

The growth respiration component in eddy CO₂ flux from a *Quercus ilex* mediterranean forest

S. RAMBAL*, R. JOFFRE, J. M. OURCIVAL, J. CAVENDER-BARES† and A. ROCHETEAU
*DREAM CEFE-CNRS, 1919 route de Mende, 34 293 Montpellier Cedex 5, France, †Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, St Paul, MN 55108, USA

Abstract

Ecosystem respiration, arising from soil decomposition as well as from plant maintenance and growth, has been shown to be the most important component of carbon exchange in most terrestrial ecosystems. The goal of this study was to estimate the growth component of whole-ecosystem respiration in a Mediterranean evergreen oak (*Quercus ilex*) forest over the course of 3 years. Ecosystem respiration (R_{eco}) was determined from night-time carbon dioxide flux (F_c) using eddy correlation when friction velocity (u_*) was greater than 0.35 m s^{-1} .

We postulated that growth respiration could be evaluated as a residual after removing modeled base R_{eco} from whole-ecosystem R_{eco} during periods when growth was most likely occurring. We observed that the model deviated from the night-time F_c -based R_{eco} during the period from early February to early July with the largest discrepancies occurring at the end of May, coinciding with budburst when active aboveground growth and radial growth increment are greatest. The highest growth respiration rates were observed in 2001 with daily fluxes reaching up to 4 g C m^{-2} . The cumulative growth respiration for the entire growth period gave total carbon losses of 170, 208, and 142 g C m^{-2} for 1999, 2001, and 2002, respectively. Biochemical analysis of soluble carbohydrates, starch, cellulose, hemicellulose, proteins, lignin, and lipids for leaves and stems allowed calculation of the total construction costs of the different growth components, which yielded values of 154, 200, and 150 g C for 3 years, respectively, corresponding well to estimated growth respiration. Estimates of both leaf and stem growth showed very large interannual variation, although average growth respiration coefficients and average yield of growth processes were fairly constant over the 3 years and close to literature values. The time course of the growth respiration may be explained by the growth pattern of leaves and stems and by cambial activity. This approach has potential applications for interpreting the effects of climate variation, disturbances, and management practices on growth and ecosystem respiration.

Keywords: biochemical compounds, ecosystem respiration, evergreen Mediterranean ecosystem, growth analysis, growth respiration, *Quercus ilex*

Received 19 December 2003; revised version received 11 February 2004; accepted 5 March 2004

Introduction

Measurement of carbon dioxide flux using the eddy correlation technique is a remarkable tool for monitoring ecosystem metabolism and has greatly contributed to our understanding of how carbon assimilation and losses through respiration are partitioned among ecosystem compartments (Baldocchi *et al.*, 2001). Re-

spiration measurements are notoriously difficult to conduct for plant organs and soil, and scaling procedures are not always easy (Damesin *et al.*, 2002). Under conditions of friction velocity, whole-ecosystem respiration can be determined from night-time eddy flux of CO₂. Whole-ecosystem respiration has been shown to be the main component in evaluating net carbon exchange in most of the European forests (Valentini *et al.*, 2000). Ecosystem respiration (R_{eco}) is often modeled as a lumped variable related empirically to temperature (Lloyd & Taylor, 1994; Enquist *et al.*, 2003), where drought is important to available soil water (Raich &

Correspondence: S. Rambal, DREAM CEFE-CNRS, 1919 Route de Mende, F-34293 Montpellier Cedex 5, France, e-mail: rambal@cefe.cnrs-mop.fr

Tufekcioglu, 2000; Reichstein *et al.*, 2002; Joffre *et al.*, 2003). R_{eco} incorporates respiration of heterotrophic organisms as well as the above- and belowground autotrophic respirations of plants (Xu *et al.*, 2001). Substrate quality also affects heterotrophic respiration but locally this property is often constant and therefore can be ignored (O'Connell, 1990). Studies of eddy fluxes have generally considered respiration as an aggregate component of ecosystem carbon exchange. In this study, however, we focus on uncoupling respiration due to growth from total ecosystem respiration.

The plant contribution to ecosystem respiration was separated into maintenance and growth components three decades ago by McCree (1970) and Thornley (1970). They proposed a simple equation using these two components, which was subsequently referred to as the growth-and-maintenance-respiration paradigm (GMRP) by Amthor (2000). According to this view, both components are important. The time course of temperature plays a key role in determining the pattern of the maintenance component. Phenology and growth patterns determine the period during which the growth component is significant (Ceschia *et al.*, 2002).

When growth is restricted or stopped, its contributions to whole-ecosystem respiration can be assumed negligible. This we will subsequently refer to as base R_{eco} and model it as a function of surface soil moisture and temperature (Reichstein *et al.*, 2002; Joffre *et al.*, 2003). The relationship can also be modeled with ambient air temperature but the soil represents the major CO_2 efflux from the system. We postulate that growth respiration, to the extent that it contributes, may be evaluated as the residual departure from simulated base R_{eco} . The same approach has been applied to separate stem growth from maintenance respiration (Sprugel & Benecke, 1991).

Following this approach, we examined growth respiration using continuous carbon flux measurements over a forest dominated by the evergreen Mediterranean oak *Quercus ilex* during 3 complete years of growth between 1998 and 2002. The present study was undertaken to: (1) examine when and how whole-ecosystem R_{eco} differed from base R_{eco} , (2) evaluate how the growth respiration rate was related to the amount of growth, and finally, (3) compare the time course of growth respiration with the growth and phenological patterns of the plant components including leaves, wood, and roots.

Methods and materials

Study site

The study site is located 35 km NW of Montpellier (southern France) in the Puéchabon State Forest

(3°35'45"E, 43°44'29"N, and elevation 270 m) on a flat plateau. This forest has been managed as a coppice for centuries and the last clear cut was performed in 1942. Vegetation is largely dominated by the overstorey evergreen tree *Q. ilex* L. This tree species is characterized by its sprouting ability after cutting or fire. New stems emerge from the root–shoot interface. This 'interface tissue' forms an enlarged structure described as a root crown or a stump. Thus, in the subsequent growth analysis we consider the new shoots or stems as a basic unit rather than as a part of the whole tree. Understorey species compose a sparse, shrubby layer (<25% cover, <2 m tall), including *Buxus sempervirens*, *Phyllirea latifolia*, *Pistacia terebinthus*, and *Juniperus oxycedrus*.

The region has a Mediterranean-type climate. Rainfall occurs largely during autumn and winter with about 75% of the total occurring between September and April. Mean annual precipitation is 872 mm with a range 550–1549 mm recorded over the past 18 years. Mean annual temperature over the same period was 13.5 °C. The forest grows on hard Jurassic limestone. Soil texture does not show trend with depth between 0 and 50 cm from the surface. Clay and sand contents are, respectively, 40% and 14%. This soil is considered a silty clay loam according to the USDA texture triangle. The soil fills up the cracks and fractures of the limestone providing a source of water throughout the long dry summers for the deep-rooted *Q. ilex*. The average stone and rock content is about 75% for the top 0–50 cm and 90% for the whole profile.

Eddy covariance measurements

Carbon and water flux measurements were acquired using the eddy covariance technique from an 11 m tall scaffolding tower about 5 m higher than the top of the dominant trees. Wind speed and ambient temperature were measured with a three-dimensional sonic anemometer (Solent R2 period 1998–1999 and R3 period 2000–2001, Gill Instruments, Lymington, UK). Air was drawn from an inlet located 20 cm apart from the sonic anemometer sensing path (height 12.2 m) and through an infrared gas analyzer (IRGA) (model LI 6262, Li-Cor Inc., Lincoln, NE, USA) with an atmospheric pressure sensor (see additional details in Rambal *et al.*, 2003). The eddy flux measurements followed the general methodology and data quality check adopted in the European UE Programs Euroflux, Medeflu, and Carboeuroflux (for a thorough account of these methods, see Aubinet *et al.*, 2000).

Ecosystem respiration (R_{eco}) was evaluated using night-time F_c . Half-hourly values of night-time F_c were considered only when $u_* > 0.35 \text{ ms}^{-1}$. R_{eco} was then

calculated as the average of the night-time F_c if more than five half-hourly periods filled these wind conditions. We compared night respiratory fluxes with the intercept of the light response curve as proposed by Falge *et al.* (2001). For the six first months of 2001, R_{eco} estimated from the light-response curves were highly significantly correlated with the night-time mean F_c with a slope of 0.78 and an intercept of $0.32 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($r^2 = 0.85$). Because of their reliability we retained the night-time data (see also Xu & Baldocchi, 2004).

Modeling base R_{eco}

To avoid interference with growth respiration, we analyzed CO_2 flux data collected outside of the period of vegetation growth (i.e. from March to June). Over the period of continuous flux measurements, 302 nights satisfied these conditions (between July 1998 and November 1999 and between July 2000 and December 2001) and were consequently considered for base R_{eco} modeling.

Base ecosystem respiration (R_{eco}) was modeled using the following equation where the rate constant of temperature is a linear function of soil moisture:

$$R_{eco} = R_{eco, \text{ref}} f(\theta) e^{(bf(\theta)+c)(t-t_{\text{ref}})/10},$$

where $f(\theta)$ is the relative water content (RWC), expressed as percent of soil water content at field capacity, t is the soil temperature at 15 cm depth, $t_{\text{ref}} = 0^\circ\text{C}$, and $R_{eco, \text{ref}}$ is the respiration under standard conditions. Best regression results were obtained with $R_{eco, \text{ref}} = 1.0625$, $b = 0.467$, and $c = 0.383$ ($n = 302$, $r^2 = 0.73$, and $\text{RMSE} = 0.54$) (see Joffre *et al.*, 2003 for more details).

Growth patterns, standing biomass, and productivity

Phenological patterns. The phenology of leaf growth was checked weekly during the growth period since 2000 using a procedure proposed by Dumerle & Mazet (1983) for both deciduous and evergreen oaks growing in areas with a Mediterranean-type climate. Fifty-five branches from 55 different trees were sampled. The spring development of the leaves was checked by observation of the apical buds. Budburst and the leafing-out process were scaled over seven stages ranging from stage 1 when the bud was completely closed to stage 7, when the new leaves were fully developed and mature. Each week, the numbers of buds at each stage was multiplied by the number of the stage and expressed as a proportion so that the final number gave the average stage of the leafing-out process over time (Blondel *et al.*, 1992).

Aboveground standing biomass. Estimation of the standing aboveground biomass required allometric

equations and stem densities per unit area by class of diameter at breast height (DBH). Stem and leaf biomass were estimated from relationships based on DBH in centimeters measured at 1.3 m height. These were established from 10 stems harvested 300 m away from the tower in 2001 and pooled with data from 14 additional stems obtained on the same site and close to the tower by Merzouki (1986). For each stem, DBH was measured, leaves were removed, oven-dried, and then weighed. The fresh mass of the stems was determined. Subsections of stem were cut, weighed fresh and then oven-dried and weighed again so that aboveground dry woody biomass could be calculated. Leaf mass and stem mass were related to DBH with both equations $21.77\text{DBH}^{1.875}$ ($r^2 = 0.92$; $S_{y,x} = 286.4$ g dry matter (DM)) and $191.6\text{DBH}^{2.171}$ ($r^2 = 0.94$; $S_{y,x} = 4945$ g DM), respectively.

The root systems and the root crowns or stumps of four trees (including all stems emerging from one stool) were excavated using a high-pressure air hose and hand tools. Perennial coarse roots, with diameter larger than ca. 5 mm, and stump, both free of soil, were oven-dried and then weighed. Stem basal area was calculated from stem diameter. Stool basal area (SBA), in cm^2 was the sum of the cross-sectional area of all live stems sustained by the excavated stool. We pooled these data with those from Canadell & Roda (1991) (two stumps) and Djema (1995) (11 stumps) obtained on *Q. ilex* coppices growing in Northeastern Spain. Based on 17 values, we found a linear relationship between SBA and the perennial belowground dry biomass: root system plus stump, 331.1SBA ($r^2 = 0.82$; $S_{y,x} = 23\,020$ g DM per stump).

Growth and litter fall. Measurements of DBH (in cm) and height (in m) were conducted annually on 439 stems. Stem volume increment was estimated by multiplying the basal area increment by the height. This simplification made use of the Leonardo da Vinci rule; he proposed that the cross-sectional area of the trunk or branch of a tree is equal to the sum of the cross-sectional areas of the branches at any higher level (Enquist, 2002). This rule has been fully verified by us with *Q. ilex* stems growing in coppices (data not shown). The volume increments per unit stem were scaled up to the whole-ecosystem using the areal densities by DBH classes. The density of the wood formed has been assumed constant and equal to 0.90 g cm^{-3} (Voulgaridis & Passialis, 1995).

Root production and turnover are notoriously difficult to measure directly. Coarse root and stool production has been assumed to be directly correlated with growth in stem diameter (Waring *et al.*, 1998). Hence, we applied a conservative hypothesis assuming that the

growth of the belowground compartment is equal to the root/shoot ratio times the growth of the stems. For the production of fine roots, we applied results from Lopez *et al.* (2001) obtained on a *Q. ilex* coppice in north-eastern Spain very similar to the Puéchabon forest. Trees fall in the same age class, and this site supports a close standing biomass with the same partition in the aboveground and belowground compartments.

Litter production was determined from 1 year of monthly collections of litter fall in 26 randomly located baskets (0.13 m^{-2} each). Litter was separated into foliage and nonfoliage elements. Nonfoliage elements were shared in elements with 1-year turnover: flowers and acorns and those with turnover greater than 1 year, i.e. woody fragments.

Results

Growth respiration

For the year 2001, we plotted the course of night-time eddy C flux, as a surrogate for whole-ecosystem respiration (R_{eco}), as well as base R_{eco} , derived from the simulation of the ecosystem respiration model driven by soil temperature and RWC of the surface soil layer (Fig. 1). We observed that the model deviated from the night F_c -based R_{eco} across the period from early February to early July with the largest discrepancies during a period centered at the end of May. During this period, simulated R_{eco} , or base R_{eco} , underestimated significantly the whole respiration of the ecosystem. We attributed this deviation to the growth respiration component of the ecosystem. The same procedure has been applied for 1999 and 2002, years for which continuous eddy fluxes measurements were available. For the 3 years, we plotted the course of the residual of R_{eco}

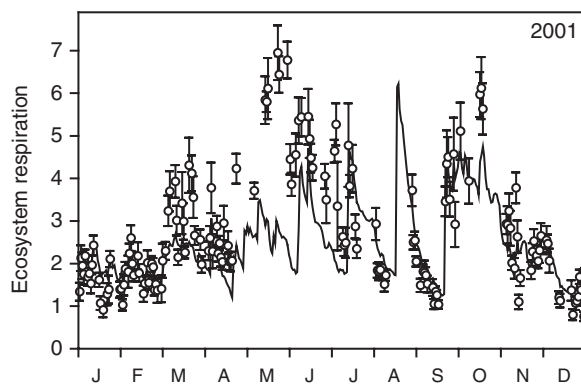


Fig. 1 Daily time course of night-time eddy C flux \pm SD and base R_{eco} obtained from the simulation of a respiration model driven by soil temperature and soil relative water content. Both respirations are expressed in g C m^{-2} .

determined from night F_c -based minus base R_{eco} , averaged over 10-day intervals (Fig. 2).

The same pattern was observed during the 3 years: growth respiration begins mid-February and ends in early July with a peak close to late May. In 2002, the growth component started mid-January but was drastically reduced later probably because of very cold conditions in February. It stopped earlier than in the previous years, likely due to very dry conditions. Higher growth respiration rates have been observed in 2001 with daily fluxes that reached up to 4 g C m^{-2} . The integrals of growth respiration for the entire growth period give total carbon losses of 170, 208, and 142 g C m^{-2} for 1999, 2001, and 2002.

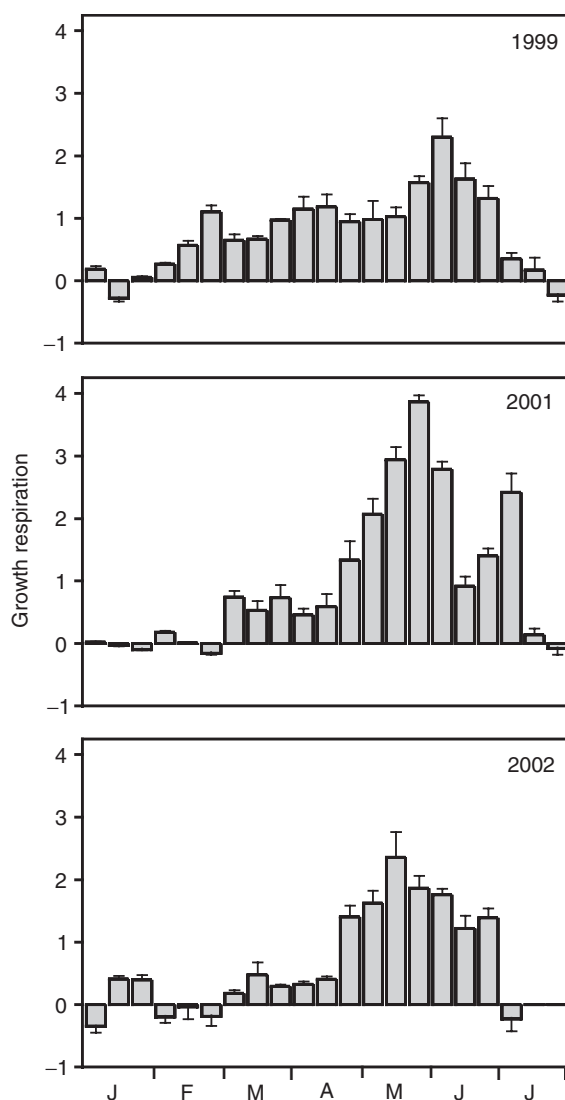


Fig. 2 Ten-day average of growth respiration (expressed in $\text{g C m}^{-2} \text{ day}^{-1}$) estimated as the residual between measured R_{eco} and base R_{eco} for 1999, 2001, and 2002.

We also calculated the average pattern of growth respiration over the 3 years. We first standardized 10-day integrals of growth respiration by dividing each one by the value for the whole growth period and subsequently averaging the standardized 10-day values over the 3 years (Fig. 3). Sixty six percent of the entire growth respiration loss occurred between May and June. Adding the last 10 days of April and the first 10 days of July allowed us to reach 80% of the total.

Estimates of annual growth from biomass production

In 2001, the density of resprouted stems was 7150 stems ha⁻¹ with a mean stem diameter of 6.8 cm. The percentage of stem with DBH < 4 cm was 12% and 12.5% for DBH > 10 cm. The whole-ecosystem basal area per ha was 30.4 m², which yields an aboveground

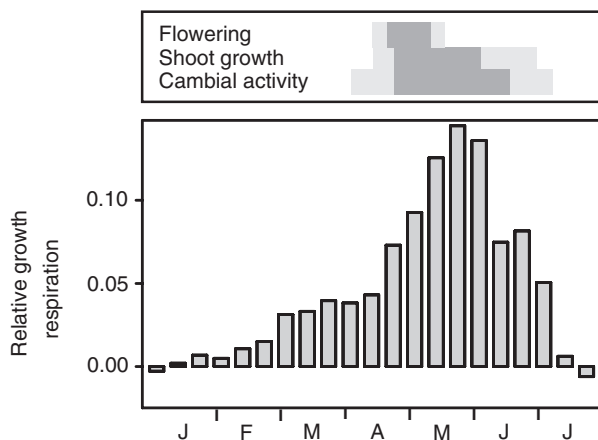


Fig. 3 Average pattern of relative growth respiration over the 3 years. Ten-day integrals of growth respiration were standardized by dividing each one by the value for the whole growth period and subsequently averaging the standardized 10-day values over the 3 years. Periods of flowering, shoot growth, and cambial activity were also presented. Light grey areas defined the period in which the growth for each compartment occurred. Dark grey areas corresponded to the most active periods.

biomass estimate of about $11\,300 \pm 2825$ g DM m⁻². The belowground component was approximately $11\,886 \pm 1783$ g DM m⁻² giving a root/shoot ratio of 1.05. Estimates of the growth components are shown for these 3 years in Table 1. They showed very large interannual variations for both leaf and stem components. Leaf litter fall ranged between 174 and 325 g DM m⁻², and stem growth ranged between 60 and 259 g DM m⁻². The biomass of fine roots was considered to be the same as the biomass recorded by Lopez *et al.* (2001), i.e., about 71 g C m⁻² with a turnover rate of 125 days. The acorn production has not been considered in our analysis because their growth starts in mid-summer. However, it reached 163, 49, and 26 g DM m⁻², respectively, for the 3 years of study.

Timing of phenological events

Strong interannual fluctuations in the beginning of phenological processes were recorded during the period of study (Table 2). Bud development and leaf growth began earlier in 2002 than in 2001 by ca. 2 weeks and earlier than in 2000 by 2–4 weeks. Flowering began 1 week earlier in 2002 than in previous years, but ended at a very similar date in all years. The duration of each phase showed less variability than the onset with mean durations of 3.8, 2.7, 1.3, and 4.5 weeks, respectively, for bud swelling, budburst, shoot elongation, and leaf maturity phases. The mean leafing scale of 3.5 was reached earlier in 2002, with an 11-day lag between 2001 and 2002, and a 19-day lag between 2000 and 2002 (Fig. 3).

Discussion

Early works of Thornley (1970), McCree (1970) and others (reviewed in Amthor, 2000) divided whole-plant respiration into two components: maintenance respiration and growth respiration. This separation was already present in Monsi (1968) with both 'constructive'

Table 1 Time course of phenological stages in the Puéchabon forest

Phenological stage	1999			2000			2001			2002		
	Onset	50	End	Onset	50	End	Onset	50	End	Beginning	50	End
Bud swelling	–	–	–	April 18	May 2	May 24	April 3	April 24	May 28	March 16	April 10	May 6
Budburst	–	–	–	May 2	May 17	June 7	April 18	May 11	June 17	April 4	April 30	May 21
Shoot elongation	–	–	–	May 10	May 25	June 13	May 9	May 18	June 15	April 23	May 11	May 28
Leaf maturity	–	–	–	May 24	June 4	July 4	May 29	June 21	July 11	May 14	June 16	July 9
Flowering	–	–	–	May 9	–	May 25	May 9	–	May 24	April 30	–	May 28

Measurements were done on 55 branches; 50 means that 50% of the branches have reached the corresponding phenological stage.

Table 2 Production in g DM m⁻² by growth compartment and year in the Puéchabon *Quercus ilex* forest

Growth compartment	1999	2001	2002
Leaf fall	174	252	325
Flowers	19	15	40
Stem growth	196	259	60
Coarse roots, stump	206	272	63
Fines roots*	71	71	71

*Biomass from Lopez *et al.* (2001a) with a turnover rate of 125 days, that is one fine root cohort within the growth period.

and maintenance respirations as the basis of his 'compound-interest law equations'. This separation has been further called the GMRP. Other paradigms have been also proposed: the growth-and-maintenance-and-wastage paradigm (GMWRP) and the general paradigm (GP). For the purpose of this study, we discuss only GMRP in detail. GMRP equations formed the basis of simple whole-plant growth models. Hesketh *et al.* (1971) wrote:

$$R = R_g + R_m = g_r G + m_r W$$

where R is the rate of respiration per unit of ground area, R_g the growth respiration component, R_m the maintenance respiration component, G the growth rate, and W the living dry biomass. The terms g_r and m_r are associated with growth respiration and maintenance respiration, respectively, g_r is a growth respiration coefficient and m_r a maintenance respiration coefficient. We expressed R , R_g , and R_m in g C day⁻¹ m⁻² and the growth rate G in g C of new biomass day⁻¹ m⁻². The living dry biomass is expressed in g C m⁻², and g_r is a growth respiration coefficient equal to the amount of C released due to growth per unit of growth and per unit of ground area, g C (g C of new biomass)⁻¹. m_r is a maintenance respiration coefficient equal to the amount of C released due to maintenance per unit of existing biomass per unit of time and per unit of ground area, g C (g C of living dry biomass)⁻¹ day⁻¹. From g_r we can derive the well-known Y_G parameter (Thornley, 1970) also called the yield of growth processes. This yield is the amount of growth per unit of C substrate used in growth processes and including that part of substrate retained in new structures with $Y_G = 1/(1 + g_r)$. It is expressed in g C of new biomass (g C of substrate used in the growth processes)⁻¹.

Construction costs

Penning de Vries *et al.* (1974) simplified their original pathway analysis method for calculating growth cost by categorizing biochemical compounds into groups.

Biochemical composition of *Q. ilex* has been intensively studied by Vivat (1995). She measured contents of soluble carbohydrates, starch, cellulose, hemicellulose, proteins, lignin, and lipids and further calculated the construction costs using the elementary costs proposed by Merino *et al.* (1984) for some Mediterranean chaparral shrub species. In her study, sun-exposed leaves sampled on our flux site and on seven nearby sites with 12 trees per site. She observed low within-site and between-site variations. The construction cost in the eddy flux site was 1.86 ± 0.03 g glucose g⁻¹ DM with a regional average of 1.82 ± 0.07 g glucose g⁻¹ DM. These values are higher than that proposed by Merino (1987) and Villar & Merino (2001) with ca. 1.51 g glucose g⁻¹ DM using a heat of combustion or calorimetric method, but for leaves with leaf mass per area largely lower than those of our site, 160 against 230 g m⁻².

For the construction cost of the wood compartment, we used results from Vivat (1995) as well, even though her analyses were done on twigs and branches only. The construction cost of the wood was lower than that of the leaves. In the flux site, the wood construction cost was 1.61 ± 0.05 g glucose g⁻¹ DM. This value was applied for the flux site to all of the wood compartments, including stems, stumps, and coarse roots. The regional average was 1.58 ± 0.07 g glucose g⁻¹ DM. For leaves and stems, underestimation of the construction cost of the lignin by 20% (see Amthor, 2003) lowered the total construction cost by 0.1 g glucose g⁻¹ or 5%.

For the fine-root compartment we used data from Martinez *et al.* (2002) obtained from Mediterranean species growing in natural conditions in southern Spain. They derived the construction costs from the biochemical compositions of the sampled material. The value for *Q. ilex* (*Q. rotundifolia* in their paper) is 1.8 g glucose g⁻¹ DM a value very close to their average value of 1.78 g glucose g⁻¹ DM for all evergreen trees, regardless of whether the soil conditions were fertile or infertile. They did show large discrepancies in values obtained from the same species growing in hydroponic conditions, i.e., 1.2 g glucose g⁻¹ DM (Martinez *et al.*, 2002). Canadell *et al.* (1999) used 1.47 g glucose g⁻¹ DM for the same species growing in very similar ecological conditions to those at Puéchabon.

From these construction costs, we derived the growth respiration coefficients g_r (Table 3). In doing so, we assumed that the carbon content in all of the plant organs was constant and equal to 0.45 g C (g C of living DM)⁻¹. g_r were 0.294, 0.194, and 0.270 g C (g C of new biomass)⁻¹ for leaves, wood, and fine roots, respectively. We further applied the leaf value of g_r to the flower compartment in our growth analysis.

Table 3 Construction cost analysis for the five growth compartments

Growth compartment	Growth cost	g_r	Y_G
Leaf fall	1.86	0.294	0.772
Flowers	1.86	0.294	0.772
Stem growth	1.61	0.194	0.838
Coarse roots, stump	1.61	0.194	0.838
Fines roots	1.80	0.270	0.787

The growth costs in g glucose g⁻¹DM of new biomass were estimated by categorizing biochemical compounds into groups. g_r is the growth respiration coefficients or the amount of C released due to growth per unit of growth and per unit of ground area, gC (g C of new biomass)⁻¹. The yields of growth processes Y_G is the amount of growth per unit of C substrate used in growth processes and including that part of substrate retained in new structures with $Y_G = 1/(1 + g_r)$. They are expressed in gC of new biomass (gC of substrate used in the growth processes)⁻¹.

Production and growth respiration

Q. ilex ecosystems show low productivity even if they appear to be one of the most productive Mediterranean-type ecosystems (Rambal, 2001). Estimating productivity in evergreen ecosystems is more difficult than in deciduous forests because litter fall is not necessarily related to annual growth. However, the basic method for estimating aboveground productivity in deciduous forests, which takes the sum of two components – the increment of growth for stem or trunk and branches plus the total litter fall – still works in evergreen ecosystems. This is because the aboveground primary productivity of *Q. ilex* ecosystems has been shown to depend largely on the amount of new leaves produced each year and their turnover rate (Bellot *et al.*, 1992). In the Puéchabon site, demographic analysis showed that the leaf life span is about 2 years and that this value is fairly constant interannually (Rapp *et al.*, 1992). For *Q. ilex* this value may increase to 3–4 years in drier habitats (Vivat, 1995). The mean yearly litter fall is a good estimator of the turnover rates for all biomass components, with a 1-year turnover rate for acorns and flowers, and about 2 years for leaves or more for woody fragments.

For the belowground compartment, we separated the growth of perennial roots and the stump from the growth of fine roots. For perennial roots and lignotubers, we assumed that root growth and shoot growth followed the same ratio as the root-to-shoot ratio evaluated for *Q. ilex* ecosystems. For fine-root production we assumed that within our analysis period, from early February to early July, only one cohort of fine roots had grown.

Table 4 Comparison of both estimates of the growth respiration cumulated over the growth period, gC

Growth respiration	1999	2001	2002
Biochemical compound	154	200	150
Eddy flux based	170	208	142
\bar{g}_r	0.255	0.239	0.254
\bar{Y}_G	0.797	0.807	0.797

We also calculated \bar{g}_r the averaged growth respiration coefficients by dividing the eddy flux-based growth respirations by the amounts of growth, gC (g C of new biomass)⁻¹ and \bar{Y}_G as $1/(1 + \bar{g}_r)$.

Combining the growth components and their associated growth respiration coefficients yielded estimates of the amount of growth respiration during the growth period. The estimates showed good agreement with growth respiration determined, using the eddy correlation method (see Table 4). So, our approach provides an independent estimate of annual growth not easily achieved through direct field measurement. Dividing the measured growth respirations by the amount of growth gave the averaged growth respiration coefficients, \bar{g}_r of 0.255, 0.239, and 0.254 gC (g C of new biomass)⁻¹ and the average yield of growth processes \bar{Y}_G of 0.797, 0.807, and 0.797 gC of new biomass (gC of substrate used in the growth processes)⁻¹ for the 3 years, respectively. These values bounded the value of 0.250 gC (gC of new biomass)⁻¹ that Waring *et al.* (1998) adopted in their growth analysis of forest ecosystems. Cannell & Thornley (2000) wrote that 'a reasonable average of direct growth yield of plant vegetative tissues is about 0.8 gC appearing in new biomass per g of C substrate utilized'. 'Transformation factors' or an 'economy ratio' in the range of 0.5–0.8 was reported by Monsi (1968).

Timing of growth respiration and phenology

Our last question concerned explaining the patterns we observed in the growth respiration. The phenology for *Q. ilex* has previously been described in detail (Floret *et al.*, 1989; Blondel *et al.*, 1992; De Lillis & Fontanella, 1992). The annual course of growth activity in Mediterranean trees or shrubs is generally related to the alternance of cold and warm seasons and of the availability of soil water (Mooney & Kummerow, 1981). Leaf growth starts at the end of April/beginning of May and continue until mid-June. Extension of the internodes of twigs starts early in spring immediately after the appearance of flowers and was rapid. It is followed by leaf expansion, which generally occurs within 2 weeks after internode expansion has stopped.

By early July, the leaves can be considered to be mature and their biochemical contents fairly constant (Damesin *et al.*, 1998). A period of stasis is generally observed from mid-July to the next growth period, the following year. In very rare cases we observe a new and brief vegetative period starting in September and lasting 3 weeks. We did not observe this phenomenon during the 3 years of this study. Flowering occurs in May with male flowers slightly preceding female flowers.

The overlapping of vegetative and reproductive growth has been intensively studied by Castro-Diez & Montserrat-Marti (1998). They showed that vegetative growth, flower bud formation and flowering were completed in less than 2.5 months. Their phenophase sequence index, an index quantifying the overlaps, ranged from 0.35 to 0.5 in three *Q. ilex* stands along an environmental gradient. An index of 0.50 means that the time period from vegetative growth to flowering is half the sum of the three basic phenophase lengths. The greater overlap has been observed in the colder site. These patterns were very similar to our site.

The rest period of the stems terminates when the cambium regains the ability to produce new vascular tissue when environment conditions are favorable. The cambium is then said to be quiescent. In ring porous trees such as *Q. ilex*, cambial reactivation spreads very quickly or even simultaneously in the whole trunk and in branches older than 1 year and proceeds basipetally in current-year shoots. Slow basipetal reactivation depends on activation of bud growth whereas simultaneous reactivation is relatively independent of bud growth. The time lag between shoot growth and simultaneous reactivation is 2 or 3 weeks in diffuse-porous species. Shoot growth occurs later than simultaneous reactivation in ring-porous species (Lachaud *et al.*, 1999).

The course of radial growth increment with time has been measured by Zhang (1987) in a *Q. ilex* stand close to the Puéchabon site and 15 km apart. Using dendrometer bands, the growth was analyzed during a 3-year period with a 1-week time step. He observed that the radial growth increased rapidly at budburst. This measurement method was not very sensitive and alternative methods may give an anatomical exact measure of cell division over time (Emmingham, 1977). However, large difficulties in determining the transition between quiescence and cambial growth, and between the swelling of cambial zone cells and the beginning and end of xylem production have been reported in the literature for evergreen Mediterranean trees (reviewed by Cherubini *et al.*, 2003). Stem dormancy began in early summer with the cessation of meristematic activity and kept on until the resumption of cell divisions. It should be noted that it is best to

consider the summer quiescent period as a period of drought-imposed rest rather than true dormancy.

During the interval between cambial cell swelling and the onset of rapid xylem production, the remaining growth respiration that could not be directly explained by the growth of the aboveground components may be attributed to fine-root growth or to reserve remobilization within the C pools. Fine-root production has been intensively studied in an evergreen oak shrub location close to our site by Kummerow *et al.* (1990). They observed the spring flush of fine roots in early April. Lopez *et al.* (2001) observed the highest fine-root productivity in winter in a *Q. ilex* ecosystem in northeastern Spain. They thus assumed no limitation to fine-root production by soil temperature. This interpretation agrees with our results. We did not find any direct evidence in our data between the onset of growth respiration and the course of soil temperature. Finally, early growth respiration that cannot be explained directly by observed growth processes (Fig. 3) is likely to be required for translocation and maintaining ion gradients and wastage respiration as described by Cannell & Thornley, (2000).

Conclusions

Four decades ago, Monsi provided the backdrop for all our ongoing activities related to the carbon cycle within terrestrial ecosystems in his talk within the 1965 Copenhagen symposium, 'Functioning of terrestrial ecosystems at the primary production level' as previously noted by Jackson *et al.* (2001). Monsi (1968) wrote: 'In order to obtain a better understanding of the relationships between photosynthetic activity and plant growth or final yield, we should investigate the internal physiology of plants as regards distribution ratio (i.e. the root/shoot ratio), rate of translocation of assimilates and rate of development of leaves, stems, and roots (i.e. the growth patterns or phenology)'. In such a context, the simple growth-maintenance respiration paradigm provides a useful approximate view of plant respiration even if it can be interpreted to explain three completely different mechanisms of plant function (Thornley & Cannell, 2000). Here, we showed that the total amounts of growth respiration were closely related to the amounts of growth of each plant components times their growth costs deduced from biochemical analysis. On average, the growth respiration coefficient or the yield of growth processes were in agreement with values given in the literature for forest ecosystems.

In conclusion, we agree with the assertion of Cannell & Thornley (2000) that 'growth respiration is easily modeled', particularly in coupling respiration with both C substrate and structure. But we add a corollary to this assertion. Most of the timing of the growth respiration

must be explained by studying the growth phenology of all the plant components. By teasing apart growth respiration from other respiration components, the approach presented here allows an easier mechanistic interpretation of how ecosystems respond to climatic change, disturbance, and management practices.

Acknowledgements

This work as part of the Medeflu project (Environment and Climate Programme ENV 4-CT98-0455) and the Carboeuroflux project (Environment Project EVK2-VT-1999-00032) was supported by the European Commission. This research is a contribution to the French Carbofor initiative.

References

- Amthor JS (2000) The McCree-de Wit-Thornley respiration paradigms: 30 years later. *Annals of Botany*, **86**, 1–20.
- Amthor JS (2003) Efficiency of lignin biosynthesis: a quantitative analysis. *Annals of botany*, **91**, 673–695.
- Aubinet M, Grelle A, Ibrom A *et al.* (2000) Estimates of the annual net carbon and water exchange of forests: the Euroflux methodology. *Advances in Ecological Research*, **30**, 113–175.
- Baldocchi D, Falge E, Gu LH *et al.* (2001) FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bulletin of the American Meteorological Society*, **82**, 2415–2434.
- Bellot J, Sánchez JR, Lledò MJ *et al.* (1992) Litterfall as a measure of primary production in Mediterranean holm-oak forest. *Vegetatio*, **99–100**, 69–76.
- Blondel J, Isenmann P, Maistre M *et al.* (1992) What are the consequences of being a downy oak (*Quercus pubescens*) or a holm oak (*Quercus ilex*) for breeding blue tits (*Parus caeruleus*). *Vegetatio*, **99–100**, 129–136.
- Canadell J, Djema A, López B *et al.* (1999) Structure and dynamics of the root system. In: *Ecology of Mediterranean evergreen oak forests* (eds Rodà F, Retana J, Gracia CA *et al.*), pp. 47–56. Springer-Verlag, Berlin.
- Canadell J, Rodà F (1991) Root biomass of *Quercus ilex* in a montane Mediterranean forest. *Canadian Journal of Forest Research*, **21**, 1771–1778.
- Cannell MGR, Thornley JHM (2000) Modelling the components of plant respiration: some guiding principles. *Annals of Botany*, **85**, 45–54.
- Castro-Diez P, Monserrat-Martí G (1998) Phenological pattern of fifteen Mediterranean phanerophytes from *Quercus ilex* communities of NE-Spain. *Plant Ecology*, **139**, 103–112.
- Ceschia E, Damesin C, Lebaube S *et al.* (2002) Spatial and seasonal variations in stem respiration of beech trees (*Fagus sylvatica*). *Annals of Forest Science*, **59**, 801–812.
- Cherubini P, Gartner BL, Tognetti R *et al.* (2003) Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. *Biological Reviews*, **78**, 119–148.
- Damesin C, Ceschia E, Le Goff N *et al.* (2002) Stem and branch respiration of beech: from tree measurements to estimations at the stand level. *New Phytologist*, **153**, 159–172.
- Damesin C, Rambal S, Joffre R (1998) Seasonal and annual changes in leaf $\delta^{13}\text{C}$ in two co-occurring Mediterranean oaks: relations to leaf growth and drought progression. *Functional Ecology*, **12**, 778–785.
- De Lillis M, Fontanella A (1992) Comparative phenology and growth in different species of the Mediterranean maquis of central Italy. *Vegetatio*, **99–100**, 83–96.
- Djema A (1995) *Cuantificación de la biomasa y mineralomasa subterránea de un bosque de Quercus ilex L.* Instituto Agronómico Mediterráneo, Zaragoza.
- Dumerle P, Mazet R (1983) Phenological stages and infestation by *Tortrix viridana* L. (Lep, Tortricidae) of the buds of 2 oaks (*Quercus pubescens* and *Q. ilex*). *Acta Oecologica-Oecologia Applicata*, **4**, 47–53.
- Emmingham WH (1977) Comparison of selected Douglas-fir seed sources for cambial and leader growth patterns in four western Oregon environments. *Canadian Journal of Forest Research*, **7**, 154–164.
- Enquist BJ (2002) Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems. *Tree Physiology*, **22**, 1045–1064.
- Enquist BJ, Economo EP, Huxman TE *et al.* (2003) Scaling metabolism from organisms to ecosystems. *Nature*, **423**, 639–642.
- Falge E, Baldocchi DD, Olson RJ *et al.* (2001) Gap filling strategies for defensible annual sums of ecosystems exchange. *Agricultural and forest meteorology*, **107**, 43–69.
- Floret C, Galan M-J, Le Floc'h E *et al.* (1989) Description of plant annual cycles: France. In: *Plant Pheno-Morphological Studies in Mediterranean Type Ecosystems* (ed. Orshan G), pp. 9–97. Kluwer Academic Publishers, Dordrecht.
- Hesketh JD, Baker DN, Duncan WG (1971) Simulation of growth and yield in cotton: respiration and carbon balance. *Crop Science*, **11**, 394–397.
- Jackson RB, Lechowicz MJ, Li X *et al.* (2001) Phenology, growth, and allocation in global terrestrial productivity. In: *Terrestrial Global Productivity* (eds Roy J, Saugier B, Mooney HA), pp. 61–82. Academic Press, San Diego, CA.
- Joffre R, Ourcival J-M, Rambal S *et al.* (2003) The key-role of topsoil moisture on CO₂ efflux from a Mediterranean *Quercus ilex* forest. *Annals of Forest Science*, **60**, 1–8.
- 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.
- Lachaud S, Catesson AM, Bonnemain JL (1999) Structure and functions of the vascular cambium. *Comptes Rendus de l'Académie des Sciences Serie III-Sciences de la Vie-Life Sciences*, **322**, 633–650.
- Lloyd J, Taylor JA (1994) On the temperature-dependence of soil respiration. *Functional Ecology*, **8**, 315–323.
- Lopez B, Sabate S, Gracia CA (2001) Fine-root longevity of *Quercus ilex*. *New Phytologist*, **151**, 437–441.
- Martinez F, Lazo YO, Fernandez-Galiano RM *et al.* (2002) Chemical composition and construction cost for roots of Mediterranean trees, shrub species and grassland communities. *Plant Cell and Environment*, **25**, 601–608.

- McCree KJ (1970) An equation for the rate of respiration of white clover plants under controlled conditions. In: *Prediction and Measurement of Photosynthetic Productivity* (ed. Setlik I), pp. 211–219. Pudoc, Wageningen.
- Merino J (1987) The costs of growing and maintaining leaves of Mediterranean plants. In: *Plant Response to Stress. Functional Analysis in Mediterranean Ecosystems* (eds Tenhunen JD, Caratarino FM, Lange OL, Oechel WC), pp. 553–564. Springer-Verlag, Berlin.
- Merino J, Field C, Mooney HA (1984) Construction and maintenance costs of Mediterranean-climate evergreen and deciduous leaves. II Biochemical pathway analysis. *Acta Oecologica/Oecologia Plantarum*, **5**, 211–229.
- Merzouki A (1986) *Les effets d'une coupe à blanc sur l'activité biologique d'un sol fersiallitique méditerranéen*. PhD, Université des Sciences et Techniques du Languedoc, Montpellier.
- Monsi M (1968) Mathematical models of plant communities. In: *Functioning of Terrestrial Ecosystems at the Primary Production Level* (ed. Eckardt FE), pp. 131–148. UNESCO, Paris.
- Mooney HA, Kummerow J (1981) Phenological development of plants in Mediterranean-climate regions. In: *Mediterranean-Type Shrublands* (eds Di Castri F, Goodall DW, Specht RL), pp. 303–307. Elsevier Scientific Publishing Company, Amsterdam.
- O'Connell AM (1990) Microbial decomposition (respiration) of litter in *Eucalyptus* forests of south-western Australia: an empirical model based on laboratory incubations. *Soil Biology and Biochemistry*, **22**, 153–160.
- Penning de Vries FWT, Brunsting AHM, van Laar HH (1974) Products, requirements and efficiency of biosynthesis: a quantitative approach. *Journal of Theoretical Biology*, **45**, 339–377.
- Raich JW, 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 Roy J, Saugier B, Mooney HA), pp. 315–344. Academic Press, San Diego, CA.
- Rambal S, Ourcival J-M, Joffre R *et al.* (2003) Drought controls over conductance and assimilation of a Mediterranean evergreen ecosystem: scaling from leaf to canopy. *Global Change Biology*, **9**, 1813–1824.
- Rapp M, EdDerfoufi F, Blanchard A (1992) Productivity and nutrient uptake in a holm oak (*Quercus ilex* L.) stand and during regeneration after clearcut. *Vegetatio*, **99–100**, 263–272.
- Reichstein M, Tenhunen JD, Rouspard O *et al.* (2002) Ecosystem respiration in two Mediterranean evergreen Holm oak forests: drought effects and decomposition dynamics. *Functional Ecology*, **16**, 27–39.
- Sprugel DG, Benecke U (1991) Measuring woody-tissue respiration and photosynthesis. In: *Techniques and Approaches in Forest Tree Ecophysiology* (eds Lassoie JP, Hinckley TM), pp. 329–365. CRC Press, Boca Raton, FL.
- Thornley JHM (1970) Respiration, growth and maintenance in plants. *Nature*, **227**, 304–305.
- Thornley JHM, Cannell MGR (2000) Modelling the components of plant respiration: representation and realism. *Annals of Botany*, **85**, 55–67.
- Valentini R, Matteucci G, Dolman AJ *et al.* (2000) Respiration as the main determinant of carbon balance in European forests. *Nature*, **404**, 861–865.
- Villar R, Merino J (2001) Comparison of leaf construction costs in woody species with differing leaf life-spans in contrasting ecosystems. *New Phytologist*, **151**, 213–226.
- Vivat A (1995) *Persistance des feuilles et bilan carboné d'un chêne méditerranéen (Quercus ilex L.). Evolution le long d'un gradient climatique*. DEA Université Montpellier II Sciences et Techniques du Languedoc, Montpellier.
- Voulgaridis EV, Passialis CN (1995) Characteristics and technological properties of the wood of mediterranean evergreen hardwoods. *Forêt Méditerranéenne*, **XVI**, 3–12.
- Waring RH, Landsberg JJ, Williams M (1998) Net primary production of forests: a constant fraction of gross primary production? *Tree Physiology*, **18**, 129–134.
- Xu L, Baldocchi DD (2004) Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. *Agricultural and Forest Meteorology*, **123**, 79–96.
- Xu M, DeBiase TA, Qi Y *et al.* (2001) Ecosystem respiration in a young ponderosa pine plantation in the Sierra Nevada Mountains, California. *Tree Physiology*, **21**, 309–318.
- Zhang SH (1987) *Contribution à l'étude de la croissance en diamètre du chêne vert (Quercus ilex L.) en relation avec le climat*. PhD, Université des Sciences et Techniques du Languedoc, Montpellier.