetation patterns on soil respiration dynamics was evident, since monthly R_s rates were consistently and significantly higher beneath tree/shrub canopies than in inter-canopy locations in the open forest and olive grove sites (by 36 and 60%, respectively). However, R_s did not differ significantly between beneath- and inter-canopy locations in the abandoned agricultural field. Furthermore, while patterns of aboveground standing biomass contributed to explain the variation in R_s in the open forest and olive grove sites, R_s was unrelated to aboveground vegetation patterns in the abandoned agricultural field. From these results, new research questions arose: (1) Why are R_s rates unrelated to standing aboveground biomass in the abandoned agricultural field?; (2) To what extent are soil C and N pools coupled to vegetation patterns in each land use?; (3) Are primary controls on spatial patterns in R_s consistent across land uses? Answering such questions will help to assess the consequences for C biogeochemical cycling and storage of woody vegetation recovery in abandoned agricultural fields, a widespread phenomenon in the western Mediterranean basin over the last 50 years, and one of the most promising options for C emission offset schemes under the Kyoto Protocol (Padilla et al., 2011; Powlson et al., 2011).

The objective of this chapter is to explore the links between heterogeneity in R_s, aboveground plant biomass and belowground properties within each land use. To accomplish this, we selected two distinctive sampling periods coinciding with annual minimum or near minimum (December) and maximum (April) rates of soil respiration in this dry Mediterranean ecosystem. In each sampling period, soil respiration, temperature and moisture, aboveground plant biomass, and belowground properties (fine root and microbial biomass, extractable dissolved organic carbon, and C and N contents in both light and heavy organic matter fractions) were measured across three different

Mediterranean land uses with the same soil texture and under similar microclimatic conditions.

Previous studies have demonstrated that woody plant establishment in former herbaceous patches can lead to soil C and N accumulation in some ecosystems (Hibbard et al., 2001; McCulley et al., 2004), although no net change or even declines have also been reported in others (Jackson et al., 2002; Kieft et al., 1998; Schlesinger and Pilmanis, 1998). Dry Mediterranean ecosystems are characterized by a set of features that constrain their resilience after cessation of disturbance (low and episodic rainfall, slow vegetation growth, potentially high litter and soil organic matter mineralization rates, slow soil C pools recovery after degradation, and a long history of cultivation; Albaladejo et al., 1998; Álvaro-Fuentes and Cantero-Martínez, 2010; Asner et al., 2003; Austin and Vivanco, 2006; Martínez-Mena et al., 2002; Vallejo et al., 2006). Thus, we hypothesized that 30 years of recovery since agriculture abandonment may not be sufficient for soil carbon pools and R_s rates to start reflecting the patchy distribution of woody vegetation in this dry Mediterranean ecosystem.

4.2. Materials and methods

4.2.1. Experimental design and soil respiration measurements

Soil CO_2 efflux was measured *in situ* with a portable soil respiration instrument (LI-6400, LI-COR, Lincoln, NB, USA) fitted with a soil respiration chamber (6400-09, LI-COR, Lincoln, NB, USA). Measurements of soil CO_2 efflux were taken according to a stratified sampling design to capture the vegetation-based variation in each land use (see Chapter 2), in order to further improve estimation accuracy and reduce sampling size (Rodeghiero and Cescatti, 2008; Xu and Qi, 2001). Three plots were selected within the open forest and abandoned agricultural field sites based on the most frequent plant cover types at each site: patches of *Pinus halepensis*, *Quercus coccifera*, and bare soil with scattered *Rosmarinus officinalis* in the open forest site; or patches of *Pinus halepensis*, *Juniperus oxycedrus*, and bare soil with scattered *Rosmarinus officinalis* in the abandoned agricultural field site. In the olive grove site, both beneath canopy and inter-canopy locations were taken into account. Twenty-four circular PVC collars (5 cm depth, 10 cm diameter) were proportionally distributed among the most frequent plant cover types in

each land use at different distances (ranging from 0.1 to 5 m) from tree/shrub stems (Fig.4.1). To minimize the effects of chamber installation, the soil collars were inserted into the soil to a depth of about 2 cm to limit root severing (Wang et al., 2005), and care was taken not to disturb the soil structure. In each sampling period, twelve of the 24 temporary collars within each land use were used for soil respiration measurements, followed by destructive harvesting as described in Section 4.2.2.
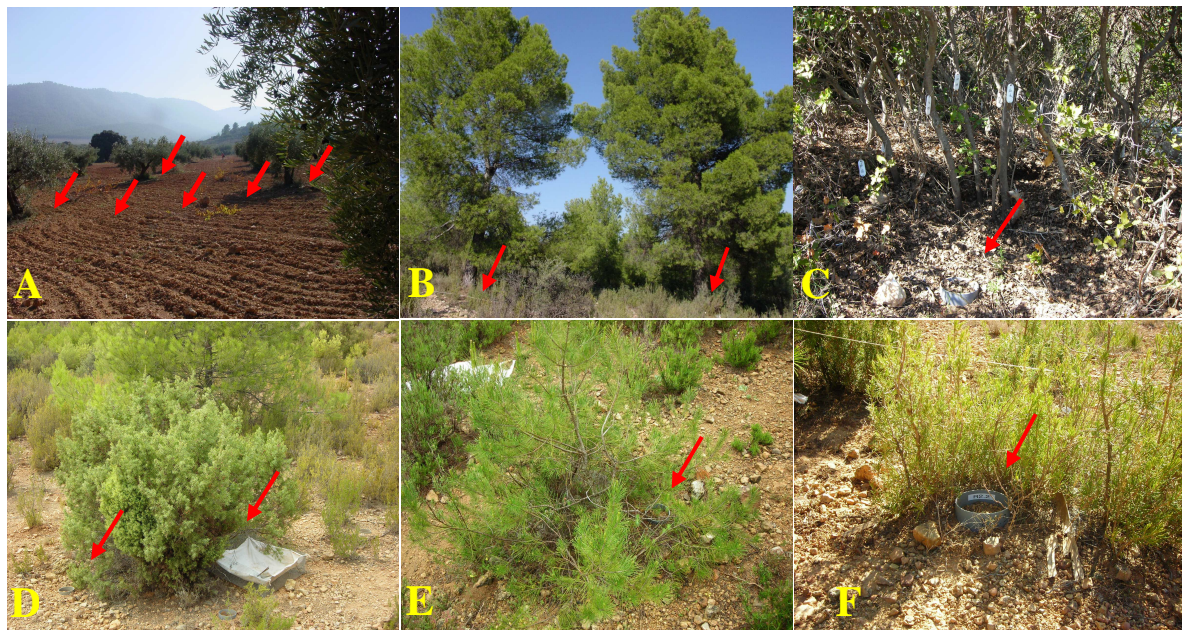
Figure 4.1. Different R_s collars beneath the most frequent plant cover types at each site: beneath-canopies and inter-canopy locations in the olive grove (A), patches of *Pinus halepensis* (B) and *Quercus coccifera* (C) in open forest, and patches of *Pinus halepensis* (E), *Juniperus oxycedrus* (D), and bare soil with scattered *Rosmarinus officinalis* (F) in the abandoned field.

Soil respiration measurements were performed between 9:00 and 12:00 (solar time), because it has been shown that these values of CO_2 efflux are representative of daily averages (Davidson et al., 1998; Mielnick and Dugas, 2000; Xu and Qi, 2001). Simultaneously with soil respiration measurements, soil temperature (T) and soil water content (SWC) were measured in the 0-15 cm depth interval at each sampling point. Soil temperature was automatically recorded with a LI-6400 soil temperature probe, and soil water content (SWC) was measured using a time domain reflectometer (TDR) (Fig.4.2A).

4.2.2. Soil cores

For each land use, soil within the twelve temporary collars was sampled destructively after measuring soil respiration rates in both December 2006 and April 2007. Soil and plant roots were sampled to a depth of approximately 15 cm, or until impeded by rocks or the limestone crust, in a circular area 10 cm in diameter (Fig. 4.2E, F). Given the nature of our soils, with an underlying caliche layer at 17-19 cm depth (Martínez-Mena et al., 2008), sampling focused on the first 0-15 cm of the soil profile, in which fine root biomass and microbial activity are highest. The depth of each core was recorded, as well as its distance to the nearest tree or shrub. Each soil core was sealed in a plastic bag and stored in a freezer (4 °C) until processed for root and microbial biomass estimates, and soil chemical analyses.

Figure 4.2. Soil respiration chamber, soil temperature probe and TDR (A), soil respiration collars beneath Aleppo pine (B), rosemary (C) and kermes-oak (D), and sampling auger (E) for plant roots and soil sampling (F).

4.2.3. Fine root biomass estimation

The soil cores were gently rinsed through a series of three successively smaller sieves (5.0, 2.0, 1.0 mm). Roots were hand-picked from the sieves and placed in a tray. The remaining soil (< 1 mm) was mixed with tap water and the floating roots were decanted into a 0.1-mm mesh sieve. The flotation procedure was repeated until no more visible roots floated to the surface.

The material collected in the 0.1-mm sieve was placed in the tray. Roots were mixed with sodium hexametaphosphate for 24 h to disperse clay particles, rinsed with tap water, and dried at 60 ºC for 4 days. Roots were sorted by diameter (< 2, and > 2 mm), and any material not derived from roots was removed before weighing the final product (fine root biomass, FRB). We were unable to distinguish live and dead roots, so they were bulked. Only fine roots (< 2 mm) were considered for the correlation and multiple regression analyses.

4.2.4. Organic matter fractionation

Soil organic matter was fractionated following the method of Echeverría et al. (2004). Soil samples were separated into two density fractions using sodium polytungstate (SPT) with prior sonification. Density fractionation included a light fraction (LF) (< 1.6 g cm^{-3}), which consists of partly decomposed plant and animal residues and presents higher concentrations of C and N in comparison to bulk soil, and a heavy fraction (HF) (> 1.6 g cm^{-3}), which contains more processed decomposition products, turns over more slowly and presents a high specific density because of its association to soil minerals (Barrios et al., 1996; Christensen, 1992). For the fractionation, 10 g of soil was placed in a 50-ml centrifuge tube with approximately 45 ml of SPT (ρ = 1.6 g cm^{-3}). The centrifuge tubes containing soil-SPT mixture were shaken on a reciprocating shaker at 300 r.p.m. for 15 min to disrupt soil aggregates. Soil aggregates were then dispersed for 2 min with a probe-type sonic disrupter (Sonics & Materials, Inc., USA). The suspensions were allowed to stand for 30 min before centrifugation to prevent mechanical occlusion of LF particles. Suspensions were then centrifuged at 2000 r.p.m. for 40 min. The supernatant with floating particles was decanted onto a Millipore AP20 glass-fiber filter (Millipore, Billerica, MA) and filtered under vacuum. Particles that had adhered to the walls of the tubes were scraped off with a spatula and washed onto filter paper. All material collected on the filter paper

was washed with at least 500 ml of deionized H_2O. The LF was dried for 24 h at 40 ° C and weighed. The residual soil in the centrifuge tubes, containing the HF, was washed at least three times with deionized H_2O, dried at 60 ° C for 72 h and weighed. Before LF and HF were analyzed for total N and organic C, using a N/C Analyzer (Flash 1112 EA, Thermo-Finnigan, Bremen, Germany), soil carbonates were eliminated from the HF using 1 M HCl.

4.2.5. Soil microbial biomass and extractable dissolved organic C estimation

Microbial biomass C was determined by the chloroform fumigation extraction procedure described by Vance et al. (1987) with some modifications. Briefly, 3 g of sieved soil (<2mm) were moistened to 40 % of maximum water-holding capacity and incubated at room temperature overnight. After soil fumigation in air-tight containers with 0.15 ml ethanol-free $CHCl_3$ for 30 min (Gregorich et al., 1990), C was extracted by head-over-head shaking (1 h, 50 rpm) with 0.5 M K_2SO_4 (1:4, w/v). The extracts were centrifuged (3400 rpm, 8 min) and the supernatant was filtered (Whatman no. 42 filter papers). Filtrates were flushed with CO_2-free air to remove residual $CHCl_3$ and extractable C was measured by using a TOC analyser (TOC-5050 A, Shimadzu). Unfumigated controls followed the same procedure. The difference between fumigated and non-fumigated C content was considered as the microbial C content, and is subsequently referred to as microbial biomass C (MBC). The non-fumigated C content was taken as a measure of soluble C in the soil (extractable dissolved organic C, EDOC) (Högberg and Högberg, 2002).

The ratio of microbial biomass C to bulk soil organic C (MBC:SOC) was computed as an index of the proportion of soil organic C that might be readily metabolized (Anderson and Domsch, 1989).

4.2.6. Aboveground biomass index

To assess the effect of aboveground biomass on soil respiration rates within each land use we used the aboveground biomass index (ABI) defined in chapter 3:

$$ABI = AB_1 / D_1 + AB_2 / D_2 + AB_3 / D_3 + \ldots + AB_n / D_n \qquad \text{Eqn. 1}$$

Where AB represents the aboveground biomass (g) of the nearby trees and/or shrubs within a 3 m radius from the collar, and D is the distance (cm) from the soil collar to their stems. Briefly, aboveground biomass was calculated from stem basal diameter measurements, by applying species-specific allometric relationships (Baeza et al., 2006, 2011; G. Barberá, unpublished data; Villalobos et al., 2006).

4.2.7. Statistical analysis

An analysis of variance (ANOVA) was performed for each site to detect differences in soil respiration rates and their potential controlling factors between sampling seasons. Prior to analysis, data were natural-log transformed to meet assumptions of normality and homogeneity of variances. Pearson correlation tests were performed separately for each sampling season to explore the relationships between soil respiration, aboveground plant biomass and belowground properties within each land use type. Soil temperature and moisture were excluded from the bivariate correlation analysis, because the effect of these microclimatic controls on R_s dynamics has been previously described in detail in chapter 3. The influence of vegetation on belowground properties was assessed by linear regression analysis, in which the soil C and N pools were considered as the dependent variables and aboveground and fine root biomass were the independent variables. As a last step, stepwise multiple regression analyses were performed separately for each season to identify the main drivers of soil respiration within each land use. Ten parameters were included in the multiple regression models explaining soil respiration: soil temperature, moisture, aboveground biomass, extractable DOC, microbial and fine root biomass, light fraction C and N content, and heavy fraction C and N content. Careful inspection of plots of regression residuals indicated normality and independence of residuals, and homogeneity of variances within sites. All statistical analyses were performed with SPSS v17 (SPSS, Chicago, IL, USA).

4.3. Results

4.3.1. Soil respiration and belowground properties in two contrasting seasons

Mean values and standard errors of soil respiration, microclimatic variables, and belowground properties within each land use type in the two contrasting seasons are given in Table 4.1. For all land uses, soil respiration rates were significantly higher in April, when temperatures and soil water contents were also higher, than in December, which is in good agreement with the strong seasonal patterns in R_s rates previously reported for this dry Mediterranean ecosystem (Chapter 3). The size of the labile C and N pools changed between sampling seasons, in contrast to the C and N contents in the heavy fraction which remained fairly stable between seasons. Soil microbial biomass was greater in April than in December for all land uses, although the difference was significant only for the open forest site. The C and N contents in the light fraction were significantly higher in December than in April in the open forest and abandoned agricultural field sites, but not in the olive grove site. Contrary to expectations, fine root biomass did not differ significantly between seasons in any of the three land uses.

Across sites, significantly higher MBC: SOC ratios were found in April (2.1 ± 0.1%, 2.0 ± 0.2%, and 1.7 ± 0.2% for open forest, abandoned agricultural field and olive grove site, respectively) than in December (1.1 ± 0.2%, 1.1 ± 0.2%, and 1.3 ± 0.2% for open forest, abandoned agricultural field and olive grove site, respectively), even though the size of the easily decomposable C pool (the sum of light fraction C content and extractable DOC) was smaller in April than in December for all the sites.

Table 4.1. Descriptive statistics (mean ± standard error, and variation coefficient) for soil respiration rates, microclimatic conditions, and belowground properties for three land use sites.

	Open forest		Abandoned agricultural field		Olive grove	
	December	**April**	**December**	**April**	**December**	**April**
R_s (µmol m^{-2} s^{-1})	1.4 ± 0.1[b]	3.2 ± 0.3[a]	1.3 ± 0.2[b]	2.8 ± 0.2[a]	0.7 ± 0.1[b]	2.6 ± 0.2[a]
T_s (°C)	8.1 ± 0.4[b]	15.3 ± 0.3[a]	6.5 ± 0.3[b]	15.4 ± 0.3[a]	7.6 ± 0.3[b]	15.8 ± 0.2[a]
SWC (%)	14.3 ± 1.8[b]	17.7 ± 1.4[a]	14.0 ± 1.0[b]	18.7 ± 0.9[a]	13.1 ± 1.1[b]	18 ± 0.5[a]
FRB (g kg^{-1} soil)	5.8 ± 1.6	7.0 ± 1.7	4.0 ± 0.6	3.7 ± 0.8	2.1 ± 0.3	2.2 ± 0.4
MBC (mg kg^{-1} soil)	489 ± 56[b]	875 ± 75[a]	454 ± 61	639 ± 70	378 ± 51	447 ± 41
EDOC (mg kg^{-1} soil)	314 ± 32[b]	620 ± 79[a]	199 ± 15	186 ± 19	108 ± 14	96 ± 11
LFC (g kg^{-1} soil)	19.8 ± 3.9[a]	12.0 ± 1.5[b]	14.1 ± 2.2[a]	9.0 ± 1.3[b]	5.8 ± 0.7	3.9 ± 0.5
LFN (g kg^{-1} soil)	0.7 ± 0.1[a]	0.5 ± 0.1[b]	0.5 ± 0.1[a]	0.3 ± 0.0[b]	0.3 ± 0.0	0.2 ± 0.0
LF C:N	29.4 ± 1.8	26.1 ± 1.3	29.9 ± 1.7	31.4 ± 1.7	21.3 ± 1.1	21.7 ± 0.3
HFC (g kg^{-1} soil)	25.0 ± 1.4	30.4 ± 2.5	22.5 ± 1.7	27.8 ± 4.4	23.1 ± 2.0	24.5 ± 3.0
HFN (g kg^{-1} soil)	2.0 ± 0.1	2.2 ± 0.1	1.7 ± 0.1[a]	1.4 ± 0.1[b]	1.4 ± 0.1	1.4 ± 0.1
HF C:N	12.8 ± 0.6	14.4 ± 1.8	13.3 ± 0.9[b]	20.1 ± 3.4[a]	18.8 ± 3.6	18.6 ± 2.9

R_s, soil respiration; Ts, soil temperature; SWC, soil water content; FRB, fine root biomass; MBC; microbial biomass C; EDOC, extractable dissolved organic C; LFC, light fraction C; LFN, light fraction N; LF C:N, C-to-N ratio in LF; HFC, heavy fraction C; HFN, heavy fraction N; HF C:N, C-to-N ratio in HF. For each land use, different letters (a-b) within the same row indicate statistically significant differences (p < 0.05) between sampling periods, according to Tukey´s test.

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4.3.2. Relationships between aboveground biomass, belowground properties and soil respiration within each site

Fewer significant correlations and also lower correlation coefficients between R_s rates, aboveground biomass and belowground properties were found in April than in December for all land uses (Tables 4.2a, b). The labile soil organic matter fractions (light fraction C and N contents, microbial biomass C, and extractable DOC) were consistently and strongly correlated correlated with one another, and to a lesser extent, with the intermediate or recalcitrant C and N pools (HFC, HFN) for all land uses in both sampling seasons. However, patterns in the relationships between vegetation attributes (e.g., aboveground and fine root biomass), belowground properties and R_s differed considerably between sites and seasons.

In the olive grove site, aboveground and fine root biomass were strongly correlated with each other (R > 0.74; P < 0.01), and both were in turn positively correlated to all belowground properties except HFC at both sampling times (R > 0.64; P < 0.01). Soil respiration was strongly correlated with all the labile soil C and N pools and vegetation attributes in December, whereas the light fraction C content was the only variable related to R_s in April.

In contrast to the olive grove site, there was no significant correlation between aboveground and fine root biomass in the open forest site for any sampling time. The correlation coefficients between vegetation attributes and the labile soil C and N pools were very high in December, but weak or non-significant in April at this site. Within-site variability in soil respiration was strongly related to above- and belowground vegetation attributes, as well as to all the labile soil C and N pools in December. However, the heavy fraction C content was the only parameter related to within-site variability in R_s rates in April.

In the abandoned agricultural field site, aboveground biomass was not correlated with fine root biomass in either December or April. A complete lack of correlation between vegetation attributes and belowground properties was observed in the abandoned agricultural field site at both sampling times. R_s was strongly related to heavy fraction C content and microbial biomass in December, whereas microbial biomass was the sole belowground parameter related to R_s rates in April at this site.

Table 4.2a Pearson´s correlations coefficients between soil respiration (R_s), aboveground plant biomass and belowground properties in December 2006 for each land use site.

	R_s	ABI	FRB	MB	EDOC	LFC	LFN	HFC	HFN
Open forest									
R_s (μmol m^{-2} s^{-1})	1.00								
ABI	**0.914****	1.00							
FRB (g kg^{-1})	**0.644***	0.417	1.00						
MBC (mg kg^{-1})	**0.624***	**0.620***	0.549	1.00					
EDOC (mg kg^{-1})	**0.905****	**0.867****	**0.588***	**0.783****	1.00				
LFC (g kg^{-1})	**0.825****	**0.809****	0.511	**0.832****	**0.874****	1.00			
LFN (g kg^{-1})	**0.887****	**0.861****	**0.614***	**0.792****	**0.919****	**0.970****	1.00		
HFC (g kg^{-1})	0.433	0.491	0.273	0.047	0.250	0.091	0.253	1.00	
HFN (g kg^{-1})	0.381	0.349	0.258	-0.167	0.250	0.091	0.253	**0.703***	1.00
Abandoned field									
R_s (μmol m^{-2} s^{-1})	1.00								
ABI	0.357	1.00							
FRB (g kg^{-1})	0.197	-0.068	1.00						
MBC (mg kg^{-1})	**0.658***	0.319	0.108	1.00					
EDOC (mg kg^{-1})	0.448	0.178	0.243	**0.732****	1.00				
LFC (g kg^{-1})	0.602	0.457	0.262	**0.951****	**0.768****	1.00			
LFN (g kg^{-1})	0.538	0.321	0.294	**0.930****	**0.724***	**0.953****	1.00		
HFC (g kg^{-1})	**0.804****	0.323	-0.143	**0.809****	0.545	**0.669***	**0.632***	1.00	
HFN (g kg^{-1})	0.595	0.483	0.309	**0.637***	**0.701***	**0.680***	**0.721***	**0.658***	1.00
Olive grove									
R_s (μmol m^{-2} s^{-1})	1.00								
ABI	**0.682***	1.00							
FRB (g kg^{-1})	**0.657***	**0.739****	1.00						
MBC (mg kg^{-1})	**0.672***	**0.802****	**0.801****	1.00					
EDOC (mg kg^{-1})	**0.704***	**0.901****	**0.899****	**0.811****	1.00				
LFC (g kg^{-1})	**0.898****	**0.647***	**0.688***	**0.842****	**0.746****	1.00			
LFN (g kg^{-1})	**0.863****	**0.747****	**0.797****	**0.874****	**0.871****	**0.962****	1.00		
HFC (g kg^{-1})	0.286	0.049	-0.014	0.014	0.057	0.264	0.166	1.00	
HFN (g kg^{-1})	0.583	**0.744****	**0.872****	**0.781****	**0.766****	0.586	**0.673***	-0.174	1.00

* P < 0.05; ** P < 0.001.
ABI, Aboveground Biomass Index; FRB, fine root biomass; MBC, microbial biomass C; EDOC, extractable dissolved organic C; LFC, light fraction C; LFN, light fraction N; HFC, heavy fraction C; HFN, heavy fraction N.

Table 4.2b. Pearson´s correlations coefficients between soil respiration rate (R_s), aboveground plant biomass and belowground properties in April 2007 for each land use site.

	R_s	ABI	FRB	MB	EDOC	LFC	LFN	HFC	HFN
Open forest									
R_s (µmol m^{-2} s^{-1})	1.00								
ABI	-0.026	1.00							
FRB (g kg^{-1})	0.289	-0.069	1.00						
MBC (mg kg^{-1})	0.004	0.412	0.551	1.00					
EDOC (mg kg^{-1})	-0.268	**0.618***	0.212	**0.865***	1.00				
LFC (g kg^{-1})	0.126	0.411	0.340	**0.757****	**0.711****	1.00			
LFN (g kg^{-1})	0.008	**0.584***	0.110	**0.632***	**0.754****	**0.933****	1.00		
HFC (g kg^{-1})	**0.635***	0.009	0.206	0.312	0.105	**0.612***	0.464	1.00	
HFN (g kg^{-1})	-0.231	0.244	-0.259	0.218	0.358	0.268	0.401	0.010	1.00
Abandoned field									
R_s (µmol m^{-2} s^{-1})	1.00								
ABI	0.466	1.00							
FRB (g kg^{-1})	-0.438	-0.252	1.00						
MBC (mg kg^{-1})	**0.845****	0.422	-0.226	1.00					
EDOC (mg kg^{-1})	0.390	0.204	0.225	0.569	1.00				
LFC (g kg^{-1})	0.363	0.536	0.276	**0.623***	**0.724***	1.00			
LFN (g kg^{-1})	0.306	0.259	0.270	0.599	**0.874****	**0.901****	1.00		
HFC (g kg^{-1})	0.292	0.340	-0.026	0.241	0.520	0.536	0.579	1.00	
HFN (g kg^{-1})	0.155	-0.412	0.098	0.350	0.377	0.295	0.582	0.347	1.00
Olive grove									
R_s (µmol m^{-2} s^{-1})	1.00								
ABI	0.302	1.00							
FRB (g kg^{-1})	0.531	**0.815****	1.00						
MBC (mg kg^{-1})	0.354	**0.902****	**0.873****	1.00					
EDOC (mg kg^{-1})	0.471	**0.759****	**0.852****	**0.729****	1.00				
LFC (g kg^{-1})	**0.636***	**0.757****	**0.953****	**0.777****	**0.935****	1.00			
LFN (g kg^{-1})	0.610	**0.762****	**0.966****	**0.801****	**0.934****	**0.996****	1.00		
HFC (g kg^{-1})	0.563	-0.054	0.038	-0.228	0.104	0.123	0.165	1.00	
HFN (g kg^{-1})	0.240	**0.810****	**0.873****	**0.873****	**0.732***	**0.792***	**0.829****	-0.334	1.00

* $P < 0.05$; ** $P < 0.001$.

ABI, Aboveground Biomass Index; FRB, fine root biomass; MBC, microbial biomass C; EDOC, extractable dissolved organic C; LFC, light fraction C; LFN, light fraction N; HFC, heavy fraction C; HFN, heavy fraction N.

4.3.3. Influence of vegetation patterns on soil carbon and nitrogen pools within each land use

Vegetation attributes (above- and fine root biomass) were included in separate regression models to assess the influence of vegetation structure (and its spatial distribution) on the spatial patterns of soil C and N pools within each land use. A tight coupling of soil C and N pools with vegetation patterns was evident in both open forest and olive grove sites (Table 4.3). Variability in all the labile C and N pools was strongly related to the vegetation biomass and distribution patterns at both sites. The C content in the heavy fraction did not track the vegetation spatial patterns at any site, while the N content in the heavy fraction was related to vegetation attributes in the olive grove site only. Interestingly, soil C and N pools were completely decoupled from vegetation patterns in the abandoned agricultural field site.

Table 4.3. Regression coefficients between vegetation attributes (aboveground and fine root biomass), and soil C and N pools in two contrasting seasons for each site.
(- non significant; * P <0.05; ** P < 0.001)

	Open forest		Abandoned field		Olive grove	
	December	April	December	April	December	April
MBC (mg kg^{-1} soil)	0.71*	0.51*	-	-	0.87**	0.89**
EDOC (mg kg^{-1} soil)	0.91**	0.46*	-	-	0.87**	0.73*
LFC (g kg^{-1} soil)	0.68*	-	-	-	0.61*	0.87**
LFN (g kg^{-1} soil)	0.74*	-	-	-	0.68*	0.92**
HFC (g kg^{-1} soil)	-	-	-	-	-	-
HFN (g kg^{-1} soil)	-	-	-	-	0.67*	0.67*
SOC (g kg^{-1} soil)	0.83**	-	-	-	0.81*	0.89**
TN (g kg^{-1} soil)	0.76*	-	-	-	0.74*	0.48*

MBC, microbial biomass C; EDOC, extractable dissolved organic C; LFC, light fraction C; LFN, light fraction N; HFC, heavy fraction C; HFN, heavy fraction N; SOC, bulk soil OC; TN, bulk soil total N.
Notes: Bulk soil organic C and total N data are from Chapter 3.

4.3.4. Factors controlling soil respiration within each land use

Multiple regression analyses (stepwise) were performed for each land use and sampling season, in order to identify the major controls on soil respiration in this dry Mediterranean ecosystem. The models that best explained within-site R_s variation in the different sampling periods are shown in Table 4.4. In the olive grove site, the light fraction C content was the single best predictor of R_s in both seasons, accounting for 67 and 41% of within-site variation in this parameter in December and April, respectively. In the open forest site, aboveground (84%) and fine root biomass (7%) together accounted for 91% of soil respiration variation in December, while the C content in the heavy fraction as a single variable explained 42% of R_s within-site variation in April. In the abandoned agricultural field site, the heavy fraction C content accounted for 70% of R_s variability in December, whereas microbial biomass (55%) and soil water content (15%) together explained 70% of R_s variability in April.

4.4. Discussion

The strong influence of aboveground biomass patterns on soil carbon pools and respiration rates was evident in both forest and olive grove sites, but not in the abandoned agricultural field site (Tables 4.2 and 4.3). This is in agreement with the results previously reported in Chapter 3, in which monthly R_s rates were consistently and significantly higher in soil beneath tree/shrub canopies than in inter-canopy locations in the open forest and olive grove sites, but not in the abandoned agricultural field site (Chapter 3, Fig. 3.3). The lack of influence of vegetation patterns on soil C pool sizes and respiration rates in the abandoned agricultural field highlights how site history can have long-lasting impacts on soil C cycling (Asner et al., 2003; Dupouey et al., 2002; Koerner et al 1997; Ruiz-Navarro et al., 2009), and the difficulty that these Mediterranean ecosystems have in recovering their original C pools and cycling patterns after disturbance (i.e., clearing of native woody vegetation for cereal cultivation; Albaladejo et al., 1998; Vallejo et al., 2006). It has often been reported that establishment of tree/shrubs on former herbaceous patches can increase markedly the near-surface (0-15 cm) soil C and N pools beneath their canopies after few decades, thus leading to a patchy spatial distribution of organic matter and nutrients, and therefore soil C dynamics (Hibbard et al., 2001; McCulley et al., 2004). However, we

found that neither soil C and N pools nor R_s rates (Table 4.3, Chapter 3, Table 3.4) are currently influenced by extant above- or belowground vegetation patterns in the abandoned agricultural field, despite the 30 years elapsed since cereal cultivation abandonment. The low aboveground standing biomass in the abandoned agricultural field site compared to the open forest and olive grove sites (Chapter 2, Table 2.1) suggests that a threshold value of aboveground biomass may need to be reached before belowground properties and R_s rates start reflecting the patchy distribution of woody vegetation in this dry Mediterranean ecosystem. In fact, the main controls on R_s variation in the old-field (heavy fraction C in December, and both soil microbial biomass and water content in April; see Table 4.4) were not directly linked to recent plant derived-C inputs to soil (e.g., extractable DOC, a conservative index of root exudate production, or light fraction C) for any sampling season.

In the open forest, on the contrary, the spatial distribution of vegetation was by far the main determinant of the spatial patterns of soil respiration observed in December, when aboveground and fine root biomass together explained 91% of the within-site variation in R_s (Table 4.4). This result was expected since vegetation structure and density have been shown to strongly influence soil C and N pools patterns, and hence soil respiration rates, in many late-successional forest ecosystems (Arevalo et al., 2010; Merbold et al., 2011; Søe and Buchmann, 2005). However, soil respiration rates in April appeared to be related only to the intermediate or recalcitrant C pool (HFC), despite two-fold greater soil microbial biomass and extractable DOC (a conservative index of root exudate production) at this time. Soil respiration peaks in April in this Mediterranean ecosystem, coinciding with maximum photosynthetic activity and net primary productivity (Chapter 3). In addition to optimal soil moisture and temperature conditions for microbial activity, the high rates of R_s in late April may be directly linked to current high rates of photosynthesis and root activity (Grünzweig et al., 2003; Högberg et al., 2001; Janssens et al., 2001; reviewed by Kuzyakov and Gavrichkova, 2010; Tang et al., 2005; Vargas and Allen, 2008). Active roots and mycorrhizal hyphae continuously exude organic materials to the surrounding soil in the form of easily decomposable substrates such as sugars, amino acids, peptides and organic acids (Gleixner et al., 2005; Grayston et al., 1997; Norton and Firestone, 1991; Sun et al., 1999). Previous studies have indicated that a photosynthesis-induced priming effect resulting from root exudate production may account for a substantial increase in SOM decomposition rates, since increased supply of easily decomposable compounds enhances microbial activity (Kuzyakov and Cheng, 2001, 2004). The pulse of exudates released by

Table 4.4. Stepwise[a] multiple linear regressions results for soil respiration (Rs, in $\mu mol\ m^{-2}\ s^{-1}$) in the open forest, abandoned agricultural field and olive grove sites in December and April.

Site	Season	Independent variables	Unstandardized partial regression coefficient	Standardized partial regression coefficient	Adj. R^2	*F*	*P* value
Open forest	December	Intercept	1.006 ± 0.060				
		Ln(ABI) (g cm^{-1})	0.088 ± 0.012	0.775			
		Fine root biomass (g kg^{-1} soil)	0.015 ± 0.005	0.304	0.908	55.04	<0.0001
	April	Intercept	0.642 ± 0.899				
		Heavy fraction C (g kg^{-1} soil)	0.086 ± 0.029	0.689	0.422	9.022	0.013
Abandoned field	December	Intercept	$- 0.656 \pm 0.412$				
		Heavy fraction C (g kg^{-1} soil)	0.088 ± 0.018	0.856	0.703	24.69	0.001
	April	Intercept	$- 0.842 \pm 0.931$				
		Microbial biomass C (mg kg^{-1} soil)	0.003 ± 0.001	0.792			
		Soil water content (%)	0.106 ± 0.044	0.410	0.706	13.00	0.003
Olive grove	December	Intercept	0.122 ± 0.131				
		Light fraction C (g kg^{-1} soil)	0.098 ± 0.021	0.840	0.672	21.48	0.001
	April	Intercept	1.557 ± 0.418				
		Light fraction C (g kg^{-1} soil)	0.272 ± 0.101	0.690	0.410	7.26	0.027

[a] Ten potential predictive variables were considered for the multiple regression models explaining soil CO_2 efflux: soil temperature, moisture, aboveground biomass, extractable dissolved organic C, microbial and fine root biomass, light fraction C and N content, and heavy fraction C and N content.

roots and mycorrhizae during spring may have stimulated microbial activity in the rhizosphere (Nobili et al., 2000) and may have enhanced decomposition of intermediate or recalcitrant soil organic matter to improve microbial access to limiting N (Kuzyakov, 2002). We suggest that an extra pulse of CO_2 may have occurred in April in those soil spots where HFC content is higher, as a result of microbial activation by root and mycorrhizal exudates (priming effect).

The olive grove site showed very little or no seasonality in the belowground properties measured in this study (Table 4.1). Aside from higher soil temperature, water content, and respiration rates in April than in December, none of the belowground properties measured differed significantly between sampling seasons at this site. The strong influence of vegetation patterns on belowground properties was expected at this site, because consistently higher rates of C and N inputs derived from leaf-litter and fine root detritus have occurred in soil beneath olive tree canopies than in the inter-canopy locations during 100 years under cultivation. In fact, light fraction C content was the main driver of R_s spatial variation at the olive grove site in both seasons (Table 4.4). These results agree with those reported by several authors (Alvarez et al., 1998; Alvarez and Alvarez, 2000; Janzen et al., 1992; Muñoz et al., 2007; Zhang et al., 2007), who found that light fraction C was the main driving factor of R_s in soils under pasture and agriculture, as well as under different tillage systems. In long-term cultivated soils, the decrease in light fraction C is more significant than that in other C fractions, because of lower plant derived-C inputs to soil and faster decomposition rates of this fraction (Barrios et al., 1996; Cambardella and Elliot, 1992; Christensen, 2000; Janzen et al., 1992). The olive grove site does not receive any amendment, so leaf and root litter inputs are the main carbon, energy and nutrient sources for soil microorganisms in this system. Despite lower microbial biomass in the olive grove than in the open forest and abandoned agricultural field, we found the highest leaf litter decomposition rates in the olive grove (Chapter 2). The narrower C:N ratios of leaf and root litter (26.4 and 34.6, respectively) in the olive grove than in the other sites (89.5 and 56.4 in the open forest, and 94.1 and 63.2, in the abandoned agricultural field, respectively) are indicative of a more easily decomposable substrate. Further, tillage operations conducted twice or three times a year break down and redistribute this labile C pool over the hill-slope (Christensen, 2000; Six et al., 1998), while enhancement of soil water erosion rates by cultivation and higher sun radiation exposure and soil temperature (Austin and Vivanco, 2006; Jacinthe et al., 2004; Throop and Archer, 2007) may further accelerate decomposition of this labile pool in the olive grove. We found that within-site R_s

variation was strongly modulated by LFC availability in the olive grove (Table 4.4), as this is the soil C pool which is more readily accessible to microbial activity.

4.5. Conclusions

Conversion of native woodland to agricultural land and subsequent land abandonment leads to profound changes in the relationships between R_s, aboveground biomass and belowground properties.

Our results suggest that long-recovery times (>30 years) may be needed and/or a threshold value of standing biomass may need to be reached before soil C and N pools and R_s rates start reflecting the patchy distribution of woody vegetation, thus highlighting the limited capacity for soil C accretion and sequestration of abandoned agricultural fields in this dry Mediterranean ecosystem.

Given that native vegetation recovery in abandoned croplands has been proposed as one of the most promising options for C emission offsets under the Kyoto Protocol, we suggest that current estimates of net increases in soil C storage during old-field succession in the Mediterranean region should be taken with caution.

References

Adachi, M., Bekku, Y.S., Rashidah, W., Okuda, T., Koizumi, H., 2006. Differences in soil respiration between different tropical ecosystems. Applied Soil Ecology 34, 258-265.

Albaladejo, J., Martínez-Mena, M., Roldan, A., Castillo, V., 1998. Soil degradation and desertification induced by vegetation removal in a semiarid environment. Soil Use and Management 14, 1-5.

Álvarez, C.R., Álvarez, R., Grigera, M.S., Lavado, R.S., 1998. Associations between organic matter fractions and the active soil microbial biomass. Soil Biology and Biochemistry 30, 767-773.

Álvarez, R., Álvarez, C.R., 2000. Soil organic matter pools and their associations with carbon mineralization kinetics. Soil Science Society of America Journal 64, 184-189.

Álvaro-Fuentes, J., Cantero-Martinez, C., 2010. Short communication. Potential to mitigate anthropogenic CO_2 emissions by tillage reduction in dryland soils of Spain. Spanish Journal of Agricultural Research 8 (4), 1271-1276.

Anderson, T.H., Domsch, K.H., 1989. Ratios of microbial biomass carbon to total organic carbon in arable soils. Soil Biology and Biochemistry 21, 471-479.

Arevalo, C.B.M., Bhatti, J.S., Chang, S.X., Jassal, R.S., 2010. Soil respiration in four different land uses systems in north central Alberta, Canada. Journal of Geophysical Research 115, doi:10.1029/2009JG001006.

Asner, G.P., Archer, S., Hughes, R.F., Ansley, R.J., Wessman, C.A., 2003. Net changes in regional woody vegetation cover and carbon storage in Texas Dryland 1937-1999. Global Change Biology 9, 316-335.

Austin, A.T., Vivanco, L., 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nature 442, 555-558.

Baeza, M.J., Raventós, J., Escarré, A., Vallejo, V.R., 2006. Fire risk and vegetation structural dynamics in Mediterranean shrubland. Plant Ecology 187 (2), 189-201.

Baeza, M.J., Santana, V.M., Pausas, J.G., Vallejo, V.R., 2011. Successional trends in standing dead biomass in Mediterranean basin species. Journal of Vegetation Science 22(3), 467-474.

Bahn, M., Janssens, I.A., Reichstein, M., Smith, P., Trumbore, S.E., 2010. Soil respiration across scales: towards an integration of patterns and processes. New Phytologist 186, 292-296.

Barrios, E., Buresh, R.J., Sprent, J.I., 1996. Organic matter in soil particle size and density fractions from maize and legume cropping systems. Soil Biology and Biochemistry 28 (2), 185-193.

Bond-Lamberty, B., Thomson, A., 2010. Temperature-associated increases in the global soil

respiration record. Nature 464, 579-582

Cambardella, C.A., Elliot, E.T., 1992. Particulate soil organic matter changes across a grassland cultivation sequence. Soil Science Society of America Journal 56, 777-783.

Casals, P., Gimeno, C., Carrara, A., López-Sangil, L., Sanz, M.J., 2009. Soil CO_2 efflux and extractable organic carbon fractions under simulated precipitation events in Mediterranean Dehesa. Soil Biology and Biochemistry 41, 1915-1922.

Christensen, B.T., 1992. Physical fractionation of soil and organic matter in primary particle size and density separates. Advances in Soil Sciences 20, 1-90.

Christensen, B.T., 2000. Organic matter in soil-structure, function and turn over. DIAS Report No. 30 Plant Production, Tjele, p.95.

Curiel-Yuste, J., Baldocchi, D.D., Gershenson, A., Goldstein, A., Misson, L., Wong, S., 2007. Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture. Global Change Biology 13, 2018-2035.

Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperature mixed hardwood forest. Global Change Biology 4, 217-227.

Dilustro, J.J., Collins, B., Duncan, L., Crawford, C., 2004. Moisture and soil texture effects on soil CO_2 efflux components in south-eastern mixed pine forest. Forest Ecology and Management 204, 85-95.

Dupouey, J.L., Dambrine, E., Laffite, J.D., Moares, C., 2002. Irreversible impact of past land use on forest soils and biodiversity. Ecology 83 (11), 2978-2984.

Echeverría, M.E., Markewitz, D., Morris, L.A., Ronald, L.H., 2004. Soil organic matter fractions under managed pine plantantions of the southeast USA. Soil Science Society of America Journal 68, 950-958.

Edwards, C.A., Reichle, D.E., Crossley, D.A.Jr., 1970. The role of soil invertebrates in turnover of organic matter and nutrients. In: Reichle, D.E. (Eds) Analysis of temperate forest ecosystems, Springer-Verlag, New York, 12-172 pp.

Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., Rumpel, C., 2007. Stability of organic carbon in depth soil layers controlled by fresh carbon supply. Nature 450, 277-281.

Gleixner, G., Kramer, C., Hahn, V., Sachse, D., 2005. The effect of biodiversity on carbon storage in soils. In: Forest Diversity and Function: Temperate and Boreal Systems (eds. Scherer-Lorenzen, M., Korner, C., Schulze, E.D.), Springer-Verlag, Berlin, Germany, 165-183 pp.

Golchin, A., Asgari, H., 2008. Land use effects on soil quality indicators in north-eastern Iran. Australian Journal of Soil Research 46, 27-36.

Grayston, S.J., Vaughan, D., Jones, D., 1997. Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. Applied Soil Ecology 5, 29-56.

Gregorich, E.G., Wen, G., Voroney, R.P., Kachanoski, R.G., 1990. Calibration of a rapid direct chloroform extraction method for measuring soil microbial biomass C. Soil Biology and Biochemistry 22, 1009-1011.

Grünzweig, J.M., Lin, T., Rotenberg, E., Schwartz, A., Yakir, D., 2003. Carbon sequestration in arid-land forest. Global Change Biology 9, 791-799.

Hibbard, K.A., Archer, S., Schimel, D.S., Valentine, D.W., 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. Ecology 82(7), 1999-2011.

Högberg, M.N., Högberg, P., 2002. Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. New Phytologist 154, 791-795.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A.F., Ekblad, A., Högberg, M.N., Nyberg, G., Ottosson-Löfvenius, M., Read, D.J., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411, 789-792.

Jacinthe, P.A., Lal, R., Owens, L.B., Hothem, D.L., 2004. Transport of labile carbon in runoff as affected by land use and rainfall characteristics. Soil and Tillage Research 77, 111-123.

Jackson, R. B., Banner, J. L., Jobbagy, E. G., Pockman, W. T., Wall, D. H., 2002. Ecosystem carbon loss with woody plant invasion of grassland. Nature 418, 623–626.

Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Guðmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N.O., Vesala, T., Granier, A., Schulze, E.D., Lindroth, A., Dolman, A.J., Jarvis, P.G., Ceulemans, R., Valentini, R., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Global Change Biology 7(3), 269-278.

Janzen, H.H., Campbell, C.A., Brandt, S.A., Lafond, G.P., Townley-Smith, L., 1992. Light-fraction organic matter in soils from long-term crop rotations. Soil Science of Society America Journal 56(6), 1799-1806.

Kieft, T. L., Carleton, S. W., Loftin, S. R., Aguilar, R., Craig, J., Skaar, D. A., 1998. Temporal dynamics in soil carbon and nitrogen resources at a grassland–shrubland ecotone. Ecology 2, 671–683

Koerner, W., Dupouey, J.L., Dambrine, E., Benoît, M., 1997. Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. Journal of Ecology 85(3), 351-358.

Kuzyakov, Y., 2002. Review: Factors affecting rhizosphere priming effects. Journal of Plant and Soil Science 165, 382-396.

Kuzyakov, Y., Cheng, W., 2001. Photosynthesis controls of rhizosphere respiration and organic matter decomposition. Soil Biology and Biochemistry 33, 1915-1925.

Kuzyakov, Y., Cheng, W., 2004. Photosynthesis controls of CO_2 efflux from maize Rhizosphere. Plant and Soil 263, 85-99.

Kuzyakov, Y., Gavrichkova, O., 2010. Time lag between photosynthesis and carbon dioxide efflux from soil: A review of mechanisms and controls. Global Change Biology 16(12), 3386-3406.

Law, B.E., Baldocchi, D.D., Anthoni, P.M., 1999. Below-canopy and soil CO_2 fluxes in a ponderosa pine forest. Agricultural and Forest Meteorology 94, 171-188.

Maestre, F.T., Cortina, J., 2003. Small-scale spatial variation in soil CO_2 efflux in a Mediterranean semiarid steppe. Applied Soil Ecology 23, 199-209.

Martínez-Mena, M., Álvarez Rogel, J., Castillo, V., Albaladejo, J., 2002. Organic carbon and nitrogen losses influenced by vegetation removal in a semi-arid soil. Biogeochemistry 61 (3), 309-321.

Martínez-Mena, M., López, J., Almagro, M., Boix-Fayos, C., Albaladejo, J., 2008. Effect of water erosion and cultivation on the soil carbon stock in a semiarid area of South-East Spain. Soil and Tillage Research 99, 119-129.

McCulley, R.L., Archer, S.R., Boutton, T.W., Hons, F.M., Zuberer, D.A., 2004. Soil respiration and nutrient cycling in wooded communities developing in grassland. Ecology 85(10), 2804-2817.

Merbold, L., Ziegler, W., Mukelabai, M.M., Kutsch, W.L., 2011. Spatial and temporal variation of CO_2 efflux along a disturbance gradient in a *miombo* woodland in Western Zambia. Biogeosciences 8, 147-164.

Mielnick, P.C., Dugas, W.A., 2000. Soil CO_2 efflux in a tallgrass prairie. Soil Biology and Biochemistry 32 (2), 221-228.

Muñoz, C., Zagal, E., Ovalle, C., 2007. Influence of trees on soil organic matter in Mediterranean agroforestry systems: an example from the "Espinal" of central Chile. European Journal of Soil Science 58, 728-735.

Norton, J.M., Firestone, M.K., 1991. Metabolic status of bacteria and fungi in the Rhizosphere of ponderosa-pine seedlings. Applied and Environmental Microbiology 57, 1161-1167.

Nobili, M., Contin, M., Mondini, C., Brookes, P.C., 2000. Soil microbial biomass is triggered into activity by trace amounts of substrate. Soil Biology and Biochemistry 33, 1163-1170.

Padilla, F.M., Vidal, B., Sánchez, J., Pugnaire, F.I., 2010. Land use changes and carbon sequestration through the twentieth century in a Mediterranean mountain ecosystem: Implications for land management. Journal of Environmental Management 91, 2688-2695.

Powlson, D.S., Gregory, P.J., Whalley, W.R., Quinton, J.N., Hopkins, D.W., Whitmore, A.P., Hirsch, P.R., Goulding, K.W.T., 2011. Soil management in relation to sustainable agriculture and ecosystem services. Food Policy 36, 572-587.

Qi, Y.C., Dong, Y.S., Jin, Z., Peng, Q, Xiao, S.S., He, Y.T., 2010. Spatial heterogeneity of soil nutrients and respiration in the desertified grasslands of Inner Mongolia, China. Pedosphere 20 (5), 655-665.

Rey, A., Pegoraro, E., Oyonarte, C., Were, A., Escribano, P., Raimundo, J., 2010. Impact of land degradation on soil respiration in a steppe (*Stipa tenacissima* L.) semi-arid ecosystem in the SE of Spain. Soil Biology and Biochemistry 43(2), 393-403.

Rodeghiero, M., Cescatti, A., 2008. Spatial variability and optimal sampling strategy of soil respiration. Forest Ecology and Management 255, 106-112.

Romanyà, J., Casals, P., Cortina, J., Bottner, P., Coûteaux, M.M., Vallejo, V.R., 2000. CO_2 efflux from a Mediterranean semi-arid forest soil. II. Effects of soil fauna and surface stoniness. Biogeochemistry 48, 283-306.

Ruiz-Navarro, A., Barberá, G.G., Navarro-Cano, J.A., Albaladejo, J., Castillo, V.M., 2009. Soil dynamics in *Pinus halepensis* reforestation: Effect of microenvironments and previous land use. Geoderma 153, 353-361.

Saiz, G., Green, C., Butterbach-Bahl, K., Kiese, R., Avitabile, V., Farrel, E.P., 2006. Seasonal and spatial variability of soil respiration in four Sitka spruce stands. Plant and Soil 287 (1-2), 161-176.

Sala, O.E., Chapin, F.S., Arnesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., et al., 2000. Biodiversity: Global biodiversity scenarios for the year 2100. Science 287, 1770-1774.

Schlesinger, W. H., Pilmanis, A. M., 1998. Plant–soil interactions in deserts. Biogeochemistry 42, 169–187.

Scott-Denton, L.E., Sparks, K.L., Monson, R.K., 2003. Spatial and temporal control of soil respiration rate in a high-elevation, subalpine forest. Soil Biology and Biochemistry 35, 525-534.

Six, J., Elliot, E.T., Paustian, K., Doran, J.W., 1998. Aggregation and soil organic matter accumulation in cultivated and native soils. Soil Science Society of American Journal 62 (5), 1367-1377.

Søe, A.R.B., Buchmann, N., 2005. Spatial and temporal variations in soil respiration in relation to stand structure and soil parameters in an unmanaged beech forest. Tree Physiology 25, 1427-1436.

Stoyan, H., De-Polli, H., Böhm, S., Robertson, G.P., Paul, E.A., 2000. Spatial heterogeneity of soil respiration and related properties at the plant scale. Plant and Soil 222, 203-214.

Sun, Y.P., Unestam, T., Lucas, S.D., Johanson, K.J., Kenne, L., Finlay, R.D., 1999. Exudation-reabsorption in mycorrhizal fungi, the dynamic interface for interaction with soil and other microorganisms. Mycorrhiza 9, 137-144.

Tang, J., Baldocchi, D.D., Xu, L., 2005. Tree photosynthesis modulates soil respiration on a diurnal time scale. Global Change Biology 11, 1298-1304.

Throop, H.L., Archer, S.R., 2007. Interrelationships among shrub encroachment, land management, and litter decomposition in a semidesert grassland. Ecological Applications 17 (6), 1809-1823.

Vallejo, R., Aronson, J., Pausas, J.G., Cortina, J., 2005. Restoration of Mediterranean woodlands, in: van Andel, J., Aronson, J. (Eds.), Restoration Ecology. The new frontier. Blackwell Science Ltd., pp. 193-207.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biology and Biochemistry 19 (6), 703-707.

Vargas, R., Allen, M.F., 2008. Environmental controls and the influence of vegetation type, fine roots and rhizomorphs on diel and seasonal variation in soil respiration. New Phytologist 179, 460-471.

Villalobos, F.J., Testi, L., Hidalgo, J., Pastor, M., Orgaz, F., 2006. Modelling potential growth and yield of olive (*Olea europaea* L.) canopies. European Journal of Agronomy 24, 296-303.

Wang, W.J., Zu, Y.G., Wang, H.M., Hirano, T., Takagi, K., Sasa, K., Koike, T., 2005. Effect of collar insertion on soil respiration in a larch forest measured with a LI-6400 soil CO_2 flux system. Journal of Forest Research 10, 57–60.

Wiant, H.V., 1967. Has the contribution of litter decay to forest soil respiration been overestimated? Journal of Forestry 65, 408-409.

Xu, M., Qi, Y., 2001. Soil-surface CO_2 efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. Global Change Biology 7, 667-677.

Zhang, J., Song, C., Wenyan, Y., 2007. Tillage effects on soil carbon fractions in the Sanjiang Plain, North China. Soil and Tillage Research 93, 102-108.

5. Factors controlling leaf-litter decomposition dynamics: dependence on litter type and site conditions

Abstract

Plant litter decomposition plays an important role in the turnover and storage of soil organic matter in terrestrial ecosystems. Conversion of native vegetation to agricultural lands and subsequent land abandonment leads to shifts in canopy structure, and consequently influences decomposition dynamics by alterations in soil temperature and moisture conditions, solar radiation exposure, and runoff and soil erosion patterns. Using the litterbag technique, we incubated leaf litter of *Pinus halepensis* and *Rosmarinus officinalis* in two Mediterranean land use types (open forest and abandoned agricultural field sites). Our objectives were: (1) to compare the mass loss rates and changes in nitrogen content of these two predominant litter types and (2) to assess whether the factors controlling decomposition dynamics differ between litter types. Fresh local litter lost between 20 and 55% of its initial mass throughout the 20-month incubation period. Rosemary litter decomposed about three-times faster than pine litter, showing net N immobilization in the early stages of decomposition, in contrast to the net N release exhibited by pine litter. The influence of site on decomposition rates was significant for both species despite the fact that no significant differences in soil temperature or water availability were found between specific locations or land uses throughout the study period. Linear models adequately explained a proportion of the cross-site variability in mass loss rates for each litter type and sampling period, but major controls on mass loss rates differed between species. Parameters related to litter quality (N content or C:N) were found to explain the variation in mass loss rates for rosemary across sites. However, differences in mass loss rates for Aleppo pine were explained by variations in ash content (an index of soil deposition on litter). Taken together, the results from this study suggest that decomposition drivers may differ depending on litter type in this Mediterranean ecosystem. While the more labile rosemary litter was degraded mainly by microbial activity, decomposition of the more recalcitrant pine litter was likely driven primarily by physicochemical processes like soil erosion and photodegradation.

5.1. Introduction

Plant litter decomposition is a key component in the terrestrial ecosystem carbon (C) and nitrogen (N) cycles, and it provides the primary source of nutrients for plants, and of both nutrients and energy for soil microorganisms (Currie, 2003). As a result of the ongoing global climate change, and the increasingly acknowledged importance of the roles of litter and soil organic matter as potential C sinks, much effort is being devoted to improving our understanding of the mechanisms driving litter decomposition dynamics and subsequent soil C storage.

Understanding the factors that control litter decomposition is particularly important in heterogeneous water-limited ecosystems, because of the small amount of soil organic matter and low availability of mineral nutrients (Carreira et al., 1996; Rashid and Ryan, 2004) compared with other ecosystems. Besides, the high mineralization rates (Martínez-Mena et al., 2002), and the episodic nature of precipitation events (Austin et al., 2004; Huxman et al., 2004) and associated soil water erosion processes (Martínez-Mena et al., 2001) might constrain the C sequestration potential of these ecosystems, making them highly susceptible to global change and prone to degradation.

Extensive research has focused on predicting litter decay rates based on climate, litter quality and soil biotic interactions (Aerts, 1997; Berg et al., 1993; 2010; Coûteaux et al., 1995; Kurz-Besson et al., 2006). However, models from mesic ecosystems are unsuited to water-limited ecosystems (Collins et al., 2008; Parton et al., 2007; Whitford et al., 1981). The differences observed as regards decomposition drivers with respect to mesic systems may be partly explained by the patchy distribution of vegetation and resources in these dry ecosystems. Unlike mesic ecosystems where vegetation cover is continuous and decomposition processes are predominantly biological (Moorhead and Sinsabaugh, 2006), plant cover patterns in water-limited ecosystems may influence decomposition rates through physicochemical processes such as photodegradation (Austin and Vivanco, 2006; Dirks et al., 2010), fragmentation by raindrop splash (Whitford, 2002), or soil erosion and runoff (Throop and Archer, 2007), even in periods in which microbial activity is constrained.

In Chapter 2, annual litter accumulation rates were estimated based on the annual litterfall inputs and decay rates of the predominant litter types within each land use site. Interestingly, we detected that the effect of site on decay rates differed between litter types.

From those results, a new research question arose concerning the factors controlling the decomposition dynamics of these two predominant Mediterranean leaf litter types (*Pinus halepensis* Miller and *Rosmarinus officinalis* L). More specifically, the objectives of this chapter were: (1) to compare the mass loss rates and changes in nitrogen content of these two predominant litter types and (2) to assess whether the factors controlling decomposition dynamics differ between litter types.

Previous analysis of main macro- and micronutrients (Table 5.1), together with a review of the available literature, indicated that these predominant Mediterranean litter types differ in chemical composition (Ben Salem et al., 1994; Berg et al., 2010; Vokou and Margaris, 1988; Dorrer et al., 2000; Minderman, 1968; Rovira and Vallejo, 2002; Traversa et al., 2011; Vokou and Liotiri, 1999). Since the influence of site on decomposition rates was not consistent between litter types, we hypothesized that the major drivers of litter decomposition dynamics in this Mediterranean ecosystem would differ between litter types. This hypothesis is based on the assumption that the recalcitrance of Aleppo pine litter is greater than that of rosemary litter, making the former much more resistant to biodegradation.

Table 5.1. Initial characteristics of the leaf litter material used in the decomposition experiment.

Litter type	*Pinus halepensis*	*Rosmarinus officinalis*
Water content (%)	4.46 ± 1.28	3.88 ± 1.28
Ash content (%)	8.1 ± 2.4	11.2 ± 1.7
%C	47.0 ± 0.42	46.65 ± 0.38
%N	0.98 ± 0.08	1.0 ± 0.08
C:N	47.56 ± 3.48	47.47 ± 4.08
%Ca	1.58 ± 0.03	1.72 ± 0.03[*]
K (ppm)	1320.62 ± 84.34	7139.46 ± 17.34[***]
Mg (ppm)	1616.68 ± 22.62	2070.61 ± 18.56[**]
Na (ppm)	904.43 ± 13.72	991.48 ± 7.01[*]
S (ppm)	561.91 ± 4.70	981.22 ± 1.51[***]
P (ppm)	11.13 ± 0.41	14.48 ± 0.02[*]
Cu (ppm)	11.29 ± 4.94	12.24 ± 0.40
Fe (ppm)	481.56 ± 1.71	570.86 ± 10.05[*]
Mn (ppm)	23.72 ± 0.07	25.52 ± 0.22[*]
Zn (ppm)	35.33 ± 0.80	204.10 ± 2.38[***]

5.2. Materials and methods

5.2.1. Canopy structure characterization

Both the open forest and the abandoned agricultural field sites were divided into the following two microsites: patches covered by *Pinus halepensis* (44-88 % estimated cover), and open intershrub patches which were sparsely covered (41-50 % estimated cover) with *Rosmarinus officinalis* shrubs. Replicate (n=4) plots (5 x 5 m) representative of each microsite were established within each land use type, and every shrub and tree stem basal diameter was measured at the end of the growing season (2007) in order to estimate aboveground biomass from species-specific allometric relationships (Baeza et al., 2006; 2011; Barberá et al., unpublished data). Mean vegetation cover (%), stem density and litter layer thickness were also determined.

5.2.2. Soil sampling and analysis

Previously to litterbag deployment, soil within the above mentioned microsites was sampled. In December 2006 and April 2007, two soil cores (10 x 15 cm) were extracted within each *microsite* x *land use* combination. Each soil core was sealed in a plastic bag and stored in a freezer (4 °C) until processed for microbial biomass estimates, and C and N analyses. Soil samples were air-dried, and sieved through a 2 mm sieve. The soil C and N content in the mineral soil (<2 mm) was measured with a N/C analyzer (Flash 1112 EA, Thermo-Finnigan, Bremen, Germany). Microbial biomass C was determined by fumigation with ethanol-free chloroform and extraction with K_2SO_4 according to the procedure described by Vance et al. (1987).

5.2.3. Litter collection and litterbag construction

In April 2007, fresh litter samples of two predominant Mediterranean litter types were collected weekly from several plastic sheets spread on the soil under tree/shrub canopies in both sites: *Pinus halepensis* needles, fine stems and fruits, and *Rosmarinus officinalis* leaves, flowers and stems. Litter samples were air-dried at room temperature. Oven-dry weight was determined for five samples per litter type after drying at 55º C for 4 days.

Figure 5.1. *Pinus halepensis* (A) and *Rosmarinus officinalis* (B) litter used in the decomposition experiment.

Samples were ground and analysed for C and N content in an elemental analyzer (Flash 1112 EA, Thermo-Finnigan, Bremen, Germany) in order to assess the initial litter % C and % N data. Subsamples (0.2 g) were combusted in a muffle furnace at 500º C for 5 h to determine initial ash content. Each litter type was thoroughly mixed before placing 3.0 g (*Rosmarinus officinalis* litter type) or 5.0 g (*Pinus halepensis* litter type) of leaves and fine stems (± 0.01 g) inside 10 x 10 cm litterbags constructed of fibreglass-nylon mesh with 1.4 mm^2 openings. The initial concentration of litter in the litterbags (500 g m^{-2} in pine and 300 g m^{-2} in rosemary) was equivalent to about two years of accumulated litter inputs, which averaged 280 and 146 g m^{-2} yr^{-1} for Aleppo pine and rosemary, respectively, in the study area (personal observation).

5.2.4. Litterbag deployment

Two fenced plots were installed next to two randomly selected Aleppo pine trees and two others next to two randomly selected rosemary shrubs in the open forest and abandoned agricultural field sites. We placed litterbags with their corresponding litter types on the soil surface inside the above-mentioned fenced plots on 19 June 2007 and followed their evolution for 20 months. A total of 72 litterbags were placed (2 litter types x 2 individuals x 6 sampling dates x 3 replicates) in the open forest and abandoned agricultural field sites. Each litterbag was carried inside an individual envelope to quantify how much litter was lost from the bags during transport. We collected 3 litterbags from each fenced plot (henceforth referred to as "location") every three or four months.

Figure 5.2. Litterbags placed on the soil surface inside the fenced plots installed next to one of the randomly selected Aleppo pine trees and rosemary shrubs in the open forest (A and B, respectively) and abandoned agricultural field (C and D, respectively).

5.2.5. Sample analyses

Litterbags were processed in the laboratory immediately after field collection. Any material not derived from litter (seedlings, stones, soil fauna or fungi) was removed by hand before the litterbags were dried at 55º C and sieved to remove mineral soil. After drying for 4 days at 55º C the litter of each litterbag was weighed to determine mass change. The litterbag contents were ground, and subsamples from each litterbag were combusted in a muffle furnace at 500º C for 5 h to determine the ash content. All data were analyzed on an ash-free dry matter basis in order to exclude any mass gain resulting from mineral soil that entered the bags. The effect of soil water erosion on litter mass loss rates was explored using the percentage of ash remaining, which has shown good correlation with decay rates in a water-limited ecosystem (Throop and Archer, 2007). Subsamples from each litterbag were analyzed for C and N content on an elemental analyzer (Flash 1112 EA, Thermo-Finnigan, Bremen, Germany).

5.2.6. Statistical analyses

Changes in litterbag mass, C content and N content throughout the study were analyzed using a three-way ANOVA. Litter type, site and time were considered the main effects. Decay constants were analyzed with a two-way ANOVA, in which litter type and site were the main effects. Hourly temperature data were condensed into daily means for each location. The effect of site on topsoil temperature and moisture were analyzed using repeated measures ANOVA. Differences in soil input into litterbags between sites were also analyzed with one-way ANOVA. Prior to analysis data were natural-log or arcsine transformed to meet ANOVA assumptions. Linear regression analyses were performed separately for each litter type to evaluate the relationships between litter mass loss and temperature, water availability or rainfall characteristics across collection dates. In addition, parameters related to litter quality (N or C:N) or soil erosion (ash content) were included into the multiple linear regression models, and the stepwise procedure was used in order to identify the main controls on decomposition rates for each litter type and collection date separately. All analyses were performed using SSPS 15.0 (Chicago, IL, USA).

5.3. Results

5.3.1. Litter mass loss

Litter quality characteristics of the leaf material used in the decomposition experiment are given in Table 5.1. Overall, rosemary litter showed significantly higher contents of macro- and micro-nutrients than Aleppo pine litter, while no significant differences in initial C and N concentrations between species were observed. Litterbag mass for both sites and litter types decreased with time (Fig. 5.3A), following a single exponential decay model (Table 5.2). However, different mass loss patterns were observed between litter types. Whereas rosemary litter showed the greatest mass loss in the first eight months of the experiment, Aleppo pine litter decomposed slowly and gradually until the last stages of the decomposition experiment, when mass loss increased considerably. For all sampling periods, rosemary litter decomposed more rapidly than Aleppo pine litter across sites ($R^2 =$ 0.742; F= 132.18; P<0.0001). After 20 months, rosemary litterbags had significantly less

remaining mass than did Aleppo pine litterbags, regardless of site (pooled across sites: rosemary = 44.77% ± 2.21% (mean ± SE), Aleppo pine = 70.25 % ± 2.21%; F= 132.18; P<0.0001).

The influence of site on mass loss rates was not consistently statistically significant throughout the decomposition experiment and differed between litter types. While a site effect on mass loss rates was apparent for rosemary litter during the first stages of the decomposition experiment, the mass loss rates of Aleppo pine litter did not differ between sites until the last stages of the decomposition experiment, when most high-intensity rainfall events and associated erosion process occurred in the experimental area (Fig. 5.5A; Martínez-Mena et al., 2011). At the end of the incubation period, the influence of site on decay rates (k) was significant for both species (Table 5.2), although no consistent patterns were observed between the two litter types. Rosemary litter decomposed faster in the open forest than in the abandoned agricultural site (R^2= 0.64; F= 41.51; P<0.0001), while decomposition rates of Aleppo pine litter were higher in the abandoned agricultural field site than in the open forest site (R^2= 0.68; F= 45.93; P<0.0001).

Table 5.2. Decay constants (k; Eqn.1), standard errors (SE) and R^2 values for Aleppo pine and rosemary leaf litter in the two land use sites.

	Pinus halepensis		*Rosmarinus officinalis*	
	k (yr^{-1})	R^2	k (yr^{-1})	R^2
Open forest	0.14 ± 0.05[b,B]	0.80	0.57 ± 0.02[a,A]	0.69
Abandoned agricultural field	0.21 ± 0.01[a,B]	0.67	0.45 ± 0.02[b,A]	0.66

Notes: Within each species, means with different lowercase superscript letter differ significantly between sites (P < 0.05). Within sites, means with different uppercase superscript letter differ significantly between species (P < 0.05).

Figure 5.3. Mean mass remaining (A), changes in N content (B) and C:N ratios (C) with time for different litter types in different sites. For each litter type, significant differences in mass remaining between sites are denoted by asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

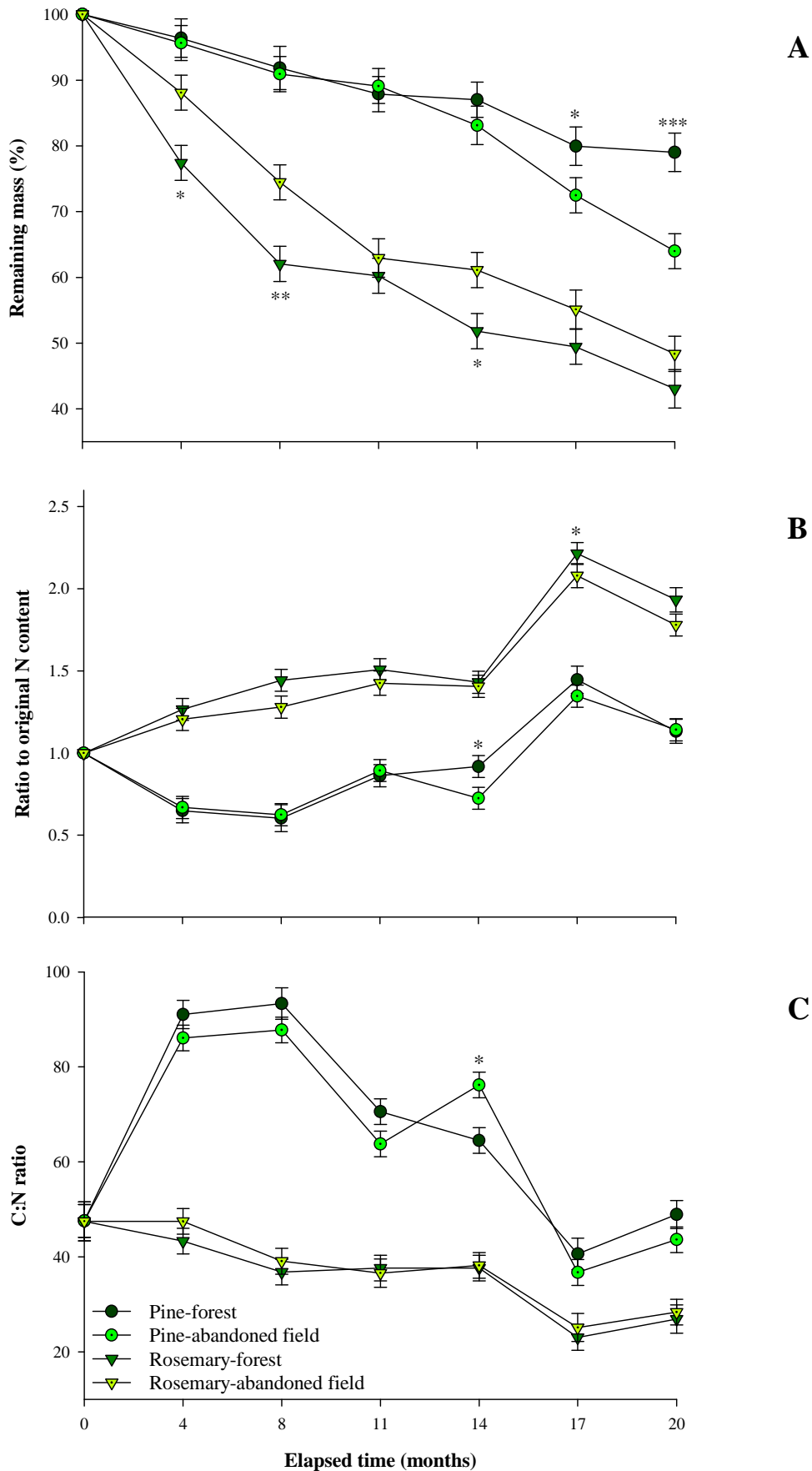**Figure 5.4.** Relationships between remaining mass and remaining carbon (A) and nitrogen (B) for Aleppo pine and rosemary litter across sites. For both species, carbon losses closely tracked mass loss patterns. However, there was a net loss of the total nitrogen mass with time for rosemary litter across sites ($y = 51.66 + 0.47x$, $R^2=0.20$), but no relationship was found between total mass loss and N loss for pine litter.
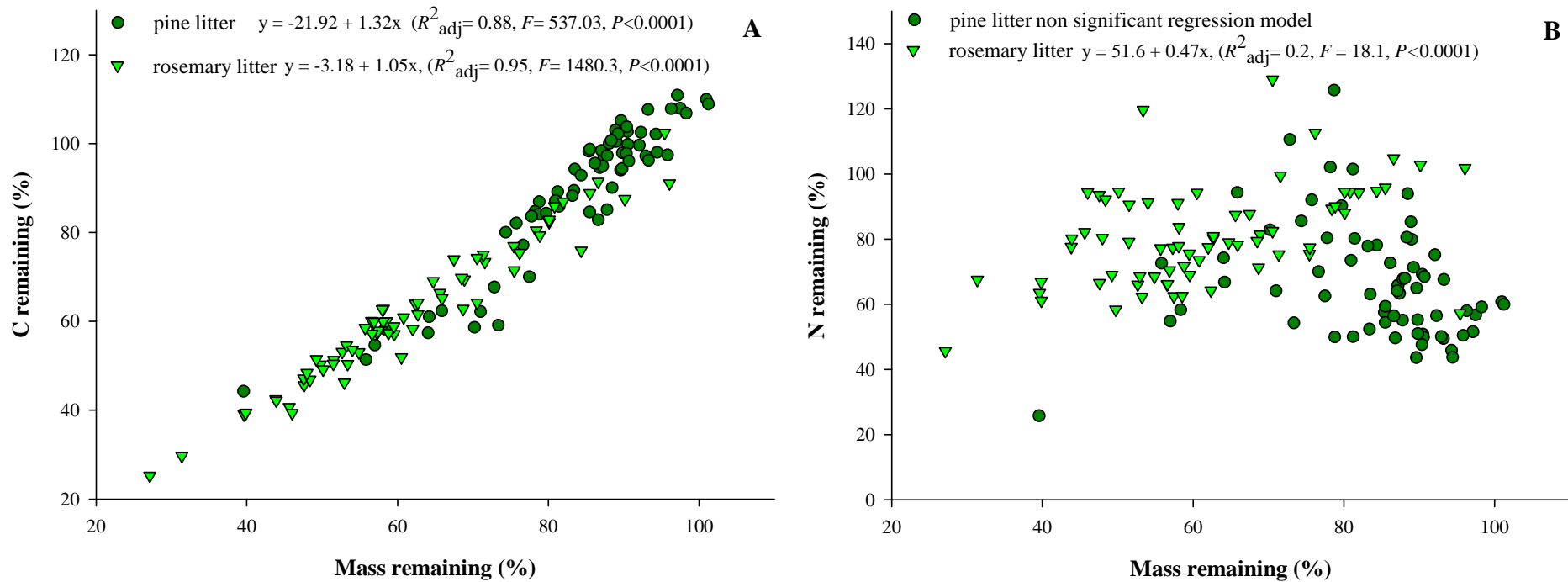
5.3.2. Changes in C and N during decomposition

Initial mean C concentration in rosemary litter was not significantly different from that in pine litter (P=0.517) (Table 5.1). For both species, C losses closely followed mass loss patterns, leading to a strong linear relationship between remaining mass and remaining C, with no significant site effects (Fig. 5.4A).

The initial nitrogen concentration in rosemary litter did not differ from that in pine litter (P=0.871) (Table 5.1). For both species, N concentration peaked at the 17-month collection date (1.87% ± 0.04% and 1.18% ± 0.04% for rosemary and pine litter, respectively), and then declined. However, before these peaks were reached, temporal patterns in N concentration differed between litter types (R^2= 0.87; F= 562.234; P <0.0001). During the first stages of decomposition rosemary litter showed net N immobilization, while pine litter showed net N release until about 20 % of the mass was lost, when net N immobilization started (Fig. 5.3B). Although higher peaks of net N immobilization were observed in the open forest than in the abandoned agricultural field site for both litter types, the influence of site on maximum net N immobilization was only significant in the case of rosemary litter (P<0.05).

Initial C:N ratios did not differ between litter types. However, temporal trends in C:N ratios differed between litter types, and subsequently the C:N ratios at the end of the incubation period also differed significantly between species (F = 794.07; P<0.0001) (Fig. 5.3C). Across sites, the C:N ratios declined significantly with time for rosemary litter (P<0.0001). Pine litter C:N ratios were much more erratic, first increasing between the 0- and 8-month collection dates, and then declining between the 8- and 20-month collection dates. However, the litter C:N ratio at the 20-month collection date did not differ from the initial one (P=0.575).

5.3.3. Canopy and soil characteristics

Whereas *Rosmarinus officinalis* patches exhibited similar canopy structure parameters across sites (50.2 ± 4.5 and 41.2 ± 4.7% plant cover, 226.7 ± 26 and 162.5 ± 6.5 g of aboveground biomass per square metre for open forest and abandoned agricultural field sites, respectively), *Pinus halepensis* patches in the open forest showed two main differences from those in the abandoned agricultural field site. First, Aleppo pine patches

exhibited greater plant cover and aboveground biomass in the open forest ($90 \pm 6.7\%$ and 990.5 ± 362.1 g m^{-2}, respectively) than in the abandoned agricultural field site ($44.5 \pm 6.0\%$ and 472.5 ± 152 g m^{-2}, respectively). Second, while there was a nearly continuous 4 cm thick litter layer beneath the Aleppo pine canopies in the open forest site, the litter layer was negligible beneath Aleppo pine canopies in the abandoned agricultural field site.

Soil in the open forest showed significantly higher microbial biomass, organic C and total N contents than in the abandoned agricultural field site (Table 5.3).

**Table 5.3.** Soil properties within each land use site (n=16).

	Open forest	**Abandoned field**
Soil organic C (g kg^{-1})	31.08 ± 2.58^a	17.08 ± 2.67^b
Soil N (g kg^{-1})	2.05 ± 0.15^a	1.43 ± 0.1^b
C:N	15.18^a	11.67^b
Soil microbial biomass (mg kg^{-1})	788.42 ± 72.9^a	550.68 ± 67^b

Numerical values are means ($\pm$ standard errors). Within each row, different superscript letters indicate statistically significant differences between sites ($P \leq 0.05$), according to Tukey´s test.

5.3.4. Rainfall, soil temperature and water availability

During the 20-month study period, rainfall events ranged from 1 mm to 70 mm, and precipitation followed the typical bimodal distribution with two rainy seasons, autumn and spring, and a dry period in summer (Fig. 5.5A). Accumulated rainfall in autumn 2008 (243 mm) was three-fold higher than that in autumn 2007 (70 mm), highlighting the high rainfall variability between years characteristic of Mediterranean regions. The highest rainfall amount and intensity recorded for a single rainfall event were 70 mm and 25 mm h^{-1} (maximum rainfall intensity in 30 minutes, I$_{30}$max) (Fig. 5.5A), which occurred in October 2008. Both soil temperature (from 5 to 30ºC) and moisture content (from 5 to 34%) varied markedly with season (Fig. 5.3B; 5.3C), and were inversely correlated with each other throughout the study period (r = -0.55, P < 0.01). There were no significant differences in soil temperature or water content between sites throughout the 20-month study period. Across sites, there was no relation between percentage mass loss, C or N content, and soil temperature, water content or any of the rainfall parameters (event size, intensity or duration). Interestingly, the ash content of the litter was strongly correlated with the total duration of rainfall events for both pine (r = 0.717, P<0.01) and rosemary (r = 0.819, P<0.01) litter throughout the study period.

Figure 5.5. Rainfall events (A), and topsoil temperature (0-3 cm) (B), and water content (0.10 cm) (C) for each land use throughout the study period. Due to technical difficulties, no data are available from 3rd September to 20th December 2007 and from 16th March to 10th June 2008 for the open forest site.
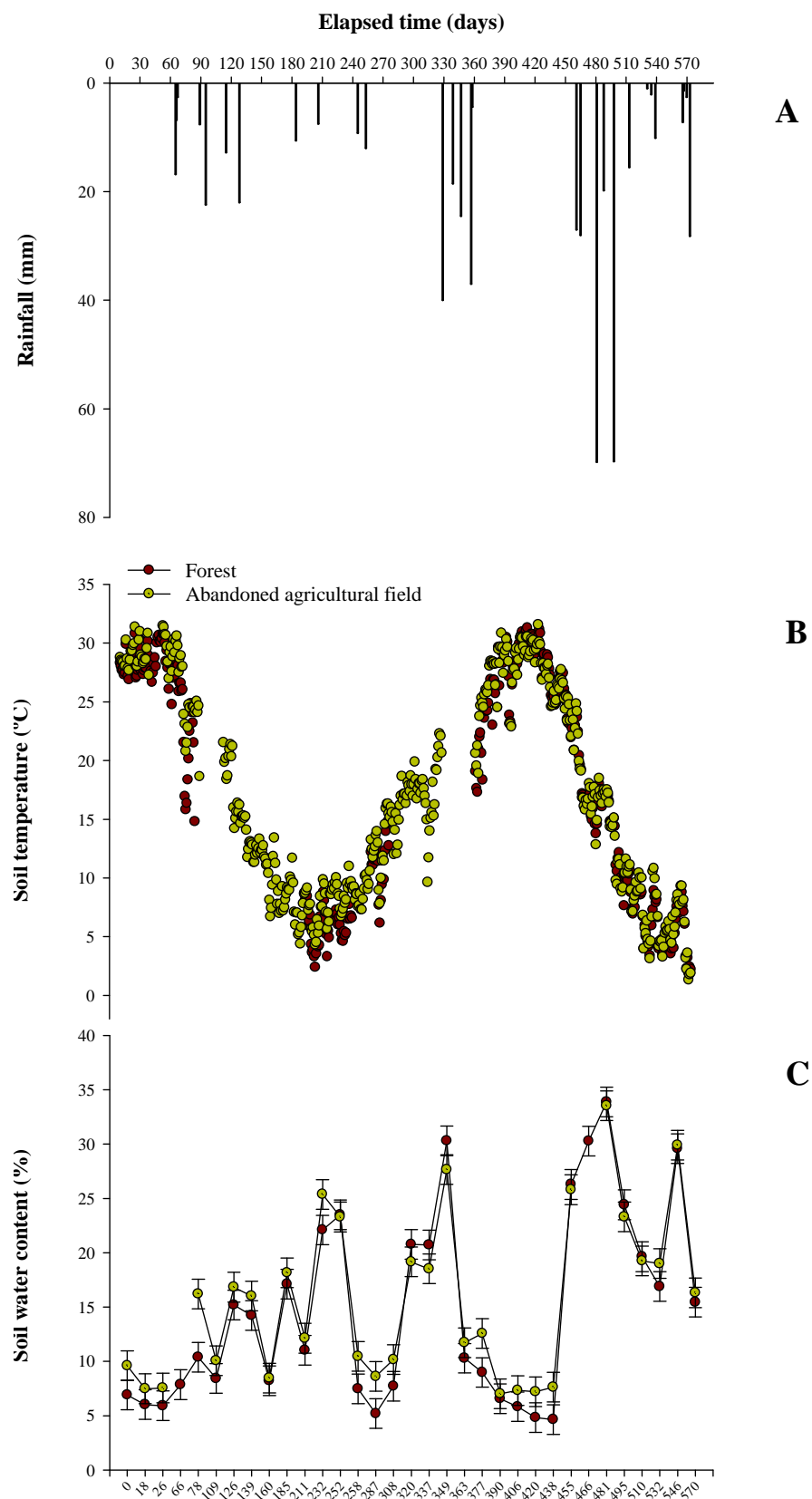
5.3.5. Soil input

Litterbag ash content, an indicator of soil deposition on litter according to Throop and Archer (2007), increased steadily with time for both litter types, and was generally greater in the abandoned agricultural field than in the open forest site for both litter types (Table 5.4). At the 20-month collection date, soil input into Aleppo pine litterbags was two-fold greater in the abandoned agricultural field than that in the open forest site (F= 43.82; P<0.0001), while rosemary litterbags did not differ significantly in the ash percentage of retrieved litter between the two sites (F= 0.58; P= 0.46).

Table 5.4. Percentage of ash in litterbags from the different land use/sites.

	% Ash			
	Pinus halepensis		*Rosmarinus officinalis*	
Time (months)	Open forest	Abandoned field	Open forest	Abandoned field
4	6.16 ± 1.61^{bcA}	7.47 ± 1.47^{cA}	12.59 ± 1.47^{bA}	11.24 ± 1.47^{cA}
8	5.11 ± 2.08^{cB}	10.41 ± 1.61^{bcA}	13.16 ± 1.47^{bB}	17.54 ± 1.47^{baA}
11	6.42 ± 1.47^{bA}	8.9 ± 1.47^{bcA}	10.26 ± 1.47^{bB}	15.74 ± 1.61^{baA}
14	6.97 ± 1.47^{bA}	10.78 ± 1.47^{bA}	13.22 ± 1.47^{bA}	14.57 ± 1.47^{bA}
17	10.49 ± 1.47^{aB}	23.19 ± 1.47^{aA}	19.46 ± 1.47^{aA}	19.79 ± 1.61^{abA}
20	9.25 ± 1.47^{aB}	19.05 ± 1.47^{aA}	17.22 ± 1.61^{aA}	20.5 ± 1.47^{aA}

Mean ± standard error (SE) for percentage ash in retrieved litter across sites. Within each species and site, values with the same lowercase superscript letters do not differ significantly from each other. Within each species, means with the same uppercase superscript letter do not differ significantly between sites (P>0.05). Averages for soil-free leaves are 8.10% ± 2.4% ash and 11.28% ± 1.71% ash (mean ± SE) for Aleppo pine and rosemary, respectively.

5.3.6. Factors controlling mass loss rates for each litter type

Parameters related to litter quality (N content or C:N) or soil erosion (ash content) were included into multiple linear regression models, and the stepwise procedure was used in order to identify the factors controlling mass loss patterns for each litter type and sampling period separately. For rosemary, parameters related to litter quality (N content or C:N) were found to explain between 33 and 37% of the variation in mass loss rates at the 14- and 17-month sampling dates, respectively. For Aleppo pine, ash content explained 44% of the variation in mass loss rates at both the 17- and 20-month sampling dates (Table 5.5).

Table 5.5. Relationship between the percentage of ash-free dry mass remaining and potential decomposition controls at each of the six collection dates.

Time (months)	*Pinus halepensis*					*Rosmarinus officinalis*				
	variable	R^2	β_0	β_1	F	variable	R^2	β_0	β_1	F
4	No model					No model				
8	N (%)	0.34	-0.252	-0.211[*]	5.69	No model				
11	No model					No model				
14	No model					N (%)	0.33	-0.43	-0.81[*]	6.46
17	Ash (%)	0.44	0.067	-0.138[**]	9.65	C:N ratio	0.37	-3.77	0.97[*]	6.92
20	Ash (%)	0.44	0.283	-0.251[**]	9.78	No model				

Data were natural-log transformed. Linear regressions were calculated for each collection date (including data for both sites); only statistically significant regression parameters are shown; * $P < 0.05$; ** $P < 0.01$.

5.4 Discussion

The litter decay constants (k = 0.14 - 0.57 yr^{-1}) and mass loss percentages (20- 55%) after 20 months observed in this study are similar to those reported for decomposition studies in other Mediterranean ecosystems (Castro et al., 2010; García-Pausas et al., 2004; Grünzweig et al., 2007; Rodríguez-Pleguezuelo et al., 2009; Rovira and Vallejo, 2002). The lack of correlation between mass loss rates and soil temperature, water availability or any of the precipitation parameters was somewhat expected, and is in agreement with the findings of several studies in other water-limited ecosystems (Kemp et al., 2003; Steinberger, 1990; Vanderbilt et al., 2008; Whitford et al., 1986), suggesting that other physicochemical processes may strongly influence the decomposition dynamics in these ecosystems.

The single exponential decay model adequately described the decomposition dynamics for both Aleppo pine and rosemary litter. However, different decomposition patterns were found between species. The fact that rosemary litter decomposed about three times faster than Aleppo pine litter across sites highlights the importance of litter chemical composition in decomposition processes in this water-limited ecosystem. In addition to lower initial concentrations of most macro- and micro-nutrients in pine litter than in rosemary litter (Table 5.1), low decomposition rates of Aleppo pine litter may further reflect the high concentrations of lignin, suberins, resins, fats and waxes (Boddi et al., 2002; Coûteaux et al., 2002), which are highly resistant to biodegradation (Minderman, 1968).

Rosemary litter appears to be more easily decomposable by microorganisms than Aleppo pine litter in this Mediterranean ecosystem. The higher decay rates observed for rosemary litter in the open forest than in the abandoned agricultural field site were consistent with the higher soil microbial biomass and respiration rates previously observed in the former than in the latter (Table 5.3; Chapter 3), suggesting that there may be greater decomposer activity in the open forest than in the abandoned agricultural field site. This assumption is supported by the fact that both species exhibited higher peaks of net N immobilization (a good indicator of microbial activity in litter decomposition studies; Aerts et al., 2006; Hobbie, 2000) in the open forest than in the abandoned agricultural field site (Fig.5.3B). Net N immobilization occurs when a new external input of N (e.g., fresh litterfall) becomes accessible to microorganisms and is converted to microbial biomass or exoenzymes (Frey et al., 2000). Despite differences in N patterns during the decomposition

process between litter types, net N immobilization peaked at the 17-month collection date for both species, shortly after the time of maximum litterfall occurrence (mid-summer) in this Mediterranean ecosystem (personal observation). Besides the higher soil microbial biomass found in the open forest in comparison to the abandoned agricultural field site, microbial decomposers in the open forest presumably have greater access to exogenous N due to higher soil mineral N and greater litterfall inputs in the open forest (Table 5.3; Table 1.1).

Conversely, mass loss rates for Aleppo pine litter were about two times higher in the abandoned agricultural field site than those in the open forest site. Aleppo pine needles, which have been identified as the most recalcitrant litter type in Mediterranean ecosystems (Berg et al., 2010; Rovira and Vallejo, 2002), resist microbial breakdown and thereby decomposition dynamics may be strongly dependent on abiotic processes. First, the higher aboveground biomass of Aleppo pine patches in the open forest in comparison to the abandoned agricultural field site may have blocked a greater fraction of the total incoming solar radiation to the soil surface, thus decreasing decomposition by photodegradation (Austin and Vivanco, 2006; Dirks et al., 2010; Henry et al., 2008; Parton et al., 2007). Greater aboveground biomass in the open forest may have also led to increased interception of rainfall, thus decreasing physical fragmentation of litter by raindrop impact and splash (Whitford, 2002). Second, the presence of a thick litter layer at the soil surface beneath Aleppo pine canopies in the open forest site may have prevented lateral transport of soil particles (Bochet et al., 2006), thus avoiding physical fragmentation of litter by abrasion (Throop and Archer, 2007; 2009). Conversely, the more open canopy of Aleppo pine patches in the abandoned agricultural field site, which lacked a litter layer on the soil surface, resulted in higher rates of soil loss and runoff (Martínez-Mena et al., 2008) and, as a consequence, a two-fold higher soil input into pine litterbags was observed at this site (Table 5.4). Interestingly, significantly higher mass loss rates of Aleppo pine litter in the abandoned agricultural field site than in the open forest site were only observed in the last stages of the decomposition experiment, when most high-intensity rainfall events and associated erosion processes occurred at this time in the experimental area (Martínez-Mena et al., 2011). In fact, the ash content was the main factor explaining mass loss rates beneath Aleppo pine canopies across sites at both the 17- and 20- month collection dates (Table 5.5), suggesting that soil water erosion was an important factor controlling litter decay during the later stages of decomposition. Soil detachment and transport processes may cause fragmentation or abrasion of litter (Throop and Archer, 2007), thus increasing the

surface area available for solar radiation exposure, which has been found to accelerate decomposition of lignin (Austin and Ballaré, 2010). Also, soil deposition may facilitate microbial litter colonization (Hamer et al., 2009; Throop and Archer, 2009), and once the lignin has been degraded mainly by sunlight, the labile compounds encapsulated in the lignin linkages become more susceptible to microbial attack (Austin and Ballaré, 2010; Foereid et al., 2010).

5.5. Conclusions

The results of this study suggest that decomposition drivers may differ depending on litter type in this Mediterranean ecosystem. Decomposition patterns of the more labile rosemary litter were controlled mainly by microbial activity, whereas decomposition of the more recalcitrant pine litter was driven mainly by abiotic factors.

The incorporation of soil erosion as an important driver of litter decomposition would be a significant step towards the development of mechanistic models of litter decomposition in Mediterranean ecosystems, where changes in vegetation structure and increases in soil erosion rates are expected as a result of future climate change.

Site-specific manipulative experiments explicitly addressing the effect of soil erosion on aboveground litter decomposition dynamics in these dry ecosystems are necessary before we can fully understand the relative importance of soil erosion with respect to other potential controlling factors such as photodegradation and litter quality.

References

Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems, a triangular relationship. Oikos 79, 439- 449.

Aerts, R., van Logtestijn, R., Karlsson, P., 2006. Nitrogen supply differentially affects litter decomposition rates and nitrogen dynamics of sub-artic bog species. Oecologia 146, 652-658.

Austin, A.T., Ballaré, C.L., 2010. Dual role of lignin in plant litter decomposition in terrestrial ecosystems. Proceedings of the National Academy of Sciences of the U.S.A. 107 (10), 4618-4622.

Austin, A.T., Vivanco, L., 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nature 442, 555-558.

Austin, A.T., Yahdjian, L., Stark, J.M., Belnap, J., Porporato, A., Norton, U., Ravetta, D.A., Schaeffer, S.M., 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141, 221-235.

Baeza, M.J., Raventós, J., Escarré, A., Vallejo, V.R., 2006. Fire risk and vegetation structural dynamics in Mediterranean shrubland. Plant Ecology 187 (2), 189-201.

Baeza, M.J., Santana, V.M., Pausas, J.G., Vallejo, V.R., 2011. Successional trends in standing dead biomass in Mediterranean basin species. Journal of Vegetation Science 22(3), 467-474.

Ben Salem, H., Nefzaoui, A., Abdouli, H., 1994. Patability of shrubs and fodder trees measured on sheep and camels. CIHEAM- Options Mediterraneennes 4, 35-48.

Berg, B., Berg, M.P., Bottner, P., Box, E., Breymeyer, A., et al., 1993. Litter mass loss rates in pine forests of Europe and Eastern United States, some relationships with climate and litter quality. Biogeochemistry 20 (3), 127-159.

Berg, B., Davey, M.P., De Marco, A., Emmett, B., Faituri, M., Hobbie, S.E., Johansson, M.B., Liu, C., McClaugherty, C., Norell, L., Rutigliano, F.A., Vesterdal, L., Virzo De Santo, A., 2010. Factors influencing limit values for pine needle litter decomposition, a synthesis for boreal and temperate pine forest systems. Biogeochemistry 100, 57-73.

Bochet, E., Poesen, J., Rubio, J.L., 2006. Runoff and soil loss under individual plants of a semi-arid Mediterranean shrubland, influence of plant morphology and rainfall intensity. Earth Surface Processes and Landforms 31, 536-549.

Boddi, S., Morassi, Bonzi, L., Calamassi, R., 2002. Structure and ultrastructure of *Pinus halepensis* primary needles. Flora 197, 10-23.

Carreira, J.A., Arevalo, J.R., Niell, F.X., 1996. Soil degradation and nutrient availability in fire-prone Mediterranean shrublands of southeastern Spain. Arid Land Research and Management 10 (1), 53-64.

Castro, H., Fortunel, C., Freitas, H., 2010. Effects of land abandonment on plant litter decomposition in a Montado system: Relation to litter chemistry and community functional parameters. Plant and Soil 333(1), 181-190.

Collins, S.L., Sinsabaugh, R.L., Crenshaw, C., Green, L., Porras-Alfaro, A., Stursova, M., Zeglin, L.H., 2008. Pulse dynamics and microbial processes in aridland ecosystems. Journal of Ecology 96, 413-40.

Coûteaux, M.M., Aloui, A., Kurz-Besson, C., 2002. *Pinus halepensis* litter decomposition in laboratory microcosms as influenced by temperature and a millipede, *Glomeris marginata.* Applied Soil Ecology 20, 85-96.

Coûteaux, M.M., Bottner, P., Berg, B., 1995. Litter decomposition, climate and litter quality. Tree 10 (2), 63-66.

Currie, W.S., 2003. Relationships between carbon turnover and bioavailable energy fluxes in two temperate forest soils. Global Change Biology 9, 919- 929.

Dirks, I., Navon, Y., Kanas, D., Dumbur, R., Grünzweig, J.M., 2010. Atmospheric water vapor as driver of litter decomposition in Mediterranean shrubland and grassland during rainless seasons. Global Change Biology 16 (10), 2799-2812.

Doerr, S.H., Shakesby, R.A., Walsh, R.P.D., 2000. Soil water repellency, its causes, characteristics and hydro-geomorphological significance. Earth Science Reviews 51, 33-65.

Foereid, B., Bellarby, J., Meier-Augenstein, W., Kemp, H., 2010. Does light exposure make plant litter more degradable? Plant and Soil 333, 275-285.

Frey, S.D., Elliot, E.T., Paustian, K., Peterson, G.A., 2000. Fungal translocation as a mechanism for soil nitrogen inputs to surface residue decomposition in a no-tillage agroecosystem. Soil Biology and Biochemistry 32, 689-698.

García-Pausas, J., Casals, P., Romanyà, J., 2004. Litter decomposition and faunal activity in Mediterranean forest soils, effects of N content and the moss layer. Soil Biology and Biochemistry 36, 989-997.

Grünzweig, J.M., Gelfand, I., Fried, Y., Yakir, D., 2007. Biogeochemical factors contributing to enhanced carbon storage following afforestation of a semi-arid shrubland. Biogeosciences 4, 891-904.

Hamer, U., Makeschin, F., An, S., Zheng, F., 2009. Microbial activity and community structure in degraded soils on the Loess Plateau of China. Journal of Plant Nutrition and Soil Science 172, 118-126.

Henry, H.A.L., Brizgys, K., Field, C.B., 2008. Between photodegradation and litter layer thickness. Ecosystems 11, 545-554.

Hobbie, S.E., 2000. Interactions between litter lignin and soil nitrogen availability during leaf litter decomposition in a Hawaiian montane forest. Ecosystems 3, 484- 494.

Huxman, T.E., Snyder, K.A., Tissue, D., et al., 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. Oecologia 141, 254-268.

Kemp, P.R., Reynolds, J.F., Virginia, R.A., Whitford, W.G., 2003. Decomposition of leaf and root litter of Chihuahuan desert shrubs, effects of three years of summer drought. Journal of Arid Environments 53, 21-39.

Kurz-Besson, C., Coûteaux, M.M., Berg, B., Remacle, J., Ribeiro, C., Romanyà, J., Thiéry, J.M., 2006. A climate response function explaining most of the variation of the forest floor needle mass and the needle decomposition in pine forest across Europe. Plant and Soil 285, 97-114.

Martínez-Mena, M., Álvarez Rogel, J., Castillo, V., Albaladejo, J., 2002. Organic carbon and nitrogen losses influenced by vegetation removal in a semi-arid soil. Biogeochemistry 61 (3), 309-321.

Martínez-Mena, M., Castillo, V., Albaladejo, J. (2001), Hydrological and erosional response to natural rainfall in a degraded semi-arid area of Southeast Spain. Hydrological Processes 15, 557-571.

Martínez-Mena, M., López, J., Almagro, M., Albaladejo, J., Castillo, V., Ortiz, R., Boix-Fayos, C., 2011. Organic carbon enrichment in sediments, Effects of rainfall characteristics under different land uses in a Mediterranean area. Catena, doi, 10.1016/j.catena.2011.02.005

Martínez-Mena, M., López, J., Almagro, M., Boix-Fayos, C., Albaladejo, J., 2008. Effect of water erosion and cultivation on the soil carbon stock in a semiarid area of South-East Spain. Soil and Tillage Research 99, 119-129.

Minderman, G., 1968. Decomposition and accumulation of organic matter in forests. Journal of Ecology 56 (2), 355-362.

Moorhead, D.L., Sinsabaugh, R.L., 2006. A theoretical model of litter decay and microbial interaction. Ecological Monographs 76 (2), 151-174.

Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44, 322-331.

Parton, W., Silver, W.L., Burke, I.C., Grassens, L., et al., 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. Science 315, 361-364.

Rashid, A., Ryan, J., 2004. Micronutrient Constraints to Crop Production in Soils with Mediterranean-type Characteristics, A Review. Journal of Plant Nutrition 27(6), 959- 975.

Rodríguez-Pleguezuelo, C.R., Durán Zuazo, V.H., Muriel Fernández, J.L., Martín Peinado, F.J., Franco Tarifa, D., 2009. Litter decomposition and nitrogen release in a sloping Mediterranean subtropical agroecosystem on the coast of Granada (SE, Spain), Effects of floristic and topographic alteration on the slope. Agriculture, Ecosystem and Environment 134, 79-88.

Rovira, P., Vallejo, R., 2002. Labile and recalcitrant pools of carbon and nitrogen in organic matter decomposing at different depths in soil, an acid hydrolysis approach. Geoderma 107, 109-141.

Steinberger, Y., 1990. Litter fall and nitrogen reabsorption in *Zygophyllum dumosum* in the Neveg Desert. Israel Journal of Botany 40 (1), 33-39.

Traversa, A., Said-Pullicino, D., D´Orazio, V., Gigliotti, G., 2011. Properties of humic acids in Mediterranean forest soils (Southern Italy), influence of different plant covering. European Journal of Forest Research, doi, 10.1007/s10342-011-0491-7

Throop, H.L., Archer, S.R., 2007. Interrelationships among shrub encroachment, land management, and litter decomposition in a semidesert grassland. Ecological Applications 17 (6), 1809-1823.

Throop, H.L., Archer, S.R., 2009. Resolving the dryland decomposition conundrum, Some new perspectives on potential drivers. In, U. Lüttge et al. (eds) Progress in Botany 70. Springer-Verlag Berlin, Heidelberg, pp 171-194.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biology and Biochemistry 19 (6), 703-707.

Vanderbilt, K.L., White, C.S., Hopkins, O., Craig, J.A., 2008. Aboveground decomposition in arid environments, Results of a long-term study in central New Mexico. Journal of Arid Environments 72, 696-709.

Vokou, D., Margaris, N.S., 1988. Decomposition of terpenes by soil microorganisms. Pedobiologia 31, 413-419.

Whitford, W., 2002. Ecology of desert systems. Academic Press, San Diego, CA.

Whitford, W.G., Meentemeyer, V., Seastedt, T.R., Cromack, K., et al., 1981. Exceptions to the AET model, deserts and clear-cut forest. Ecology 62 (1), 275-277.

Whitford, W.G., Steinberger, Y., MacKay, W., Parker, L.W., Freckman, D., Wallwork, J.A., Weems, D., 1986. Rainfall and decomposition in the Chihuahuan desert. Oecologia 68, 512-515.

General Conclusions

1. Across land uses, approximately one-third of the whole ecosystem C was stored belowground, which is consistent with the observed C allocation patterns within each land use. Overall, more than 60 % of the C is allocated belowground (soil and roots), highlighting the importance of including total belowground C accumulation when estimating net primary productivity in these dry Mediterranean ecosystems.

2. Overall, the annual net productivity values provided by this study combining both TBCA (non steady-state model) and biomass-inventory approaches were in reasonable agreement with the estimates for other Mediterranean ecosystems provided by studies using the eddy-covariance approach.

3. Use of the steady-state model is not advisable in these Mediterranean ecosystems because, in our sites at least, it underestimates the belowground C sequestration capacity, particularly in the abandoned agricultural field, where storage may be increasing more rapidly.

4. The results of this thesis stress the importance of soil respiration in the soil carbon balance and emphasize the need to consider its response to rain pulses in estimates of net carbon annual losses in dry Mediterranean ecosystems.

5. Mean Q_{10} values alone may not be indicative of the sensitivity of soil respiration to temperature at ecosystem level in drought-stressed regions, where low soil water contents strongly limit the response of root and microbial activity to temperature.

6. Both aboveground biomass and rewetting indices were found to be suitable tools to explain soil respiration variability in dry Mediterranean ecosystems.

7. This thesis provides valuable insights into the role of vegetation patterns in shaping belowground properties and C dynamics in the open forest and olive grove sites. However, the lack of correlation between vegetation patterns, soil C and N pools and respiration rates in the abandoned agricultural field suggests that long-recovery times (>30 years) may be needed and/or a threshold value of standing biomass may need to be reached before soil C and N pools and R_s rates start reflecting the patchy distribution of woody vegetation. This

highlights the limited capacity of abandoned agricultural fields for soil C accretion and sequestration in dry Mediterranean ecosystems such as that studied.

8. The expected decrease in plant cover in Mediterranean ecosystems as a result of future climate change may increase the vulnerability of these heterogeneous ecosystems, since the inter-canopy locations are shown to be more sensitive to environmental fluctuations.

9. Annual C losses by water erosion were negligible compared to soil respiration (less than 1% across all land uses) and had little influence on the estimates of TBCA. However, water erosion should not be overlooked when estimating TBCA in these Mediterranean ecosystems because of: i) the direct effect of soil water erosion on net primary production patterns (nutrient source and sinks), and ii) its interaction with the litter and soil organic matter decomposition dynamics.

10. The role of water erosion in the carbon balance needs to be assessed over long time periods (e.g., decades) and larger spatial scales (e.g. subcatchment or catchment). Moreover, the net effect of soil detachment, transport and deposition on litter decomposition dynamics will need to be clarified before we can fully understand the role of water erosion in the organic C balance in Mediterranean ecosystems.

11. This thesis provides a useful database of carbon pools and fluxes along a land use intensification gradient in a dry Mediterranean ecosystem, which can help understand the soil C cycling and storage capacity, and hence improve land management for C emission offset schemes under the Kyoto Protocol ("clean development mechanism").

Appendixes

Appendix I. Soil profile in the open forest

City: Cehegín
Location: Burete
U.T.M. coordinates: 4212852.35 N; 607725.62 E
Altitude: 650 m.a.s.l
Landform: Medium-gradient hill, strongly sloping (10-12%)
Land use: Non-managed forest
Vegetation: *Pinus halepensis, Rosmarinus officinalis, Juniperus oxycedrus, Quercus coccifera, Thymus sp., Rhamnus lycioides.*
Parent material: limestone Coluvium
Drainage conditions: well drained
Stoniness: Stony
Rock outcrops: moderately rocky
Salt: None
Erosion: Moderate water sheet erosion
Soil classification: Petrocalcic Calcisol (IUSS-WRB, 2006); Typic Petrocalcid (USDA, 2006)

MACROMORPHOLOGICAL DESCRIPTION

Hor.	Depth, cm	
	0-19	Dark yellow red (10YR4/4, moist) and light yellow red (10YR6/4, dry). Loam. Medium subangular blocky structure moderately developed. Sofá, friable, sticky and slightly plastic. Common fine pores. Many coarse angular gravels and limestones. Slightly hard thin crusts. Few biological activity. Common fine roots. Abrupt smooth boundary to
	+19	Continuous, platy, extremely cemented and indurated carbonates.
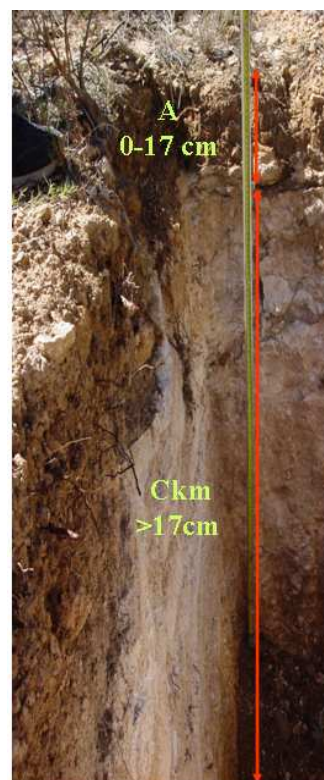
ANALYTIC DATA

Hor	Depth,cm	O.M. %	C %	N mg/100g	C/N	CO$_3$Ca%	pH H$_2$O	pH ClK
A	0-19	2.32	1.35	144.13	9.37	41.18	8.02	7.38
Ckm	+19					84.30		

Hor.	T cmol(+)kg^{-1}	E.C. dSm^{-1}	H$_2$O 0.5 atm.	H$_2$O 15 atm
A	16.24	0.55	30.84	14.88

TEXTURE

Hor.	<2	2-20	20-50	50-100	100-250	250-500	500-1000	1000-2000µm
A	28.1	31.2	10.2	4.5	4.4	4.5	8.3	8.9

Appendix II. Soil profile in the abandoned agricultural field

City: Cehegín
Location: Burete
U.T.M. coordinates: 4213733.34 N; 607295.91 E
Altitude: 599.66 m.a.s.l.
Landform: Medium-gradient hill, strongly sloping (10-12%)
Land use: Non-managed old-field
Vegetation: *Rosmarinus officinalis, Pinus halepensis, Juniperus oxycedrus, Thymus sp, Cistus clusii.*
Parent material: limestone Triasic marl coluvium
Drainage conditions: well drained
Stoniness: Stony
Rock outcrops: non rocks
Salt: None
Erosion: Moderate water sheet and rill erosin
Human influence: Cultivated with cereal for several years until abandonment in 1980
Soil classification: Haplic Regosol (Calcaric) (IUSS-WRB, 2006); Typic Torriorthent (USDA, 2006)

MACROMORPHOLOGICAL DESCRIPTION

Hor.	Depth, cm	
	0-17	Dark brown (7.5YR5/5, moist) and light brown (7.5YR6/4, dry). Loam. Medium subangular blocky structure weakly developed. Soft, friable, very sticky and plastic. Extremely calcareous. Few fine and medium distinct white mottles. Common very fine pores. Few irregular coarse gravel, mainly sandstones. Very few fine roots. Gradual and irregular boundary to
	17-42	Brown (7.5YR5/4, moist) and light brown (7.5YR6/4, dry). Loam. Massive. Slightly hard, friable, very sticky and plastic. Extremely calcareous. Few medium and coarse distinct white mottles of disperse powdery lime. Few very fine and fine pores. Few irregular coarse gravel and stones, mainly sandstones. Very few fine and medium roots. Clear and irregular boundary to
	+42	Yellowish-red (7.5YR6/5, moist) and yellowish-red (7.5YR7/5, dry). Loam. Massive. Hard, friable, very sticky and plastic. Very few fine pores. Common gravel and few irregular sandstones and limestones. Very few very fine roots.
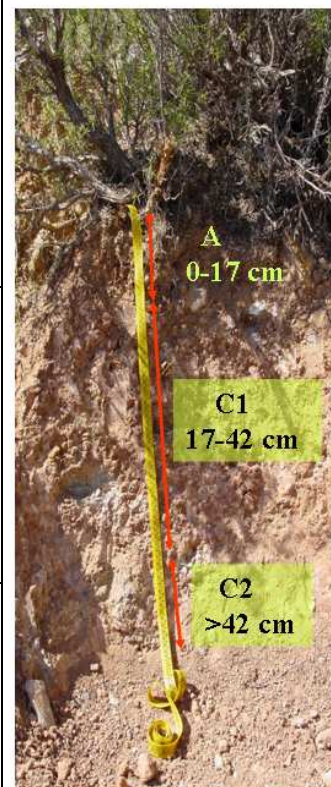
ANALYTIC DATA

Hor.	Depth, cm	O.M. %	C %	N mg/100g	C/N	$CO_3Ca\%$	pH H_2O	ClK
A	0-17	1.05	0.61	106.50	5.73	32.32	8.30	7.34
C1	17-42	0.53	0.31	71.12	4.36	35.33	8.38	7.40
C2	+42	0.38	0.22	39.67	5.55	34.89	8.28	7.29

Hor.	T cmol(+)kg^{-1}	C.E. dSm^{-1}	H_2O 0.5 atm.	15 atm
A	10.28	0.80	26.29	11.88
C1	9.25	0.36	21.11	11.81
C2	8.83	0.28	21.31	12.00

TEXTURE

Hor.	<2	2-20	20-50	50-100	100-250	250-500	500-1000	1000-2000µm
A	26.1	28.6	14.2	4.7	5.7	5.6	7.5	7.7
C1	26.7	27.7	20.7	3.9	4.6	9.8	4.2	2.5
C2	23.3	26.8	21.8	4.6	5.5	5.1	6.1	6.8

Appendix III. Soil profile in the olive grove

City: Cehegín
Location: Burete
U.T.M. coordinates: 4213049.49 N; 607858.72 E
Altitude: 606.82 m.a.s.l.
Landform: Medium-gradient hill, strongly sloping (10-12 %)
Land use: Olive grove
Parent material: Limestone colluviums
Drainage conditions: Well drained
Stoniness: none
Rock outcrops: non rocks
Salt: None
Erosion: Moderate to severe water sheet erosion
Human influence*:* Ploughed following the contours lines and small ridges with a moderate erosion.
Soil classification: Hypercalcid Calcisol (IUSS-WRB, 2006); Typic Haplocalcic (USDA, 2006).

MACROMORPHOLOGICAL DESCRIPTION

Hor.	**Depth, cm**	
	0-20	Dark brownish-gray (7.5YR5/6, moist) and light brownish-gray (7.5YR6/4, dry). Loam. Fine subangular blocky structure weakly developed. Soft, very friable, sticky and slightly plastic. Common very fine and few fine and medium pores. Few gravel and very few and angular limestones. . Few fine and medium roots. Clear smooth boundary to
	+20	Yellowish-red (7.5YR6/6, moist) and yellowish-red (7.5YR8/6, dry). Silt loam. Massive. Slightly hard, friable, sticky and slightly plastic. Few fine and very fine pores. Slightly cemented. Common medium to coarse prominent white mottles with a clear boundary. Very few gravels and angular limestones. Common irregular to spherical calcium carbonate with iron oxide nodules with pinkish-white colour. Few roots.
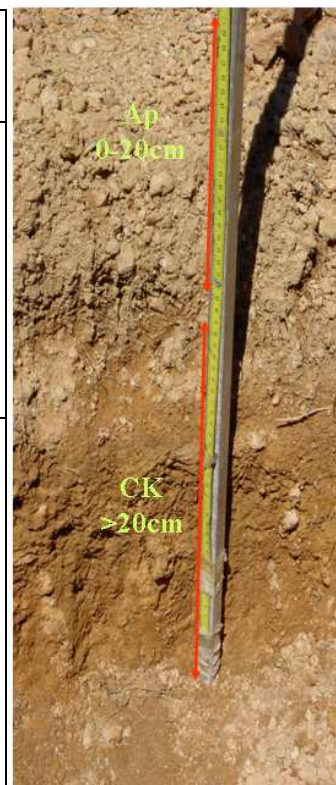
ANALYTIC DATA

Hor	Depth, cm	O.M. %	C %	N g/100g	C/N	CO_3Ca %	pH H_2O	ClK
Ap	0-20	1.15	0.67	99,47	6.74	61.90	8.13	7.36
Ck	+20	0.47	0.28	53.46	5.24	63.25	8.27	7.35

Hor.	T $cmol(+)kg^{-1}$	C.E. dSm^{-1}	H_2O 0.5 atm.	15 atm
Ap	12.02	1.16	21.84	10.89
Ck	11.10	0.46	19.77	7.77

TEXTURE

Hor.	<2	2-20	20-50	50-100	100-250	250-500	500-1000	1000-2000μm
A	22.3	23.7	17.8	5.9	6.8	7.0	10.5	6.0
Ck	19.7	33.6	17.2	5.6	5.4	6.2	8.7	3.6