



Litter decomposition in Mediterranean ecosystems: Modelling the controlling role of climatic conditions and litter quality

Guido Incerti^b, Giuliano Bonanomi^a, Francesco Giannino^c, Flora Angela Rutigliano^d, Daniela Piermatteo^d, Simona Castaldi^d, Anna De Marco^f, Angelo Fierro^f, Antonietta Fioretto^e, Oriana Maggi^g, Stefania Papa^e, Anna Maria Persiani^g, Enrico Feoli^b, Amalia Virzo De Santo^f, Stefano Mazzoleni^{a,*}

^a Dipartimento di Arboricoltura, Botanica e Patologia Vegetale, Università di Napoli "Federico II", Via Università 100, Portici 80055 (NA), Italy

^b Dipartimento di Scienze della Vita, Università di Trieste, Via Giorgieri 10, 34100 Trieste, Italy

^c Dipartimento di Ingegneria Agraria, Agronomia e Territorio, Università di Napoli "Federico II", Via Università 100, Portici (NA), Italy

^d Dipartimento di Scienze Ambientali, Seconda Università di Napoli, Via Vivaldi 43, 81100 Caserta, Italy

^e Dipartimento di Scienze della Vita, Seconda Università di Napoli, Via Vivaldi 43, 81100 Caserta, Italy

^f Dipartimento di Biologia Strutturale e Funzionale, Università di Napoli Federico II, Via Cinthia, 80126 Napoli, Italy

^g Dipartimento di Biologia Ambientale, Sapienza Università di Roma, P.le Aldo Moro, 5, 00185 Roma, Italy

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ABSTRACT

A new process-based model of litter decomposition, characterized by detailed climatic data input and simple litter quality parameters, is proposed. Compared to existing litter carbon models, specific implementations for temperature and moisture limiting effects have been adopted. The model is capable to represent decomposition processes in Mediterranean ecosystems, with summer drought slowing down, even at optimal temperatures, the litter decay rates of sclerophyll plants whose leaf masses are rich in structural compounds and low in N content. The model was calibrated by a best fitting procedure of two different datasets. First, unpublished results of litterbag experiments on leaf litter of 9 Mediterranean species, decomposing under controlled and not limiting temperature and water conditions, have been used to estimate the decay rate dependency from litter quality that was defined by only three initial C pools (labile, stable and recalcitrant compounds) instead of traditional N-based indices. Second, a set of published data from three medium-term field experiments on a single species, *Phillyrea angustifolia*, decomposing under different climatic conditions, have been used to estimate the limiting effects of temperature and moisture. The model was then validated against published data on seven other species and showed a correct reproduction of the major patterns of litter mass loss during decomposition processes of other seven different Mediterranean species. The model simulations, satisfactory for different litter types under a wide range of climatic conditions, suggest that factors which were not taken into account, such as initial litter N contents, microclimatic variations related to stand structure, soil chemistry and texture, and microbial communities, are not very significant for assessing decomposition dynamics in Mediterranean ecosystems. The minimal requirements of input data, the simple structure, and the easiness of parameterisation make our model, among the many other available litter carbon models, an attractive alternative for different research purposes, at least for Mediterranean ecosystems.

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1. Introduction

In terrestrial ecosystems, a major fraction of net primary production is yearly delivered as leaf litter, exfoliated tissues, and exudates, which sustain the detrital food chain. A great diversity of organisms consume litter materials to obtain energy, also pro-

viding the main carbon and nutrient contribution to the forest floor (Berg and McLaugherty, 2008).

Litter decomposition is a complex phenomenon led by both biotic (Hättenschwiler et al., 2005) and abiotic factors such as leaching and UV radiation (Austin and Vivanco, 2006; Weider et al., 2009). The rate of litter decomposition is affected by climatic variables, litter quality, and soil biota (Aerts, 1997; Virzo De Santo et al., 1993). Temperature and water availability are the major controlling factors of litter decomposition rate at global and regional scales (Liski et al., 2003), but the relative importance of litter quality com-

* Corresponding author. Tel.: +39 081 7754850; fax: +39 081 7760104.
E-mail address: stefano.mazzoleni@unina.it (S. Mazzoleni).

pared to climate can change at lower spatial scales. For instance, decomposition rates of Scots pine needles vary across boreal forests more according to substrate quality rather than to climatic conditions (Berg and McClaugherty, 2008). Similarly, a prevailing effect of litter quality over climate has been reported for wet tropical forests (Tanner, 1981; Weider et al., 2009). On the contrary, in Mediterranean ecosystems the peculiar dynamics of climatic conditions are critical for litter and soil organic matter decomposition. In summer, high temperature and low moisture, leading to persistent drought, can strongly limit microbial growth and activity (Criquet et al., 2004; Fioretto et al., 2005) whereas, the milder and wetter spring and autumn seasons induce higher metabolic rates of microbes temporarily enhancing the litter decomposition rates (Coûteaux et al., 1995).

In general, it is well established that litter quality can be crucial to assess the decomposition rate (Meentemeyer, 1978). Plant litter is an organic material composed of many different chemical compounds with a wide range of turnover times (Rovira and Vallejo, 2007). In this respect, the quality of litter can be defined as a quantitative index of how difficult its degradation is by the soil microflora (Rovira et al., 2008), reflecting the relative proportion of the different chemical components. In addition, litter quality radically changes during the course of decomposition as a consequence of the different degradation rates of the various chemical constituents (Berg and McClaugherty, 2008; Papa et al., 2008).

In detail, soluble substances and labile compounds (carbohydrates, proteins, a fraction of microbial biomass, and other simple compounds) are rapidly degraded by fast growing microorganisms requiring high N concentration (Swift et al., 1979). The first decomposition phase, in addition to the litter morphological characteristics, is supposedly regulated by labile C and N availabilities (Melillo et al., 1989) affecting the microbial respiration that converts the organic carbon to CO₂. Differently, cellulose and lignin, the most abundant stable and resistant litter components, as well as suberin, resins and waxes, are slowly degraded in later stages of decomposition which have been reported as mainly regulated by lignin content (Coûteaux et al., 1995; Rutigliano et al., 1996). Several studies demonstrated that C/N and lignin/N ratios, reflecting the proportion of N to the whole C pool and to the most resistant compound, are useful indices for predicting litter decomposition rate (Melillo et al., 1982; Taylor et al., 1989). Also, it has been reported that lignin content exerts a major control on decomposition for lignin-rich litters, compared to N availability (Taylor et al., 1989). In Mediterranean ecosystems, sclerophyll plants, adapted to seasonal drought, limit water loss by producing thick and dense leaves tissue, with high leaf mass, due to high content of structural compounds, and low N content per unitary area (Kazakou et al., 2009). Both the high content of structural compounds and the low N availability slow down leaf litter decomposition (Cornwell et al., 2008).

Given the complexity of the decomposition process and the high number of interacting factors, many mathematical models have been proposed to predict litter decomposition and soil organic matter decay (Burke et al., 2003; Moorhead et al., 1996), reflecting the concept of litter decomposition following an exponential decay process (Olson, 1963). However, the potential effects of global environmental changes on litter and soil organic matter quality and turnover (Cox et al., 2000) have stimulated the interest on mechanistic models to simulate organic matter transformations in terrestrial ecosystems.

The process of litter decomposition is included in the majority of biogeochemical models simulating carbon dynamics and other ecosystem processes, from annual to millennium scale. The main examples are CENTURY (Parton et al., 1987), RothC (Coleman and Jenkinson, 1996), LPJ (Sitch et al., 2003), and the Biome-

(Running and Gower, 1991) BGC (Bio Geochemical Cycles) models. These detailed models are often used for simulations at regional or global level (e.g. Gholz et al., 2000), whereas their application at lower scale, particularly in Mediterranean ecosystems, is much less reported (e.g. Romanyà et al., 2000; Hoff et al., 2002). As pointed out in a comparative analysis by Burke et al. (2003), each model proposes a different response function of litter decay rate to temperature. In spite of contrary evidence (Berg and McClaugherty, 2008), such response functions are assumed fixed across ecosystem types and climatic locations. Further, all the empirical functions controlling the decomposition–temperature relationships have been calibrated with a few and limited data sources, none of which from Mediterranean areas, irrespective whether the models were afterward tested in such systems.

Other models, considerably simpler, have been used to represent the decomposition process at short-term, usually weeks, for agronomic-related applications, such as CropSyst (Stockle et al., 1994) and LEACHM (Hutson and Wagenet, 1992), and at long-term, such as “Hockey Stick” model (Feng and Li, 2001) and ICBM – Introductory C Balance Model (Kätterer and Andrén, 2001). Among these, the simple Yasso model (Liski et al., 2005; Tuomi et al., 2009) was developed for long-term decomposition predictions, taking into account climate and litter quality, in temperate or cold ecosystems.

The absence of a specific decomposition model able to capture the climatic peculiarities of Mediterranean ecosystems and to predict the related litter decomposition dynamics in such context, gives scope to this work. The underlying hypothesis is that a correct prediction of litter decomposition dynamics in Mediterranean environment requires detailed climatic data and litter quality parameters, with the latter not defined by classical N-based indices, but by three initial pools indicated as labile, stable and recalcitrant compounds (Palosuo et al., 2005). Then, the main objective of this work is to present a new process-based model of litter decomposition dynamics, specifically focused on Mediterranean ecosystems.

2. Materials and methods

2.1. Litter decomposition experiment in controlled condition

The experiment was aimed at estimating the value of maximum potential decomposition rates of leaf litter of Mediterranean species, as a function of litter quality (i.e. the maximum potential decay rate for each initial litter pool, see Section 2.4). Since decomposition in open field mainly depends on litter quality, temperature, and water availability (Gholz et al., 2000), the experiment was carried out under controlled conditions, not limiting decay rates in terms of temperature and water availability.

A set of nine species widespread in the Mediterranean environments and representing a wide range of litter quality (Bonanomi et al., 2010; Lecerf et al., 2007) were selected from different vegetation types located in the Campania Region, Southern Italy. The species pool included three evergreen shrubs (*Arbutus unedo*, *Coronilla emerus* and *Phyllirea angustifolia*), one broadleaf evergreen tree (*Quercus ilex*), two conifers (*Picea abies* and *Pinus pinea*), and three deciduous trees (*Castanea sativa*, *Populus nigra* and *Quercus pubescens*). One of these species is a nitrogen-fixing legume (*C. emerus*).

Freshly abscised leaves were collected by placing nets under plants of natural communities (n° plants > 20 randomly selected individuals for each species), dried (40 °C for 5 days) and then stored at room temperature. Proximate cellulose and lignin content of undecomposed litters were assessed as hydrolysable fraction and non-hydrolysable materials, respectively, following Gessner (2005).

Table 1
Plant species litters used in the experiment and modelling work. Data used for calibration of the maximum potential decomposition rates of litter pools (K_L , K_S , and K_R) refer to unpublished results from experiments in controlled conditions. Calibration of limiting effects of temperature and moisture (LF_T and LF_θ) is based on published data of *Phyllirea angustifolia* leaf litter decomposition in three different years under field conditions. Validation was done on published data of leaf litter decomposition of seven different species in field conditions.

Species	Calibration of K_L , K_S , and K_R	Calibration of LF_T and LF_θ	Validation	Field site	Reference	Climatic time series	Decomposition days
<i>Abies alba</i>	–	–	✓	Taburno	Virzo De Santo et al. (2002)	28.11.89–22.01.92	785
<i>Arbutus unedo</i>	✓	–	–				180
<i>Castanea sativa</i>	✓	–	–				180
<i>Cistus incanus</i>	–	–	✓	Castel Volturno	Fioretto et al. (2003, 2005)	12.1.98–25.2.01	1140
<i>Coronilla emerus</i>	✓	–	–				180
<i>Myrtus communis</i>	–	–	✓	Castel Volturno	Fioretto et al. (2003, 2005)	12.1.98–25.2.01	1140
<i>Picea abies</i>	✓	–	–				180
<i>Pinus laricio</i>	–	–	✓	Terzigno	Virzo De Santo et al. (2002)	22.11.89–3.10.91	680
<i>Pinus pinea</i>	✓	–	✓	Terzigno	Virzo De Santo et al. (2002)	22.11.89–16.1.92	180, 785
<i>Pinus sylvestris</i>	–	–	✓	Terzigno	Virzo De Santo et al. (2002)	22.11.89–3.10.91	680
<i>Populus nigra</i>	✓	–	–				180
<i>Quercus ilex</i>	✓	–	✓	Castel Volturno	Papa et al. (2002) Fioretto et al. (2005)	14.12.98–16.12.01	180, 1098
<i>Quercus pubescens</i>	✓	–	–				180
<i>Phyllirea angustifolia</i>	✓	✓	–	Castel Volturno	De Marco et al. (2004) De Marco et al. (2004) Maisto et al. (2011)	21.12.00–11.3.03 26.7.02–30.6.04 6.10.06–13.11.07	810 705 403

Decomposition experiments were carried out in microcosms placed in a growth chamber under controlled temperature ($22 \pm 2^\circ\text{C}$ night and $25 \pm 2^\circ\text{C}$ day) and water availability (everyday watering to field capacity with distilled water), according to the litterbag method (Berg and McClaugherty, 2008). Large (20×20) terylene litterbags (mesh size 2 mm) were filled with 6 g of dry leaf litter and placed inside trays (30 cm deep, 100 cm for each side). A microbial inoculum obtained by mixing 10 g of soil taken from the fields where litter where collected (top 10 cm) and 90 g of water, was added in order to improve the start up of the decomposition process (Bonanomi et al., 2011). The microbial inoculum was sprayed over the litterbag. Litterbags were harvested after 30, 90 and 180 days of decomposition for a total of 216 litterbags (9 species \times 3 sampling dates \times 8 replicates). Bags were dried in the laboratory (40°C until constant weight was reached) and the remaining material weighted.

2.2. Field experiments of litter decomposition

Leaf litter decomposition experiments, carried out in Campania Region (Southern Italy) over the last 20 years (Table 1) have been used for model calibration (data reported by De Marco et al., 2004; Maisto et al., 2011) and validation (Fioretto et al., 2003, 2005; Papa et al., 2002; Virzo De Santo et al., 2002). The whole database (Table 1) includes 10 time series of decomposition, ranging from 403 to 1140 days, for leaf litter of 8 Mediterranean species, coupled with corresponding daily time series of temperature and precipitation. For one (*P. angustifolia*) of the considered species, the database includes three time series (De Marco et al., 2004; Maisto et al., 2011) that were used for model calibration. Such data drawn from decomposition measurements performed in climatically different years on a single species, and thus largely independent from differences in morphological and chemical properties, have been used to estimate the limiting effects of temperature and moisture on decomposition rate. The remaining 7 datasets were used for model validation.

The field experiments were carried out at 3 different sites (Table 2). The Terzigno site is located on the south-eastern slope of Monte Vesuvius. The 1944 eruption of the volcano covered the area with a lapillus layer about 1 m thick. On volcanic lapillus *P. pinea* forest was planted in place of mixed forest occupying the site before the eruption. The stand has a very sparse understory of herbs and young oaks (*Q. ilex* and *Q. pubescens*). The soil is a Typic Vitrixerand with a weakly developed A horizon (5–10 cm). An experimental

plot was located on a gentle slope to the west (Virzo De Santo et al., 1993).

The Monte Taburno site is covered by an 80–100-year-old *Abies alba* forest planted on a site formerly covered by *Fagus sylvatica* forest. An experimental plot was located on a gentle north-east-facing slope. A sparse understory of herbs and *F. sylvatica* recruitment occurs in the plot. The soil, a Typic Hapludand (Rutigliano et al., 2001), forms a deep profile on the pyroclastic parent material (Virzo De Santo et al., 1993).

The Castel Volturno site is located in a Nature Reserve on a flat coastal area of ca. 268 ha with alluvial deposit dunes composed of loose siliceous-calcareous marine sand and pyroclastic products. Vegetation is a mosaic of different plant patches, including low and high Mediterranean maquis, i.e. the vegetation dominated by sclerophyll evergreen shrubs typical of the Mediterranean basin. Within this site, two plots in different vegetation types were used for decomposition experiments: the low Mediterranean maquis, a shrubland burned in 1976, covered by *Cistus incanus*, *Myrtus communis*, *Rhamnus alaternus*, *Asparagus acutifolius*, *P. angustifolia* and *Pistacia lentiscus*, and the coppice wood of *Q. ilex* with sporadic *P. pinea* trees (Fioretto et al., 2005). The soil of the low maquis is a Typic Xeropsamment, the soil of the *Q. ilex* coppice wood is a Mollic Xeropsamment (Rutigliano et al., 2001).

In each plot, litter was collected by net traps during the period of fall peak, i.e. May–June for leaf litters (*Q. ilex*, *P. angustifolia*, *M. communis* and *C. incanus*), at Castel Volturno site, and October, for needle litters of *P. pinea*, *P. laricio* and *P. sylvestris* (at Terzigno site) and *A. alba* (at Monte Taburno site). Each litter was mixed to obtain a homogeneous sample, air-dried and stored at room temperature (20 – 25°C) until sample preparation. Undecomposed litters were analyzed for content of total water soluble substances, organic C and lignin, as reported in Fioretto et al. (2005) and Virzo De Santo et al. (1993). Cellulose content was measured only in leaf litters (Fioretto et al., 2005), whereas cellulose content of needle litters was obtained from literature data (Chadwick et al., 1998, for *P. sylvestris*; Chadwick et al., 1998; Ibrahima et al., 1995; Sariyildiz et al., 2005 for species closely related to *A. alba*, *P. pinea* and *P. laricio*).

Decomposition was determined by measuring litter mass loss. For leaf litter, the litter-bag method (Fioretto et al., 2005) was used. About 3.5 g of air-dried leaf litter were confined in litter bags ($16 \times 10 \text{ cm}^2$, for the *C. incanus* and *M. communis* leaves, and $26 \times 22 \text{ cm}^2$, for *Q. ilex* leaves) made of terylene net with a mesh size of 1 mm and incubated on litter layer by metal pegs. At each

Table 2

Field sites of decomposition experiments. Location, vegetation, climatic and pedologic data are reported for each site.

Site	Lat./long.	Altitude (m)	Plant cover	Mean annual temperature (T) (°C)	Mean annual precipitation (P) (mm)	Lang aridity index (P/T)	Litter thickness (cm)	Soil pH	SOM content (upper A, %)
Terzigno	40°49'N 14°28'E	250	<i>P. pinea</i> forest	13.2	960	73	3.4	6.0 ^b	58.4 ^a 6.1 ^b 1.1 ^c 19.0 ^b
Taburno	41°06'N 14°36'E	1100	<i>A. alba</i> forest	7.9	2166	274	1.8	6.0 ^b	14.2 ^c 4.1 ^b (1)
Castel Volturno	40°57'N 13°55'E	6–9	Mediterranean vegetation	18.6	680	37	n.d.	8.4 (1) 8.0 ^b (2)	23.8 (2)

n.d.: not recorded.

(1) Low maquis; (2) *Q. ilex* wood.^a Humus layer.^b Upper 5 cm.^c 5–10 cm.

sampling 18 bags were collected, dried at 75 °C and weighed in order to determine remaining mass (Fioretto et al., 2005). The study lasted 1140 days for *C. incanus* and *M. communis*, 1098 days for *Q. ilex* and 810, 705, and 403 days for the three experiments with *P. angustifolia*.

The mass loss of needle litters was measured by linear determination method (Gourbière, 1986). In particular, about 600 g of air-dried needle litters were exposed in containers (100 × 100 cm² and 5 cm high) with the top cover and bottom being made of terylene net with a mesh size of 1.5 mm. At each sampling date, about 20 g of needle litter of each plant species was collected from container and sub-divided in 5 replicates. After drying at 75 °C and weighing, the length and weight of the needles contained in each replicate was measured, by placing the needles end-to-end (Virzo De Santo et al., 1993). The study period was 785 days for *P. laricio* and *P. pinea*, and 680 for *P. sylvestris* and *A. alba*.

2.3. The model

The model is based on the concept that decomposition process proceeds following an exponential decay function (Olson, 1963). Following a well-accepted approach (Adair et al., 2008; Liski et al., 2005) measured initial litter chemistry was used to divide leaf litter mass (C , g) into three different pools: “stable” (S) was percent cellulose, “recalcitrant” (R) was lignin-like compounds, and “labile” (L) was the difference between 100% and the sum of S and R , intended as non-polar and water soluble extractives. It follows that:

$$C = L + S + R \quad (1)$$

The C partitioning in these three compartments is implemented by a species-specific distribution vector $[\alpha_L, \alpha_S, \alpha_R]$ with $\sum_{i=L,S,R} \alpha_i = 1$ and $L = \alpha_L \cdot C$, $S = \alpha_S \cdot C$ and $R = \alpha_R \cdot C$.

The three groups of compounds are then decomposed at their own rates independent of their origin, losing a proportion of their mass over unit time, according to the following equations:

$$\begin{aligned} \frac{dL}{dt} &= -k_L \cdot L \\ \frac{dS}{dt} &= -k_S \cdot S \\ \frac{dR}{dt} &= -k_R \cdot R \end{aligned} \quad (2)$$

where t is time (day), k_L , k_S and k_R are the decomposition rates of labile, stable, and recalcitrant components, respectively.

From Eq. (1) and the mathematical solution of Eq. (2), it follows that:

$$C(t) = \alpha_L \cdot C_0 \cdot e^{-k_L t} + \alpha_S \cdot C_0 \cdot e^{-k_S t} + \alpha_R \cdot C_0 \cdot e^{-k_R t} \quad (3)$$

where C_0 is litter C mass at time $t=0$. Dynamic of litter mass remaining is then calculated as percentage of initial litter C mass: $MR_{\%}(t) = (C(t)/C_0) \cdot 100$

Hence, inter-specific differences of decomposition dynamics due to litter quality are exclusively referred to the species-specific fraction of the three main litter components, not including N content or N related indexes such as C/N and lignin/N ratio.

In the model, temperature and litter moisture content are considered as the main environmental factors affecting litter decomposition in Mediterranean ecosystems. Daily temperature (T , °C) is an input parameter, while volumetric litter moisture content (θ , %) is calculated by applying a NASA-CASA-like equation (Potter et al., 1993), as a function of daily precipitation (P , mm) and potential evapo-transpiration (ETP , mm), the latter calculated according to Thornthwaite (1948), obtaining the equation:

$$\frac{d\theta}{dt} = \frac{1}{L_{th} \cdot L_{po}} \cdot \left[\min(P, (L_{th} \cdot L_{po})(1 - \theta)) - ETP \frac{1 + a}{1 + a \cdot \theta^b} \right] \quad (4)$$

where L_{th} (mm) and L_{po} (mm³_{air} mm⁻³_{bulk}) are litter thickness and porosity, and a and b texture-dependent empirical coefficients.

The effects of T and θ on decomposition rates are implemented as two scalar limiting factors (LF_T and LF_{θ} , respectively), both ranging between 0 and 1, with the minimum having a multiplying reducing effect on the maximum potential decomposition rates K_L , K_S , K_R :

$$k_i(t) = K_i \cdot \min(LF_T(t), LF_{\theta}(t)) \quad (5)$$

with $i = [L, S, R]$.

In this way, equal weight is given to the relative importance of T and θ , by considering the reducing effect on decay rates as produced by the most limiting of two independent factors. Moreover, the limiting effect of moisture shortage is decoupled from that of temperature, providing a model adapted to decomposition dynamics in Mediterranean ecosystem, where summer drought can slow down decomposition even at optimal temperatures (Criquet et al., 2004; Fioretto et al., 2005). As a consequence, new equations for the temperature and moisture scalars have been implemented. The scalars were calculated as parametric functions of T and θ . In the case of temperature, the curves reported for the suite of models reviewed by Burke et al. (2003) were evaluated. After calibration (see Section 2.4), a logistic increase of decomposition rates was

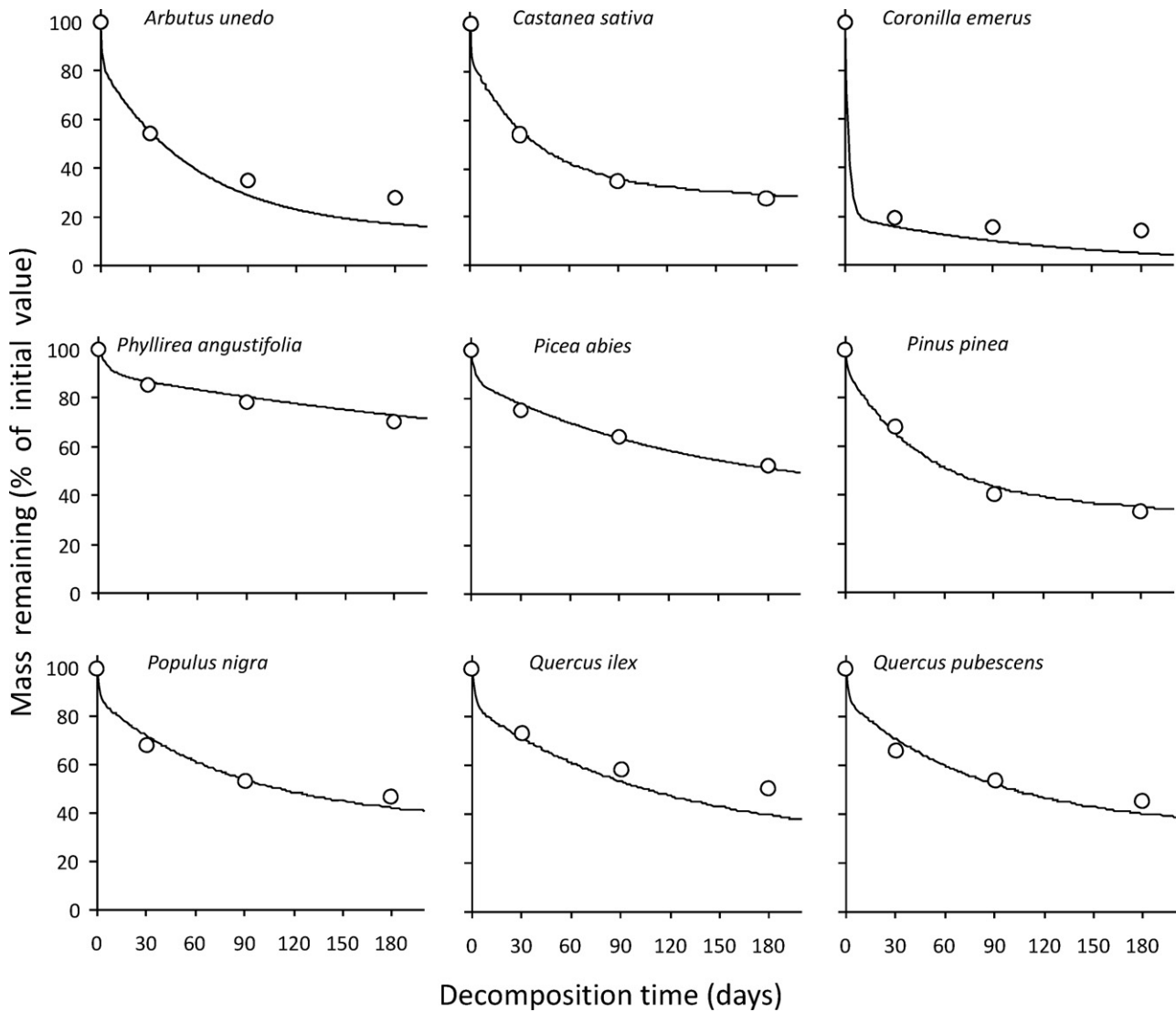


Fig. 1. Observed (white dots) and simulated (black lines) decomposition dynamics for leaf litterbags of 9 species decomposing in controlled optimal conditions ($22 \pm 2^\circ\text{C}$ at night, $25 \pm 2^\circ\text{C}$ during the day, watering to field capacity).

used, reaching its maximum value at $T_m = 30^\circ\text{C}$, and decreasing at values higher than $T_M = 35^\circ\text{C}$:

$$LF_T = \begin{cases} \frac{1}{1 + b \cdot e^{-c \cdot T}} & T < T_m \\ 1 & T_m \leq T \leq T_M \\ e^{-\left(\frac{T-a}{d}\right)^2} & T > T_M \end{cases} \quad (6)$$

In the case of litter moisture content, after calibration, a gaussian increase and a linear decrease of decomposition rate were used, corresponding to values lower than $\theta_m = 40\%$ and higher than $\theta_M = 90\%$, respectively:

$$LF_\theta = \begin{cases} h \cdot e^{-[(\theta-m)/n]^2} & \theta < \theta_m \\ 1 & \theta_m \leq \theta \leq \theta_M \\ -r \cdot \theta + s & \theta > \theta_M \end{cases} \quad (7)$$

2.4. Model calibration

Potential maximum decomposition rates (K_i , see Eq. (5)) for the three litter pools were estimated by fitting model simulations to data of percent mass remaining in leaf litter of nine species decom-

posing in controlled and not limiting conditions of temperature and water availability (see Section 2.1). An iterative procedure of linear programming was applied to Eq. (3) to minimize the residuals of simulated and observed $\text{MR}_\%$, based on the following constraints: $K_L > K_S > K_R$.

The effects of temperature and litter moisture content were calibrated by adjusting the levels of parameters in Eqs. (6) and (7) to best fitting of published data (De Marco et al., 2004; Maisto et al., 2011) from decomposition experiments carried out at Castel Volturno site on three datasets of *P. angustifolia* leaf litter (Tables 1 and 2). An iterative linear programming procedure based on the numerical optimization "simplex" algorithm (Himmelblau, 1972; Nelder and Mead, 1965) was applied, consisting in changing the parameter values one at a time, running a model simulation, recording the model fit of experimental data, and repeating until reaching the maximum model fit, in terms of coefficient of determination (R^2). For model simulations, the litter moisture equation (Eq. (4)) was parameterised according to climatic time series and litter properties recorded at the field site, using average values both for litter thickness ($L_{th} = 26 \text{ mm}$) and litter porosity ($L_{po} = 0.65 \text{ mm}^3_{\text{air}} \text{ mm}^{-3}_{\text{litter}}$). Calibrated values for parameters in Eqs. (6) and (7) were $a = 35$, $b = 100$, $c = 0.4$, $d = 9$, and $h = 2.5$, $m = 0.65$, $n = 0.22$, $r = -10$, $s = 10$, respectively.

2.5. Model simulations and validation

In order to validate the decomposition model, a set of simulation exercises was run, and the outputs statistically compared to the validation dataset (Fioretto et al., 2003, 2005; Papa et al., 2002; Virzo De Santo et al., 2002). Litter quality data and maximum potential decomposition rates for labile, stable and recalcitrant pools were applied in model runs simulating experimental conditions at the field sites. Real climatic time series for rainfall and temperature recorded at each site were used as model inputs, and Eq. (4) was parameterised according to litter properties recorded at the field sites (Table 2). Finally, Eqs. (6) and (7), parameterised as described above (Section 2.4), were applied to simulate the limiting effects of temperature and litter moisture content on litter decomposition.

3. Results

Model calibration led to a satisfactory prediction of potential decay rates for the three litter fractions ($K_L = 0.799$, $K_S = 0.008$, $K_R = 0.004$), and of litter mass loss dynamics in optimal controlled conditions (Fig. 1). Highly significant linear regression of simulated and observed values of mass remaining were obtained, both for each species and for all pooled data (Fig. 2). It is noteworthy that highly significant predictions were obtained for nine species covering a very wide spectrum of litter quality, ranging from slow-decomposing sclerophyll leaves of *P. angustifolia* and *Q. ilex* and needles of *P. abies* to the extremely rapid decaying leaf litter of the nitrogen fixing legume *C. emerus*. Although this result is due to an efficient parameter optimization, it is worth noting that it was possible to predict inter-specific differences of decomposition dynamics, at least in controlled and optimal conditions of temperature and water supply, based on a simple exponential model with three pools. In addition, this approach allowed an estimation of the potential decomposition rates for each litter pool, independent from the species-specific distribution vector of labile, cellulose and lignin-like compounds.

The calibration of the limiting effects of temperature and litter moisture content on decay rates produced likely shapes (Fig. 3A and B), with highly significant linear regression of simulated and observed percent mass remaining (Fig. 4). This result indeed confirms the possibility of predicting litter decomposition dynamics in Mediterranean environment, based on the limiting effects of temperature and moisture content on litter decay rates. Despite considering leaf litter of one species only, the parameterisation of the response to the limiting factors was based on a representative dataset of real climatic conditions including a total of 1918 daily data.

Concerning the model validation with field decomposition data, simulations correctly reproduced the patterns of litter mass

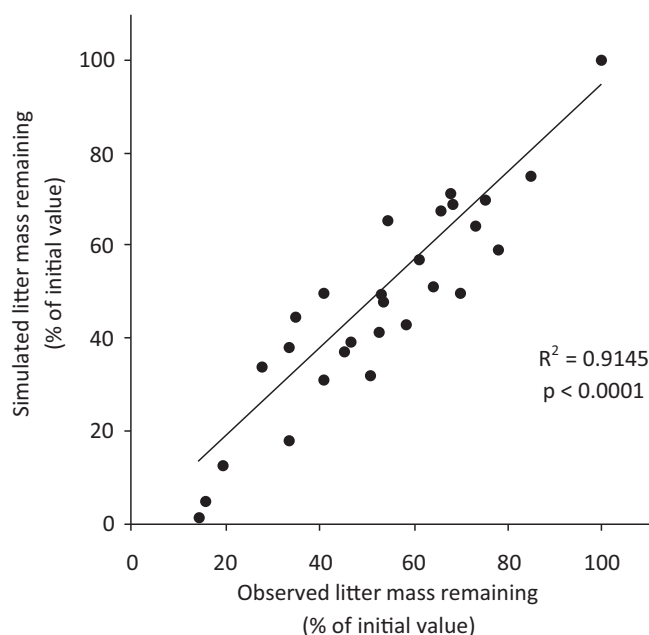


Fig. 2. Linear correlation (coefficient of determination and associated P -value) between simulated and observed litter mass remaining in litterbags of nine species decomposing in controlled optimal conditions.

remaining during the decomposition process of 7 leaf litter species in three different sites (Fig. 5). This constituted a consistent validation because the highly fitting outputs with real data were obtained without any further empirical adjustment of the model. However, some differences in model performance between the species were found. Leaf litter decomposition of sclerophyll species, both trees and shrubs, was predicted with high statistical significance. A lower statistical power, though still significant, was found in the prediction of *Pinus* needles and *Q. ilex* leaves decomposition. In detail, the model underestimated the litter mass remaining during the whole decomposition period (Fig. 5), with an average deviation from observed data equal to 11.0%, 11.8%, 14.9%, and 21.1% for *P. pinea*, *P. sylvestris*, *Q. ilex*, and *P. laricio*, respectively.

4. Discussion

The model proposed in this study correctly predicted medium-term litter decomposition dynamics (up to 4 years) in Mediterranean ecosystems, encompassing a wide range of environmental conditions (from coastal maquis to high mountain) and plant litter types (7 species). Our model, similarly to other existing tools (e.g. Tuomi et al., 2009), is based on three litter pools and scalars for the

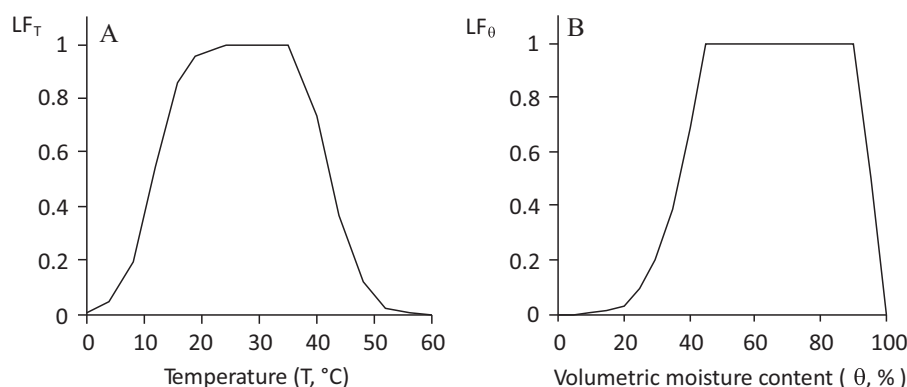


Fig. 3. Shape of scalar factors limiting decomposition rates as function of temperature (A) and litter moisture (B), as resulting from model calibration.

limiting effects of temperature and moisture on decay rates. However, our approach is novel for the mathematical implementation of such effects. Our new implementation makes it possible to predict decomposition dynamics even in the absence of data on N and P content of litter, where the limiting effects of temperature and moisture are a major factor affecting litter decay rate. Applications of other existing models, such as Century (Parton et al., 1987) and DayCent (Del Grosso et al., 2001), require input data on amount and timing of nutrient amendments in order to correctly predict decomposition rates in these ecological conditions.

4.1. Effect of litter quality

In our model, the three C pools L , S , R define the initial litter quality based on conventional elemental and proximate analysis of plant litter (Berg and McClaugherty, 2008). In other litter and soil organic matter models, initial organic matter is subdivided in a variable number of pools, ranging from one (e.g. TEM model, Raich et al., 1991) to six (e.g. CENTURY model, Parton et al., 1994). Recently, Adair et al. (2008), by comparing similar models with 1, 2 or 3 pools, concluded that 3 pools are necessary to correctly predict long-term (10 years) litter decomposition, which is consistent with our findings. During the model implementation, a comparative analysis of mass loss simulations were done with different model versions, based on either one, two, or three pools. We found a statistical gain (improvement of R^2 of simulations vs. observations) of 6% and 39%,

passing from one- to two- and three-pools, respectively (Fig. S1). On the other hand, a higher number of pools did not provide any significant advantage, making the model parameterisation more difficult.

The major differences between our model and other previous, structurally similar, 3-pools models (Adair et al., 2008; Palosuo et al., 2005) are in the assessment procedure of the fraction-specific decomposition rates (K_S , K_L , K_R). Our estimates of potential decay rate for the labile fraction (Fig. S2) were lower compared to Adair et al. (2008) ($K_L = 0.79$ vs. >1). For cellulose and lignin-like pools (Fig. S2), our data were respectively either much lower ($K_S = 0.008$ vs. 0.76) or higher ($K_R = 0.004$ vs. 0) compared to published values (Adair et al., 2008). This could depend by differences in the chemical definition of the three litter pools or in the related decay rates estimation approaches. Our method seemingly provided better estimates compared to previous models which were either parameterised on few standard materials (two litter types for Yasso model, Liski et al., 2005), or not reporting the source of the k values used as a model input for the different litter pools (Burke et al., 2003).

In contrast with the correct model behavior in simulating the decomposition of deciduous and evergreen leaf litter, the mass remaining of the three *Pinus* species (*P. laricio*, *P. pinea* and *P. sylvestris*) has been underestimated by our model – and, consequently, mass loss rate has been overestimated – with an average deviation from experimental data of 15.2%. A possible explana-

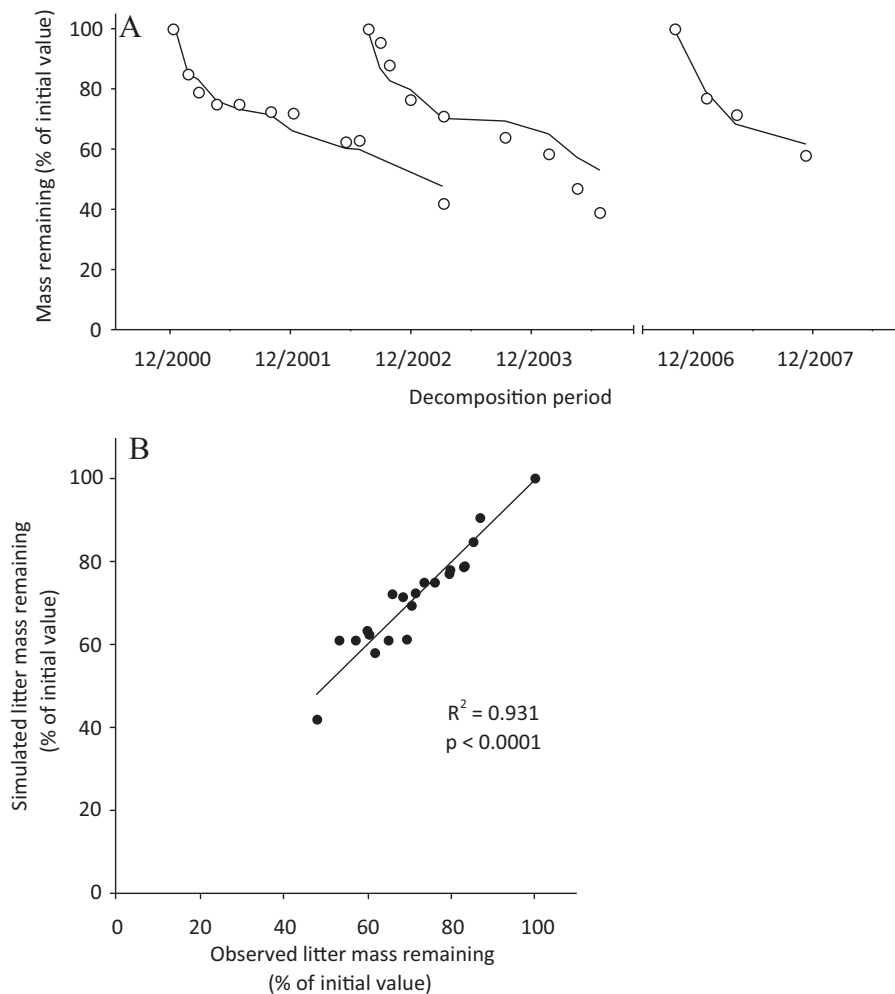


Fig. 4. Decomposition dynamics of litter mass remaining from three field experiments at Castel Volturno site on leaf litterbags of *Phillyrea angustifolia* (see Table 2). (A) White dots – observations; black lines–simulations. (B) Linear correlation between simulated and observed data with coefficient of determination and associated P -value.

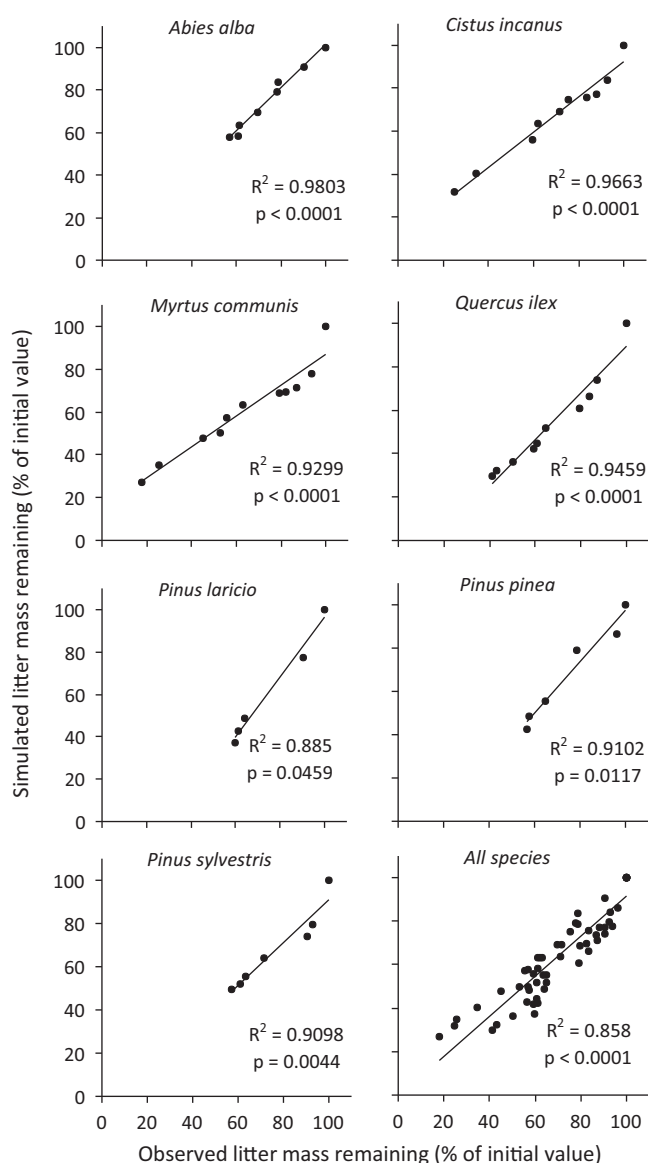


Fig. 5. Model validation. Linear correlation (coefficient of determination and associated P -value) between simulated and observed data of litter mass remaining in litterbags of 7 species (Table 1) decomposing in 3 different experimental fields (Table 2).

tion is that *Pinus* litter may contain inhibitory compounds, such as resins, that are not represented by the three pools approach. The slight underestimation reported for *Q. ilex* could be related to the abundant inhibitory compounds of sclerophyll Mediterranean species, that have been shown to slow down decomposition and mineralization by forming recalcitrant complexes with organic matter, as in the case of high molecular-weight condensed tannins (Castells et al., 2004; Hättenschwiler and Vitousek, 2000). However, these substances are implicitly included in our representation of litter quality, as recalcitrant non-hydrolysable materials. Other studies reported cases of simulations deviating from observed data. Palosuo et al. (2005), in an application of Yasso model to long-term litter decomposition in Canadian ecosystems, found the mass loss either over- or underestimated for the grass *Festuca hallii* and the conifer *Larix laricina*, with such incorrect predictions related to the extreme values of some litter chemical parameters (O -alkyl carbon and phenol concentration for *F. hallii* and *L. laricina*, respectively). Tuomi et al. (2009), fitting simulations by Yasso07 model with a large dataset of litterbag decomposition experiments, noticed a

higher mass loss rate in European litterbag measurements compared to the North or Central American ones. It was related to the larger mesh size and smaller litter mass used in the European litter bags, which may have caused more leaching, and thus overestimates of mass loss in Europe.

Nitrogen content and N related indexes such as C/N and lignin/N ratios have been often used as quality parameters in litter and organic matter models (for review see Burke et al., 2003). Our results, consistently with Palosuo et al. (2005), indicate that the exclusion of N as input variable does not preclude the possibility of correct predictions of short- and medium-term litter decay rates. This seems to apply well to Mediterranean ecosystems where litter decomposition can be slowed down by both climatic factors (summer drought) and poor litter quality (litter rich in structural compounds). This hypothesis is also partially supported by the meta-analysis study of Knorr et al. (2005) reporting that N additions enhanced the decomposition of high-quality litters, while reduced the mass losses of low-quality litters. Moreover, a contrasting effect of a high N concentration has been observed during decomposition process, with a general speeding up in the early stage (Fioretto et al., 2008) and a slowing down of both the late stage of lignin decay and of the whole decomposition process (Berg and Laskowsky, 2006; Rutigliano et al., 1996).

4.2. Effect of climatic conditions

Previous litter decomposition models reported biome-specific biases due to the intrinsic difficulty of representing all possible environmental conditions. For instance, Adair et al. (2008) reported that their model, capable of an accurate description of the general patterns of long-term litter decomposition across many ecosystems, failed in some specific conditions. Specifically, this occurred for root litter in wetlands and aboveground materials in semi-arid ecosystems and related to anaerobic conditions and UV effects, respectively, both factors not considered by the model.

Mediterranean ecosystems are characterized by warm and dry summer seasons with litter layers sporadically wetting by rainfall events, but still subject to very rapid drying afterwards, much faster compared to underground soil conditions (Criquet et al., 2004). Obviously, this limiting water availability bears negative effects on the litter decay rates. In order to represent the dynamics of this process, we modelled the litter moisture content by a specifically adapted NASA-CASA sub-model (Potter et al., 1993) able to describe the rapid litter wetting and drying cycles on the basis of daily rainfall and temperature time series. This approach is radically different from other models. According to Burke et al. (2003), in other models the effect of moisture content is often implemented as a scalar dampening linear or exponential increases in k with temperature, as in Biome-BGC (Hunt et al., 1996) and RothC (Coleman and Jenkinson, 1996), or shifting the temperature at which k is greatest, as in CENTURY (Parton et al., 1987) and FAEWE (Van der Peijl and Verhoeven, 1999). Furthermore, the effects of water limitations has been usually implemented by calculating aggregated climatic metrics, e.g. among many others mean annual or monthly temperature and actual or potential evapo-transpiration (Burke et al., 2003). Such data have been used to calculate general abiotic scalars, such as DEFAC (Decomposition factor based on temperature and moisture, Kelly et al., 2000; Parton et al., 1994), or the climate decomposition index (CDI), used by Parton et al. (2007), which incorporates monthly temperature and rainfall. At global and regional scales, this approach has been reported as effective to predict long-term organic matter decomposition, but it is clearly unable to capture the rapid and critical changes of litter moisture in semi-arid environments.

In our model, we considered the minimum of the two scalars for both temperature and moisture as a multiplicative limiting factor

of decay rates. In this way, the effects of litter moisture content and temperature were decoupled, with equal importance of the two independent climatic factors in determining the model prediction. Most models fix either maximum or baseline decomposition rates that are modified by temperature and moisture scalars (Coleman and Jenkinson, 1996; Hunt et al., 1996; Parton et al., 1994). All proposed temperature scalars represent decomposition increasing with temperature (at least up to 30 °C, Burke et al., 2003), but there is little agreement among different models regarding the shape of the temperature–decomposition relationship. Scalar shape represents a major, not sufficiently assessed, difference among models, directly affecting the shape of k -temperature relationships. We used a methodology to calibrate the scalar by best fitting of experimental data under a wide range of Mediterranean climatic conditions, and the resulting logistic/gaussian shape of temperature scalar (Fig. 3A), beside differing from all other published models, was well in accordance with that used in CENTURY model (Burke et al., 2003; Parton et al., 1994), though the latter is based on an exponential and an arctangent functions, for the monthly and daily versions, respectively. Burke et al. (2003) in a review on modelling of temperature effects on decomposition, concluded with a specific point of consensus on how simulation models treated temperature–decomposition relationships. A Q_{10} of 1 to 3 is likely for temperatures between 17 and 22 °C. Our temperature scalar fits with these suggestions, with Q_{10} , varying between 1.00 and 1.79 within the specified temperature range, and rapidly increasing at temperature <15 °C, consistently with the RothC, CENTURY and FAWE models (Burke et al., 2003). Hence, compared to previous decomposition models, the peculiar shape of our temperature scalar, producing highly fitting simulations, could be regarded as an improved fine-tuning for Mediterranean ecosystems.

5. Conclusions

By means of a new process-based model, specifically developed for Mediterranean ecosystems, it has been possible to correctly predict leaf litter decomposition of several species across different environments. In the model, litter quality is represented with the well-accepted three-pool approach, whereas specific implementations for temperature, and especially moisture limiting effects, have been adopted. In summary, the minimal requirements of input data, the simple structure and the easiness of parameterisation for different research purposes make our model an attractive alternative among the many litter carbon models. However, there are a number of factors also affecting decomposition processes, which we did not take into account due to their negligible importance in Mediterranean conditions, including initial N and P contents of litter, microclimatic variation related to stand structure, and site factors such as soil chemistry, texture, and microbial communities. Future modelling approaches focusing on semiarid ecosystems should include the effects of ultraviolet radiation that are nowadays considered a major factor in aboveground litter decomposition (Austin and Vivanco, 2006; Gallo et al., 2009).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.apsoil.2011.06.004.

References

- Adair, E.C., Parton, W.J., Del Grosso, S.J., Silver, W.L., Harmon, M.E., Hall, S.A., Burke, I.C., Hart, S.C., 2008. Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates. *Glob. Change Biol.* 14, 2636–2660.
- Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79, 439–449.
- Austin, A.T., Vivanco, L., 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature* 422, 555–558.
- Berg, B., Laskowsky, R., 2006. Litter decomposition: a guide to carbon and nutrient turnover. *Adv. Ecol. Res.* 38, 20–71.
- Berg, B., McClaugherty, C., 2008. *Plant Litter: Decomposition, Humus Formation and Carbon Sequestration*, second ed. Springer-Verlag, Berlin, Heidelberg, 341 pp.
- Bonanomi, G., Incerti, G., Antignani, V., Capodilupo, M., Mazzoleni, S., 2010. Decomposition and nutrient dynamics in mixed litter of Mediterranean species. *Plant Soil* 331, 481–496.
- Bonanomi, G., Incerti, G., Barile, E., Capodilupo, M., Antignani, V., Mingo, A., Lanzotti, V., Scala, F., Mazzoleni, S., 2011. Phytotoxicity, not nitrogen immobilization, explains plant litter inhibitory effects: evidence from solid-state ^{13}C NMR spectroscopy. *New Phytol.* doi:10.1111/j.1469-8137.2011.03765.x.
- Burke, I.C., Kaye, J.P., Bird, S.P., Hall, S.A., McCulley, R.L., Somerville, G.L., 2003. Evaluating and testing models of terrestrial biogeochemistry: the role of temperature in controlling decomposition. In: Canham, C.D., Lauenroth, W.K. (Eds.), *Models in Ecosystem Science*. Princeton University Press, Princeton, NJ, pp. 225–253.
- Castells, E., Peñuelas, J., Valentine, D.W., 2004. Are phenolic compounds released from the Mediterranean shrub *Cistus albidus* responsible for changes in N cycling in siliceous and calcareous soils? *New Phytol.* 162, 187–195.
- Chadwick, D.R., Ineson, P., Woods, C., Pearce, T.G., 1998. Decomposition of *Pinus sylvestris* litter in litter bags: influence of underlying native litter layer. *Soil Biol. Biochem.* 30, 47–55.
- Coleman, K., Jenkinson, D.S., 1996. RothC-26.3 – a model for the turnover of carbon in soil. In: Powlson, D.S., Smith, P., Smith, J.U. (Eds.), *Evaluation of Soil Organic Matter Models, Using Existing Long-Term Datasets*. Springer-Verlag, Heidelberg, pp. 237–246.
- Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Diaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.V., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol. Lett.* 11, 1065–1071.
- Coûteaux, M.M., Bottner, P., Berg, B., 1995. Litter decomposition, climate and litter quality. *Tree* 10, 63–66.
- 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.
- Criquet, S., Ferre, E., Farnet, A.M., Le Petit, J., 2004. Annual dynamics of phosphatase activities in an evergreen oak litter: influence of biotic and abiotic factors. *Soil Biol. Biochem.* 36, 1111–1118.
- De Marco, A., Forte, A., Gentile, A.E., Virzo De Santo, A., 2004. Elemental composition and litter decomposition of *Phillyrea angustifolia* L. at burned and unburned. In: Arianoutsou, M., Papanastasis, V.P. (Eds.), *Proceedings of the 10th MEDECOS Conference*. Millipress, Rotterdam, pp. 49–50.
- Del Grosso, S.J., Parton, W.J., Mosier, A.R., Hartman, M.D., Brenner, J., Ojima, D.S., Schimel, D.S., 2001. Simulated interaction of carbon dynamics and nitrogen trace gas fluxes using the DAYCENT model. In: Schaffer, M., Ma, L., Hansen, S. (Eds.), *Modeling Carbon and Nitrogen Dynamics for Soil Management*. CRC Press, Boca Raton, FL, pp. 303–332.
- Feng, X., Li, Y., 2001. An analytical model of soil organic carbon dynamics based on a simple “hockey stick” function. *Soil Sci.* 166, 431–440.
- Fioretto, A., Di Nardo, C., Papa, S., Fuggi, A., 2005. Lignin and cellulose degradation and nitrogen dynamics during decomposition of three leaf litter species in a Mediterranean ecosystem. *Soil Biol. Biochem.* 37, 1083–1091.
- Fioretto, A., Papa, S., Fuggi, A., 2003. Litter-fall and litter decomposition in a low Mediterranean shrubland. *Biol. Fertil. Soils* 39, 37–44.
- Fioretto, A., Papa, S., Pellegrino, A., Fuggi, A., 2008. Leaf litter decomposition dynamics in Mediterranean area. In: Tian-Xiao, L. (Ed.), *Soil Ecology Research Developments*. Nova Science Publishers, Hauppauge, NY, pp. 31–61.
- Gallo, M.E., Porras-Alfaro, A., Odenbach, K.J., Sinsabaugh, R.L., 2009. Photoacceleration of plant litter decomposition in an arid environment. *Soil Biol. Biochem.* 41, 1433–1441.
- Gessner, M.O., 2005. Proximate lignin and cellulose. In: Graca, M.A.S., Bärlocher, F., Gessner, M.O. (Eds.), *Methods to Study Litter Decomposition. A Practical Guide*. Springer Verlag, The Netherlands, pp. 115–120.
- Gholz, H.L., Wedin, D.A., Smitherman, S.M., Harmon, M.E., Parton, W.J., 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Glob. Change Biol.* 6, 751–765.

- Gourbière, F., 1986. Méthode d'étude simultanée de la décomposition et des mycoflores de conifères *Abies alba*. *Soil Biol. Biochem.* 18, 155–161.
- Hättenschwiler, S., Tiunov, A.V., Scheu, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annu. Rev. Ecol. Syst.* 36, 191–218.
- Hättenschwiler, S., Vitousek, P.M., 2000. The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends Ecol. Evol.* 15, 238–243.
- Himmelblau, D.M., 1972. *Applied Nonlinear Programming*. McGraw-Hill, New York, NY, 498 pp.
- Hoff, C., Rambal, S., Joffre, R., 2002. Simulating carbon and water flows and growth in a Mediterranean evergreen *Quercus ilex* coppice using the FOREST-BGC model. *Forest Ecol. Manage.* 164, 121–136.
- Hunt Jr., E.R., Piper, S.C., Nemani, R., Keeling, C.D., Otto, R.D., Running, S.W., 1996. Global net carbon exchange and intra-annual atmospheric CO₂ concentrations predicted by an ecosystem process model and three-dimensional atmospheric transport model. *Glob. Biogeochem. Cycles* 10, 431–456.
- Hutson, J.L., Wagenet, R.J., 1992. LEACHM: leaching estimation and chemistry model: a process-based model of water and solute movement, transformations, plant uptake and chemical reactions in the unsaturated zone. Version 3.0. Dept. CSS Research Series, 93-3. Cornell University, Ithaca, New York, 143 pp.
- Ibrahima, A., Joffre, R., Gillon, D., 1995. Changes in litter during the initial leaching phase: an experiment on the leaf litter of Mediterranean species. *Soil Biol. Biochem.* 27, 931–939.
- Kätterer, T., Andrén, O., 2001. The ICBM family of analytically solved models of soil carbon, nitrogen and microbial biomass dynamics – descriptions and application examples. *Ecol. Model.* 136, 191–207.
- Kazakou, E., Violle, C., Roumet, C., Pintor, C., Gimenez, O., Garnier, E., 2009. Litter quality and decomposability of species from a Mediterranean succession depend on leaf traits but not on nitrogen supply. *Ann. Bot.* 104, 1151–1161.
- Kelly, R.H., Parton, W.J., Hartman, M.D., Stretch, L.K., Ojima, D.S., Schimel, D.S., 2000. Intra-annual and interannual variability of ecosystem processes in shortgrass steppe. *J. Geophys. Res.* 105, 20093–20100.
- Knorr, M., Frey, S.D., Curtis, P.S., 2005. Nitrogen additions and litter decomposition: a meta-analysis. *Ecology* 86, 3252–3257.
- Lecerf, A., Risnoveanu, G., Popescu, C., Gessner, M.O., Chauvet, E., 2007. Decomposition of diverse litter mixtures in streams. *Ecology* 88, 219–227.
- Liski, J., Nissinen, A., Erhard, M., Taskinen, O., 2003. Climatic effect on litter decomposition from arctic tundra to tropical rainforest. *Glob. Change Biol.* 9, 575–584.
- Liski, J., Palosuo, T., Peltoniemi, M., Sievänen, R., 2005. Carbon and decomposition model Yasso for forest soils. *Ecol. Model.* 189, 168–182.
- Maisto, G., De Marco, A., Meola, A., Sessa, L., Virzo De Santo, A., 2011. Nutrient dynamics in litter mixtures of four Mediterranean maquis species decomposing in situ. *Soil Biol. Biochem.* 43, 520–530.
- Meentemeyer, V., 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* 59, 465–472.
- Melillo, J.M., Aber, J.D., Linkins, A.E., Ricca, A., Fry, B., Nadelhoffer, K.J., 1989. Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. *Plant Soil* 115, 180–198.
- Melillo, J.M., Aber, J.D., Muratore, J.F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63, 621–626.
- Moorhead, D.L., Sinsabaugh, R.L., Linkins, A.E., Reynolds, J.F., 1996. Decomposition processes: modelling approach and applications. *Sci. Total Environ.* 183, 137–149.
- Nelder, J.A., Mead, R., 1965. A simplex method for function minimization. *Comput. J.* 7, 308–313.
- Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44, 322–331.
- Palosuo, T., Liski, J., Trofymow, J.A., Titus, B.D., 2005. Litter decomposition affected by climate and litter quality – testing the Yasso model with litterbag data from the Canadian intersite decomposition experiment. *Ecol. Model.* 189, 183–198.
- Papa, S., Curcio, E., Lombardi, A., D'Orlando, P., Fioretto, A., 2002. Soil microbial activity in three evergreen oak (*Quercus ilex*) woods in a Mediterranean area. In: Violante, A., Huang, P.M., Bollag, J.-M., Gianfreda, L. (Eds.), *Soil Mineral–Organic Matter–Microorganism Interactions and Ecosystem Health*. Developments in Soil Science, vol. 28B. Elsevier Science B.V., pp. 229–237.
- Papa, S., Pellegrino, A., Fioretto, A., 2008. Microbial activity and quality changes during decomposition of *Quercus ilex* leaf litter in three Mediterranean woods. *Appl. Soil Ecol.* 40, 401–410.
- Parton, W.J., Ojima, D.S., Cole, C.V., Schimel, D.S., 1994. A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture, and management. *Quantitative Modelling of Soil Forming Processes*, SSSA Special Publication, vol. 39, pp. 147–167.
- Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in great plains grasslands. *Soil Sci. Soc. Am. J.* 51, 1173–1179.
- Parton, W., Silver, W.L., Burke, I.C., Grassens, L., Harmon, M.E., Currie, W.S., King, J.K., Adair, E.C., Brandt, L.A., Hart, S.C., Fasth, B., 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science* 315, 361–364.
- Potter, C.S., Randerson, J.T., Field, C.B., Matson, P.A., Vitousek, P.M., Mooney, H.A., Klooster, S.A., 1993. Terrestrial ecosystem production: a process model based on global satellite and surface data. *Glob. Biogeochem. Cycles* 7 (4), 811–841, doi:10.1029/93GB02725.
- Raich, J.W., Rastetter, E.B., Melillo, J.M., Kicklighter, D.W., Steudler, P.A., Peterson, B.J., Grace, A.L., Moore, B.I., Vörösmarty, C.J., 1991. Potential net primary productivity in South America: application of a global model. *Ecol. Appl.* 1, 399–429.
- Romanyà, J., Cortina, J., Falloon, P., Coleman, K., Smith, P., 2000. Modelling changes in soil organic matter after planting fast-growing *Pinus radiata* on Mediterranean agricultural soils. *Eur. J. Soil Sci.* 51, 627–641.
- Rovira, P., Kurz-Besson, C., Coûteaux, M.M., Vallejo, V.R., 2008. Changes in litter properties during decomposition: a study by differential thermogravimetry and scanning calorimetry. *Soil Biol. Biochem.* 40, 172–185.
- Rovira, P., Vallejo, V.R., 2007. Labile, recalcitrant, and inert organic matter in Mediterranean forest soils. *Soil Biol. Biochem.* 39, 202–213.
- Running, S.W., Gower, S.T., 1991. Forest-BGC, a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiol.* 9, 147–160.
- Rutigliano, F.A., Fierro, A.R., D'Ascoli, R., Virzo De Santo, A., 2001. Factors influencing the stability of organic carbon pool in some Mediterranean soils. *J. Med. Ecol.* 2, 113–121.
- Rutigliano, F.A., Virzo De Santo, A., Berg, B., Alfani, A., Fioretto, A., 1996. Lignin decomposition in decaying leaves of *Fagus sylvatica* L. and needles of *Abies alba* Mill. *Soil Biol. Biochem.* 28, 101–106.
- Sariyildiz, T., Anderson, J.M., Kucuk, M., 2005. Effects of tree species and topography on soil chemistry, litter quality, and decomposition in Northeast Turkey. *Soil Biol. Biochem.* 37, 1695–1706.
- Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K., Venevsky, S., 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Glob. Change Biol.* 9, 161–185.
- Stockle, C.O., Martin, S., Campbell, G.S., 1994. CropSyst, a cropping systems model: water/nitrogen budgets and crop yield. *Agric. Syst.* 46, 335–359.
- Swift, M.J., Heal, O.W., Anderson, J.M., 1979. *Decomposition in Terrestrial Ecosystems*. Blackwell Scientific Publications, Oxford, London, Edinburgh, Melbourne, 372 pp.
- Tanner, E.V.J., 1981. The decomposition of leaf litter in Jamaican montane rain forests. *J. Ecol.* 69, 263–273.
- Taylor, B.R., Parkinson, D., Parsons, W.F.J., 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70, 97–104.
- Thornthwaite, C.W., 1948. An approach toward a rational classification of climate. *Geogr. Rev.* 38, 55–94.
- Tuomi, M., Thum, T., Järvinen, H., Fronzek, S., Berg, B., Harmon, M., Trofymow, J.A., Sevanto, S., Liski, J., 2009. Leaf litter decomposition – estimates of global variability based on Yasso07 model. *Ecol. Model.* 220, 3362–3371.
- Van der Peijl, M.J., Verhoeven, J.T.A., 1999. A model of carbon, nitrogen and phosphorus dynamics and their interactions in river marginal wetlands. *Ecol. Model.* 118, 95–130.
- Virzo De Santo, A., Berg, B., Rutigliano, F.A., Alfani, A., Fioretto, A., 1993. Factors regulating early-stage decomposition of needle litters in five different coniferous forests. *Soil Biol. Biochem.* 25 (10), 1423–1433.
- Virzo De Santo, A., Rutigliano, F.A., Berg, B., Fioretto, A., Puppi, G., Alfani, A., 2002. Fungal mycelium and decomposition of needle litter in three contrasting coniferous forests. *Acta Oecol.* 23, 247–259.
- Weider, W.R., Cleveland, C.C., Townsend, A.R., 2009. Control over litter decomposition in wet tropical forests. *Ecology* 90, 3333–3341.