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## **“Ecosystem respiration in a Mediterranean Turkey oak forest: eddy covariance and chamber-based models comparison”**

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## Abstract

Eddy covariance and up-scaled chamber measurements were used to estimate ecosystem respiration (Reco) in a *Quercus cerris* L. coppice forest in Central Italy. The annual variation of Reco and its components, was analyzed in relation to seasonal changes in soil temperature and soil moisture. Chamber measurements on soil, stems and leaves were carried out between June 2010 and December 2012. Each plot was chosen to be always within the footprint of the eddy covariance tower installed in the forest compartment.

The ecosystem respiration and its main components shown a strong seasonal variability. Summer aridity played a crucial role on the observed reduction of respiration that was evident both in soil and stem CO<sub>2</sub> efflux rates. Soil respiration ( $R_s$ ) and stem respiration ( $R_{\text{stem}}$ ) increased from winter to spring, decreased in summer and suddenly increased in autumn after rainfall events. A different trend was showed by leaf dark respiration ( $R_l$ ) that increased from spring to summer and decreased in autumn.

Based on up-scaled chamber measurements, ecosystem respiration ( $\text{Reco}_{\text{cuv}}$ ) showed a significant temporal variation over the year.  $R_s$  and  $R_{\text{stem}}$  followed the same trend of ecosystem respiration estimated by eddy covariance ( $\text{Reco}_{\text{eddy}}$ ) with a reduction during summer months consequently to summer drought. On the contrary,  $R_l$  peaked in August and decreased in autumn and was responsible for the decoupling of the two Reco estimates. The total annual  $\text{Reco}_{\text{eddy}}$  chosen as reference was  $9.11 \text{ t C ha}^{-1} \text{ y}^{-1}$ , while the total annual contribution of  $R_s$ ,  $R_{\text{stem}}$  and  $R_l$  was 6.79, 1.77 and  $4.74 \text{ t C ha}^{-1} \text{ y}^{-1}$ , respectively. Thus, the relative contribution of each component was 51% for the soil, 13% for the stem and 36% for leaves, confirming that whole ecosystem respiration is dominated by soil respiration.  $\text{Reco}_{\text{cuv}}$  was 32% larger than ecosystem respiration estimated by eddy covariance.

Through model validation techniques was possible to quantify the uncertainty. The results showed that method of estimation used, sample size, and biotic and abiotic factors influencing the respiration rates, can lead to both underestimation and overestimation higher than 50%. The main contribution of errors was showed by stem CO<sub>2</sub> efflux because of the bad model performance during the growing period. Therefore, the sources of uncertainty identified suggest that the comparison between the estimation of  $\text{Reco}_{\text{cuv}}$  and  $\text{Reco}_{\text{eddy}}$ , is feasible only if the errors are minimized. An adequate sample size, use of prediction models suitable for Mediterranean environments and, standardized methods as much as possible, are needful.



## Riassunto

La tecnica *eddy covariance* e le misure con cuvetta scalate a livello ecosistemico, sono state usate per stimare la respirazione ecosistemica (Reco) in un bosco ceduo di *Quercus cerris* L. in Italia centrale. La variazione annuale della Reco e delle sue componenti è stata analizzata in relazione alle variazioni stagionali di temperatura e umidità del suolo. Le misure di efflusso di CO<sub>2</sub> con cuvetta dal suolo, dai fusti e dalle foglie sono state effettuate tra giugno 2010 e dicembre 2012. L'area sperimentale è stata scelta per essere sempre dentro la *footprint* della torre *eddy covariance* installata nella particella forestale oggetto di studio. La respirazione dell'ecosistema e le sue componenti principali hanno mostrato una forte variabilità stagionale. L'aridità estiva ha svolto un ruolo cruciale nella riduzione di respirazione ed è stata evidente sia nei tassi di efflusso di CO<sub>2</sub> dal suolo che dai fusti. I tassi di respirazione del suolo (R<sub>s</sub>) e dei fusti (R<sub>stem</sub>) sono aumentati dall'inverno alla primavera, sono diminuiti in estate e sono improvvisamente aumentati in autunno dopo alcuni eventi piovosi. Un andamento diverso è stato mostrato dalla respirazione fogliare (R<sub>l</sub>), che è aumentata dalla primavera all'estate ed è diminuita in autunno. Sulla base delle misure da cuvetta scalate, la respirazione ecosistemica (Reco<sub>cuv</sub>) ha mostrato una significativa variazione temporale nel corso dell'anno. R<sub>s</sub> e R<sub>stem</sub> hanno seguito lo stesso andamento della respirazione ecosistemica stimata con la tecnica *eddy covariance* (Reco<sub>eddy</sub>) con una riduzione durante i mesi estivi, a causa della siccità. Al contrario, R<sub>l</sub> ha raggiunto un picco nel mese di agosto ed è poi diminuita in autunno essendo così responsabile del disaccordo delle due stime di Reco. La Reco<sub>eddy</sub> annuale, scelta come riferimento, è stata stimata pari a 9.11 t C ha<sup>-1</sup> anno<sup>-1</sup>, mentre, il contributo totale annuo di R<sub>s</sub>, R<sub>stem</sub> e R<sub>l</sub> è stato di 6.79, 1.77 e 4.74 t C ha<sup>-1</sup> anno<sup>-1</sup>, rispettivamente. Pertanto il contributo relativo di ciascuna componente è stato del 51% per il suolo, del 13% per i fusti e del 36% per le foglie, confermando che la respirazione ecosistema è dominata dalla respirazione del suolo. Reco<sub>cuv</sub> è stata maggiore della Reco<sub>eddy</sub> del 32%.

Attraverso tecniche di validazione è stato possibile quantificare l'incertezza delle stime. I risultati hanno dimostrato che il metodo di stima utilizzato, la dimensione del campione, e i fattori biotici e abiotici che influenzano i tassi di respirazione, possono portare sia ad una sottostima che ad una sovrastima superiore al 50%. Il contributo maggiore all'errore di stima è stato dato dall'efflusso di CO<sub>2</sub> a causa delle cattive prestazioni del modello durante il periodo di crescita. Pertanto, le fonti di incertezza individuate suggeriscono che il confronto tra la stima di Reco<sub>cuv</sub> e Reco<sub>eddy</sub>, è fattibile solo se sono ridotti al minimo gli errori quindi, utilizzando un campione di dimensioni adeguate, modelli di previsione adatti ad ambienti mediterranei e metodi standardizzati di misura.



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## **1. INTRODUCTION**



To predict long-term trends in carbon sequestration by ecosystems, it is necessary to understand the responses of ecosystem respiration, defined as the sum of soil microbial, root, leaf and stem respiration to environmental factors (Johnson et al., 1996; Valentini et al., 2000; Vourlitis & Oechel, 1999). A consensus exists with respect to the importance of temperature and water availability in determining ecosystem CO<sub>2</sub> emissions. Several reviews have examined the analysis and description of temperature induced increases in soil respiration (Kätterer et al., 1998; Kirschbaum, 1995; Lloyd & Taylor, 1994). Less consistent results have been recorded with respect to the influence of soil moisture on respiration, so that different functions describing the dependence have been applied (Davidson et al., 1998; Epron et al., 1999; Fang & Moncrieff, 1999; Norman et al., 1992). Information on the processes controlling net carbon gain have often been obtained in extreme habitats, e.g. shaded, hot or cold but, respiration may be more important than photosynthesis in controlling interannual variability in net ecosystem production (Valentini et al., 2000). The Mediterranean environment is special in that prolonged drought reoccurs annually in a relatively predictable, simple manner with a long-term slow drying of the system followed by rewetting. Thus, Mediterranean sites are ideal to examine temporal changes in ecosystem carbon balance in response to soil water availability and temperature (Di Castri, 1981; Rovira & Vallejo, 1997). Long-term effects of warming and drying can only be obtained from forests in which seasonal drought is a regular feature. In order to better understand the effects of environmental factors on respiration fluxes, in the current study, stem, soil and leaf CO<sub>2</sub> efflux of a Mediterranean deciduous species, turkey oak (*Quercus cerris* L.) were measured. The study was conducted in a coppice forest in Central Italy and a comparison between the up-scaled chamber measurements and ecosystem respiration estimated by eddy covariance was carried out.

## 1.1 Stem CO<sub>2</sub> efflux

Interest in stem respiration is increasing as many quantitative estimates show that it is a large component of the annual carbon balance of forest ecosystems. The stem CO<sub>2</sub> efflux ( $R_{\text{stem}}$ ), accounts for 11% - 23% and 40% - 70% of the carbon assimilated in temperate and tropical forest ecosystems, respectively (Ryan et al. 1995; Chambers et al. 2004). In previous studies conducted in Mediterranean forests,  $R_{\text{stem}}$  varies in the range between 8% -11% (Guidolotti et al., 2013; Maseyk et al., 2008; Wieser et al., 2009).

Despite stem CO<sub>2</sub> efflux is an important component of forest ecosystem carbon budgets and net ecosystem CO<sub>2</sub> exchange, little is known about R<sub>stem</sub> in Mediterranean forests. It is important quantify the contribution and the evolution of CO<sub>2</sub> through the different seasons. Few studies have examined the seasonal respiration throughout an entire year. Some have shown that the response of respiration to temperature clearly varies among months (Guidolotti et al., 2013; Paembonan, et al., 1991). Temperature sensitivity of stem respiration is usually expressed in terms of Q<sub>10</sub> (the rate of change in respiration resulting from a 10°C increase in temperature). Numerous studies on temperature sensitivity of stem respiration have been conducted across different forest types of the world and reported different Q<sub>10</sub> values, varying from 1.00 to 6.40 (Acosta et al., 2011; Damesin et al., 2002; McGuire et al., 2007).

R<sub>stem</sub> is a complex process composed of different sources of CO<sub>2</sub> and with many controlling factors (Teskey et al., 2008). Due to the large effect that temperature has on rates of respiration, it has often been used to predict R<sub>stem</sub>. However, the relationships between R<sub>stem</sub> and temperature vary greatly. In some studies, strong correlations have been reported. For example, in different study on *Pinus* spp. R<sub>stem</sub> was strongly correlated with stem temperature (T<sub>stem</sub>) (Xu et al., 2000; Zha et al., 2004). In other studies, R<sub>stem</sub> was correlated with a time-lagged T<sub>stem</sub> (Kim et al., 2007; Lavigne & Ryan, 1997; Lavigne, 1996; Ryan et al., 1995; Acosta et al., 2008). Zach et al. (2009) found that for trees in tropical montane forest, R<sub>stem</sub> was independent from T<sub>stem</sub> in the wet season, but was well correlated with T<sub>stem</sub> in the dry season. Other studies have found weak, or non-existent, correlations between R<sub>stem</sub> and temperature in trees. Teskey & McGuire (2002) found that R<sub>stem</sub> was poorly correlated with T<sub>stem</sub> in *Quercus alba* trees, Bowman et al. (2005) reported that diel variation in R<sub>stem</sub> could not be explained by T<sub>stem</sub>. Chambers et al. (2004) reported that there was no relationship between R<sub>stem</sub> and T<sub>stem</sub> in Central Amazon tropical forest. Zach et al. (2010) found that R<sub>stem</sub> was completely uncoupled from the diel pattern of T<sub>stem</sub>. They observed positive, negative, and completely uncoupled relationships between R<sub>stem</sub> and T<sub>stem</sub> in 20 mature canopy trees during the dry season in a tropical montane forest. Taken together, these results suggest that temperature is not always a reliable predictor of R<sub>stem</sub>.

Temperature exerts strong control on the rate of cellular metabolism but there are many other factors that can complicate the relationship between this rate and the amount of CO<sub>2</sub> on stem surface. Among these are the CO<sub>2</sub> absorption and transport in the transpiration stream (Saveyn et al., 2007a; Teskey & McGuire, 2002), the long radial diffusion pathways of CO<sub>2</sub> and high bark resistance to gaseous diffusion (Ceschia et al., 2002; Stockfors, 2000), the corticular photosynthesis, especially important for young stems and branches (Cernusak & Marshall, 2000;

Sprugel, 1990; Wittmann et al., 2001; Wittmann & Pfanz, 2007, 2008; Wittmann et al., 2006), the cambial activity, substrate supply and growth (Damesin et al., 2002; Stockfors & Linder, 1998) and other environmental and physiological factors that either directly or indirectly affect  $R_{\text{stem}}$  including sap flow, phenology, stem oxygen concentration, solar radiation, and water deficits (Aubrey & Teskey, 2009; Bowman et al., 2005; Brito et al., 2010; Damesin et al., 2002; Gruber et al., 2009; Maieret al., 2010; Meir et al., 2008; Saveynet al., 2007b; Zach et al., 2010). Within the same species, trees of different size have different stem  $\text{CO}_2$  efflux rates because size also appears to influence  $R_{\text{stem}}$ . Diameter at breast height (DBH) has been found to be correlated with  $R_{\text{stem}}$  in tropical and temperate forests (Bowman et al., 2005; Chambers et al., 2004; Kim et al., 2007; Zach et al., 2008) and in a Mediterranean montane beech in Central Italy (Valentini et al., 1996). However, Kim et al. (2007) reported that  $R_{\text{stem}}$  in *Pinus densiflora* stand decreased with increasing diameter.

Several previous studies have shown differences between stems for volume-based or area-based respiration (Sprugel, 1990; Stockfors, 2000), but these differences are rarely considered when scaling-up to the stand level. Many studies have shown differences among trees for stem maintenance and growth respiration, which were correlated to live cell volume and annual dry-matter production, respectively (Ryan, 1990). Thus is important determining the best unit of scale. The unit chosen (surface area, sapwood volume) can greatly affect the final results. Surface area, for instance, was found to be the best unit for expressing maintenance respiration of *Picea abies* (Stockfors & Linder, 1998) because the living cells were concentrated in the outer wood. Nevertheless, (Ryan, 1990) found maintenance respiration of *Pinus contorta* and *Picea engelmannii* was better estimated by sapwood volume. Stockfors (2000) in a study on *Picea abies*, showed that respiration at the breast height generally provided an acceptable estimate of respiration of the whole stem, especially if surface area was used as unit for scaling up. About the sampling height, he found that for a tree with an even distribution of living cells in the stem, scaling-up whole-year respiration by sapwood volume causes only small errors (7% - 12%) disregarding sample height. For a tree with living cells concentrated near the surface, scaling up by surface area produce an equally small error (2% - 14%) if the sample is taken at 140 cm height or higher.

Differences in stem respiration could be the result of differing site characteristics, but evaluations of stem respiration also depend on measurement and calculation methods. Quantifying the stem respiration of a forest ecosystem requires  $\text{CO}_2$  efflux measurements in the field to build or validate simulation models. Some difficulties are involved in scaling-up from

local and non continuous field respiration measurements to estimates of carbon loss at the ecosystem level for the duration of one year.

Most studies concerning stem respiration have been done on conifers. Investigations of other woody species, especially deciduous broadleaved trees, need to be expanded.

## **1.2 Soil respiration**

Soil respiration is an important component of forest carbon balance, accounting for 60% - 80% of total ecosystem respiration ( $R_{eco}$ ) and significantly affecting the interannual variability of net ecosystem production (Law et al., 1999; Law et al., 2001; Matteucci et al., 2000).

The contribution of  $R_s$  to  $R_{eco}$  may differ among ecosystems, depending on site biomass (Longdoz et al., 2000), vegetation type (Janssens et al., 1999) or plant age (Buchmann, 2000; Tedeschi et al., 2006).

Several biotic and abiotic factors influence soil  $CO_2$  production: soil temperature and moisture (Epron et al., 1999; Law et al., 1999), soil organic matter quantity and quality (Coûteaux et al., 1995; Taylor et al., 1989), root and microbial biomass, root nitrogen content (Rey et al., 2002; Ryan et al., 1996), soil acidity and texture and site productivity (Raich & Schlesinger 1992; Raich & Potter 1995). Several examples of equations expressing the dependence on soil temperature (Davidson et al., 1998; Kucera & Kirkham, 1971; Witkamp, 1966) or soil water content (Carlyle & Than, 1988; Hanson et al., 1993; Rout & Gupta, 1989; Reichstein et al., 2003; Yuste et al. 2005) have already been provided. It is recognized that these factors usually account for 80% of temporal variability of soil  $CO_2$  efflux. However, no agreement, either on the shape of the relationship (Lloyd & Taylor, 1994) or on the measurement procedure for these factors (depth, time and spatial frequency) has been achieved (Reichstein & Beer, 2008).

Temperature has been the most often studied factor influencing soil respiration and all studies confirm a nonlinear positive direct relationship between temperature and soil respiration. Several shapes have been proposed and the most commonly used are reviewed by Kätterer et al. (1998), Kirschbaum (1995) and Lloyd & Taylor (1994). The simplest is the exponential  $Q_{10}$  relationship (the rate of change in respiration resulting from a  $10^\circ C$  increase in temperature).

Due to temperature related increases in respiration, ecosystems will become a net source of  $CO_2$  by 2050, although it is not clear which effect the drought would have on the full accounting of carbon dynamics (Cox et al., 2000). The effect of soil water status on soil respiration has been

described empirically via absolute or relative measures of volumetric water content and soil water potential as reviewed by Rodrigo et al. (1997). The relationship between soil water status and soil-respiratory processes is complex, since many individual processes vary with soil water content, in particular gas and solute diffusion, enzyme activities, and growth and mortality of microorganisms (Killham, 1994; Marshall et al., 1996). Also rewetting events often increase soil respiration, which can be explained by remineralization of dead biomass or by desorption processes, which make labile substrate available to microbes (Orchard & Cook, 1983). After a long soil drying and subsequent rewetting, soil respiration rates can exceed rates under well watered conditions before the drying (Birch, 1958). This effect has been found being of importance also for ecosystem carbon dynamics (Borken et al., 2003; Jarvis et al., 2007; Xu & Baldocchi, 2004). Thus, despite the obvious importance of biological control of soil respiration, empirical models have often focused mainly on the abiotic controls. Even for global and interannual variation, models are developed that predict soil respiration solely from climate variables (Raich et al., 2002; Raich & Potter, 1995).

Respect to temperature, less consistent results have been recorded about the influence of soil moisture on respiration and different functions describing the dependence have been applied: linear (Epron et al., 1999; Norman et al., 1992) exponential (Davidson et al., 1998; Fang & Moncrieff, 1999) and hyperbolic (e.g. Hanson et al., 1993).

Climatic variables determine most of the temporal variability in soil respiration at different scales (Davidson & Janssens, 2006; Janssens et al., 2001; Pregitzer et al., 2000). In this study an empirical model, originally developed to estimate ecosystem respiration, that accounts for variation in temperature and soil moisture, was fitted to the data of two years and, an evaluation of the model accuracy was performed.

### **1.3 Leaf respiration**

A key factor in determining the biosphere's response to global climate change is the impact of the abiotic environment on rates of leaf respiration (Ryan, 1991; Valentini et al., 2000; Atkin et al., 2008).

Leaf respiration represents a major source of CO<sub>2</sub> release in plants. Mitochondrial respiration produces much of the metabolic energy and carbon skeletons necessary for the growth and maintenance of plant tissues. In this process, between 25 and 75% of the carbon gained daily through photosynthesis is released into the atmosphere in the form of CO<sub>2</sub> (Amthor, 2000).

In natural condition air temperatures vary diurnally and seasonally and leaf dark respiration ( $R_l$ ) is very sensitive to short-term changes in temperature (Körner & Larcher, 1988; Atkin et al., 2005; Tjoelker et al., 2001). Understanding the effect of variation in temperature on respiratory  $\text{CO}_2$  loss is fundamental for predicting plant growth in a changing global environment. However,  $R_l$  may increase less markedly, remain unchanged or even decline in response to long-term rises in temperature (Atkin et al., 2005).

The degree to which leaf respiration changes with temperature is highly variable, with  $Q_{10}$  values varying from 1.4 to 4 (Azcón-Bieto, 1992).  $Q_{10}$  values differ between species (Larigauderie & Körner, 1995) and are influenced by the metabolic state of the tissue and the growth environment (Covey-Crump et al., 2002; Tjoelker et al., 2009). To fully predict variations in leaf respiration under field conditions, an understanding is needed on how other abiotic factors (e.g. drought) influence rates of leaf respiration at any given reference temperature and how such factors shape responses of  $R_l$  to temperature. Moderate drought often results in lower rates of  $R_l$  (Atkin & Macherel, 2009; Flexas et al., 2005; Lawlor & Cornic, 2002), with  $R_l$  sometimes increasing in response to more severe drought (Flexas et al., 2005; Slot et al., 2008). Drought may influence the temperature dependence of  $R_l$  depending on the duration and severity of stress, because drought-induced restrictions of photosynthesis can reduce short-term temperature dependence of  $R_l$  (Slot et al., 2008). Rodríguez-Calcerrada et al. (2011) in a study on *Quercus ilex* L., a Mediterranean tree species tolerant of drought and extreme temperatures, observed that leaf respiration decreased with increasing water deficit suggesting that drier conditions projected for the Mediterranean may attenuate the stimulation of leaf respiratory  $\text{CO}_2$  release by global warming. Thus, how rates of  $R_l$  of deciduous trees in Mediterranean regions respond to differences in soil moisture and air temperature is essential for reliable prediction of the impact of climate change on ecosystem functioning.

## 1.4 Ecosystem respiration

Two methods, widely used to estimate ecosystem respiration, are the chamber-based measurements and eddy covariance. The eddy covariance technique has provided an useful tool to continuously measure net ecosystem exchange (NEE) from hourly to daily, annual and interannual periods (Aubinet et al., 2000; Baldocchi, 2003). However, eddy covariance measurements do not provide direct information on component fluxes.

Chamber-based methods are most frequently used to estimate ecosystem CO<sub>2</sub> flux due to their low cost and ease of use (Epron et al., 1999; Lavigne et al., 1997; Ryan, 1990; Tang et al., 2008; Xu & Qi, 2001; Zha et al., 2004). Nevertheless, chamber-based measurements are only made on a small portion of the surface or biomass, and a large effort is required to collect sufficient data to scale up to the entire ecosystem. It is important that sufficiently large representative samples of components are measured in the chamber to obtain accurate estimates of average respiration rates (Janssens & Ceulemans, 1998; Janssens et al., 2001; Savage et al., 2008; Zha et al., 2007). At the same time, these samples are subjected to uncertainties associated with so-called chamber effects (Mosier & Bouwman, 1990).

To up-scale the chamber measurements predictive models are used, often based on the influence of abiotic factors on respiration rates (e.g. Guidolotti et al., 2013; Law et al., 1999; Tang et al., 2008; Wang et al., 2010a). Mathematical models have a wide-spread use in environmental applications but the applied models typically only render an approximate description of the system under study. Data from field measurements are compared with the corresponding model predictions. In its most elementary form this comparison is performed mainly qualitatively by visually inspecting the agreement between observed data and model predictions; more sophisticated approaches express the agreement between data and model quantitatively in terms of misfit measures (Janssen & Heuberger, 1995), which typically are functions of the error between measurements and model predictions. A given method may have low bias but its performance (accuracy estimation) may be poor due to the high variance. Moreover, problems of over-fitting can occur when a model is excessively complex or because the model can perform less well on a new data set than on the data set used for fitting. In order to avoid over-fitting, it is necessary to use additional techniques as cross-validation (Tetko et al., 1995).

Eddy covariance technique provide an estimation of carbon, water and energy exchanges between an ecosystem and the atmosphere without any perturbation over relatively large terrains (Foken et al., 2012). The measured net ecosystem exchange (NEE) of CO<sub>2</sub> between the ecosystem and the atmosphere reflects the balance between gross primary production (GPP) and ecosystem respiration (Reco). For understanding the mechanistic responses of ecosystem processes to environmental change it is important to separate these two flux components. As indicate in (Lasslop et al., 2010) two approaches are conventionally used: (1) respiration measurements made at night are extrapolated to the daytime or (2) light-response curves are fit to daytime NEE measurements and respiration is estimated from the intercept of the ordinate, which avoids the use of potentially problematic night time data.

Methods that rely on night-time data for partitioning may be biased due to the frequent night-time suppression of turbulence and dominance of advective fluxes not measured by conventional eddy covariance systems (Aubinet, 2008; Feigenwinter et al., 2004; Goulden et al., 1996). The second common approach extrapolating respiration from light-response curves conditioned on daytime data, usually does not account for the fact that NEE varies both as a function of temperature (mostly affecting Reco) and vapour pressure deficit (affecting GPP via stomatal regulation), among other factors (Lasslop et al., 2010). Lasslop et al. 2010, improved the method based on light-response curves taking into account the temperature sensitivity of respiration and the vapour pressure deficit (VPD) limitation of photosynthesis. In this way they improved the model's ability to reproduce the asymmetric diurnal cycle during periods with high VPD, and enhances the reliability of Reco estimates given that the reduction of GPP by VPD may be otherwise incorrectly attributed to higher Reco. Lasslop et al. 2010, demonstrated that the uncertainty arising from systematic errors, such as advection, low turbulence, decoupling of the flow, differences in the footprint during the night compared with daytime or the choice of model and extrapolation, clearly dominates the overall uncertainty of the estimates. Moreover, it was shown by different authors (Aubinet et al., 2000; Goulden et al., 1996; Gu et al., 2005; Papale et al., 2006), that independently of the problems related to data acquisition, eddy flux measurements can underestimate the net ecosystem exchange during periods with low turbulence and air mixing.

Comparisons of eddy covariance and chamber-based estimations of Reco ( $\text{Reco}_{\text{eddy}}$  and  $\text{Reco}_{\text{cuv}}$ , respectively) have been made previously. This was often done by comparing eddy covariance Reco estimations with estimated fluxes calculated by scaling-up component fluxes measured in small samples (Goulden et al., 1996; Law et al., 1999; Tang et al., 2008). However, with respect to Mediterranean forests, the lack of comparable data on response of  $\text{CO}_2$  exchange measured using eddy covariance and chamber-based methods presents problems for interpretation (Tang et al. 2008), especially relative to measurements taken simultaneously at the same sites using the two different methods. In this study, chamber-based measurements were used to measure the  $\text{CO}_2$  fluxes in soil, stem and foliage through the year. Furthermore, the eddy covariance system was used as a reference for comparison with the up-scaled chamber measurements because, despite the uncertainties associated with the two methods, comparison of  $\text{Reco}_{\text{cuv}}$  and  $\text{Reco}_{\text{eddy}}$  may provide valuable information about ecological processes, such as patterns in carbon allocation to above and belowground forest compartments.

## 1.5 Objectives

- Examine seasonal patterns of the ecosystem respiration components in response to environmental variables.
- Extrapolate the chamber-based measurements to an annual budget of stand scale ecosystem.
- Quantify seasonal and annual components of ecosystem respiration fluxes in *Quercus cerris* L. coppice forest in Central Italy.
- Compare the eddy covariance technique with the chamber-based method for estimating ecosystem respiration.
- Evaluate the uncertainty of model performance to up-scale the chamber measurements.
- Evaluate the uncertainty derived from the application of different  $u^*$  thresholds to filter periods with low turbulence and air mixing.



## **2. MATERIALS AND METHODS**



## 2.1 Site description

The forest of Roccarespampani is in Central Italy, in the province of Viterbo (42°23'N, 11°55'E, 120 -160 m above sea level). The forest is a *Quercus cerris* L. coppice and covers over 1420 ha in a fairly flat area. The phytoclimatic zone is Lauretum. The climate is Mediterranean, with an average annual temperature of 14 °C and an annual rainfall of 750 mm. The rainfall distribution is irregular, with a drought period in summer of approximately 2 months. The cold is not intense but rather extended from November to April. The average minimum temperature of the coldest month ranges from 2.3 to 4 °C.

*Q. cerris* is the dominant overstorey species, but *Q. pubescens* L., *Q. suber* L. and *Q. ilex* L. occur sporadically. In addition to oaks, we found *Fraxinus ornus* L., *Ulmus minor* Mill., *Ostrya carpinifolia* Scop., *Carpinus orientalis* L., *Acer monspessulanum* L. and *A. campestre* L., *Pyrus communis* L., *Phillyrea latifolia* L., *Olea europea* L. var. *oleaster*. Understorey vegetation is a Mediterranean-type macchia with shrubs of *Prunus spinosa*, *Ruscus aculeatus*, *Cytisus scoparius*, *Colutea arborescens*, *Cornus mas*, *C. sanguinea* and *Crataegus monigyna*, that are more dense in recently coppiced stands. The herbaceous layer is largely made up of grasses, which develop in spring, dry off in summer and regrow to some extent after the first autumn rains; in the older stands, herbs are limited to canopy gaps and is mainly composed of the following species: *Hedera helix*, *Cyclamen hederifolium* and *repandum*, *Alliaria petiolata*, *Allium pendulinum*, *Clinopodium vulgare*, *Brachypodium sylvaticum*, *Thymus vulgaris*.

Leaf flushing occurs in late April, while leaf abscission starts in December. The forest has been managed as a 'coppice with standards' over the last 200 years, with a rotation cycle varying between 15 and 20 years in length. Currently, the forest is arranged as a chronosequence of 45 compartments, each of about 26 ha, with coppice shoots in the range of 0–20 years. Coppicing consists of selective logging of trees in each compartment, leaving standards about every 10 m. The trees are kept for about three coppice rotations so that the oldest trees in the forest are between 45 and 60 years old. The result is a mosaic of compartments of different age-stands ranging from 0 to 20 years after coppicing.

The development and structure of the sprouts and the standards looks good, as well as the health condition of the population, which denotes the absence of standing dead trees and few signs of "decay of oak species". Nearly 100 stems (standards) per hectare are left standing at each harvest; the trees are kept for about three coppice rotations. Standards have an average diameter of 26.1 cm and average height of 17 m. Suckers have an average diameter of 11.0 cm and average height of 13 m. The diametric curve of distribution presents a bell shape asymmetrical to

the right, typical of coppice with release of standards, with the highest frequencies in correspondence with the class 10. The density is equal to 3735 sprouts and 1007 stumps per hectare. The density of shoots per stump is approximately 3.7. The diametric distribution is shown in Fig. 2.1.

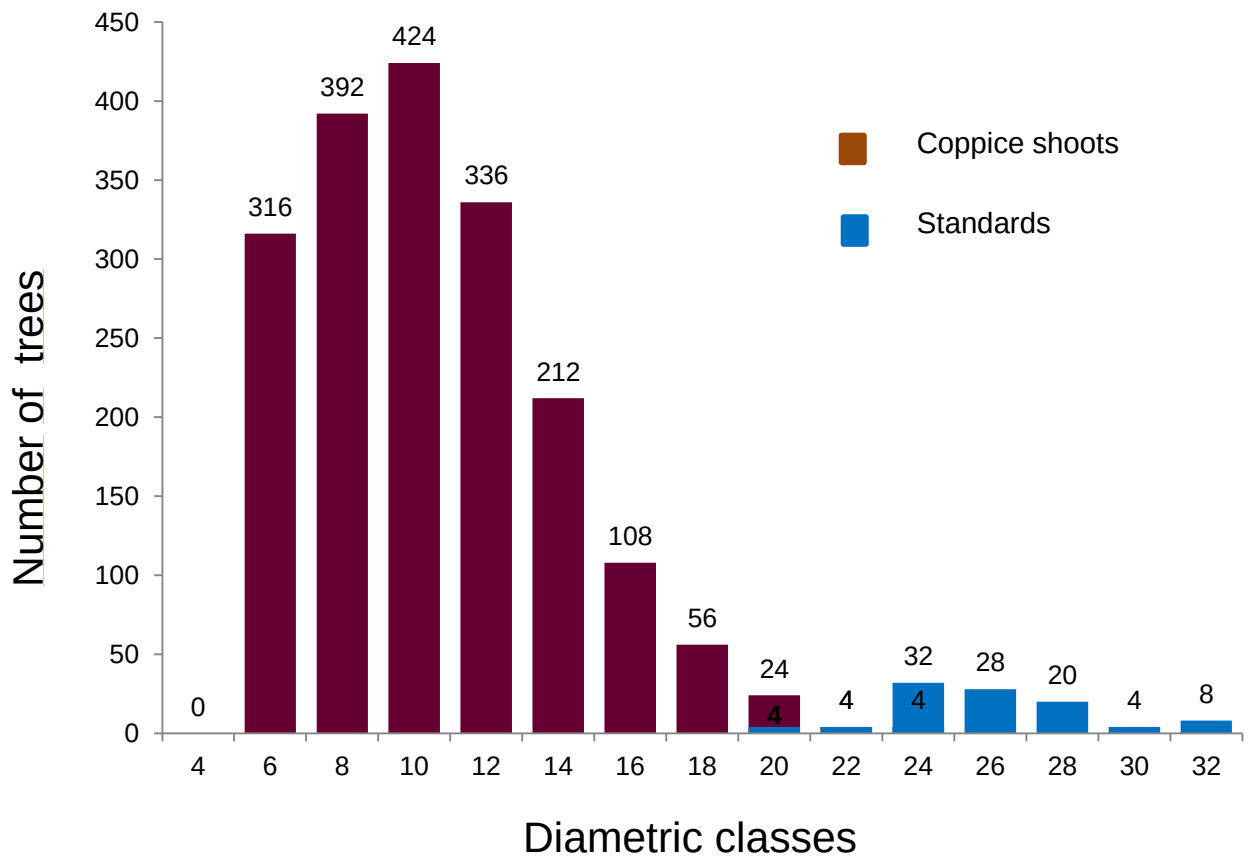


**Fig. 2.1 - Diametric distribution of standards and coppice shoots. The distribution has the typical shape of a coppice with release of standards.**

The highest root density occurs in the top 20 cm, with most roots penetrating down to 50 cm; no carbonates are present in the soil profile (Tedeschi et al., 2006).

The underlying rock is of volcanic origin and the soil is a 90 cm deep Luvisoil (FAO classification). The geological substratum is derived from the sedimentation of material of volcanic origin on pre-existing marine deposits, mostly sand. The presence of crystallized clay and the migration of clay are characteristic of this kind of soils and is a phenomenon due to the alternation of wet and dry periods.

In the Tab. 2.1 are shown the results of a soil pit of 1m depth (Manca, 2003). The profile describes a well-drained soil, with an aquifer depth greater than 1 m and the absence of suspended aquifers on waterproof substrates. Rocky outcrops and stoniness are absent and there are no signs of erosion.

|                    |                 |                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
|--------------------|-----------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <b>Horizon H</b>   | cm 0            | Litter consists mainly of turkey oak leaves                                                                                                                                                                                                                                                                                                                                                                                                                           |
| <b>Horizon O</b>   | cm 0-3          | Abundant presence of fine roots. Lower limit with the horizon below abruptly. Lumpy texture, very friable, slightly sticky when wet; little plastic; voids and cracks absent; medium-sized pores (1-3 mm) and of Class IV (2-5%). Absent veins, crystals, concretions, nodules, carbonates cutans. Abundant biological activity, with many fine roots (25-200 of 100 cm <sup>-2</sup> ). Color 5 YR 2/2 in the wet state and 5 YR 4/3 at the same dry. No skeleton.   |
| <b>Horizon A</b>   | cm 4-23         | The limit to the horizon is less clear (2-5 cm). Cracks very thin (<1 mm), fine pores (0.5-1mm) and Class III (0.5-2%); polyhedral structure sub angular, strongly developed, medium-sized (10-20 mm), compact, sticky when wet , very plastic; medium biological activity, with 10-25 fine roots to 100 cm <sup>-2</sup> , concretions of the organic type. Color 5 YR 2/4 in the wet state, 5 YR 3/4 dry.                                                           |
| <b>Horizon Bt</b>  | cm 24-65        | The lower limit is clear (2-5 cm); clayey texture; structure strongly developed, prismatic, medium; very compact; sticky when wet, plastic; limited biological activity, with 10-25 fine roots to 100 cm <sup>-2</sup> , often in black color and in decomposition; very thin cracks; very fine pores and of class II (0.5 - 1%); color in field 5YR 4/6, dry 5 YR 4/8.                                                                                               |
| <b>Horizon Btx</b> | cm 66-90        | The horizon is characteristic of a massive clayey frangipan. The lower limit is gradual; highly developed structure, laminated, medium, moist is very compact, wet is sticky and very plastic, the fine roots are few (1-10 100 cm <sup>-2</sup> ), black and in decomposition. Organic type concretions. Skeleton appreciably from the tactile point of view; very thin cracks, very fine pores of class I (<0.1%); when wet the color is 5YR 3/6, dry is 7.5 R 5/6. |
| <b>Horizon C</b>   | More than 90 cm | Lower limit gradual, structured and lacking of any degree of aggregation; crumbly texture; sticky and plastic; pores and cracks absent; few roots, very fine (<1 mm); this and abundant skeleton, color 10 R 3/4 and in the dry state 10 R 4/6.                                                                                                                                                                                                                       |

Tab. 2.1 - Results of a soil pit of 1m depth with description of the soil profile.

This study is focused in a compartment of about 24 ha and the stand was 19-years-old at the beginning of the study period. In the compartment, an eddy covariance system has been running since 1998 measuring fluxes of CO<sub>2</sub> and H<sub>2</sub>O vapour.

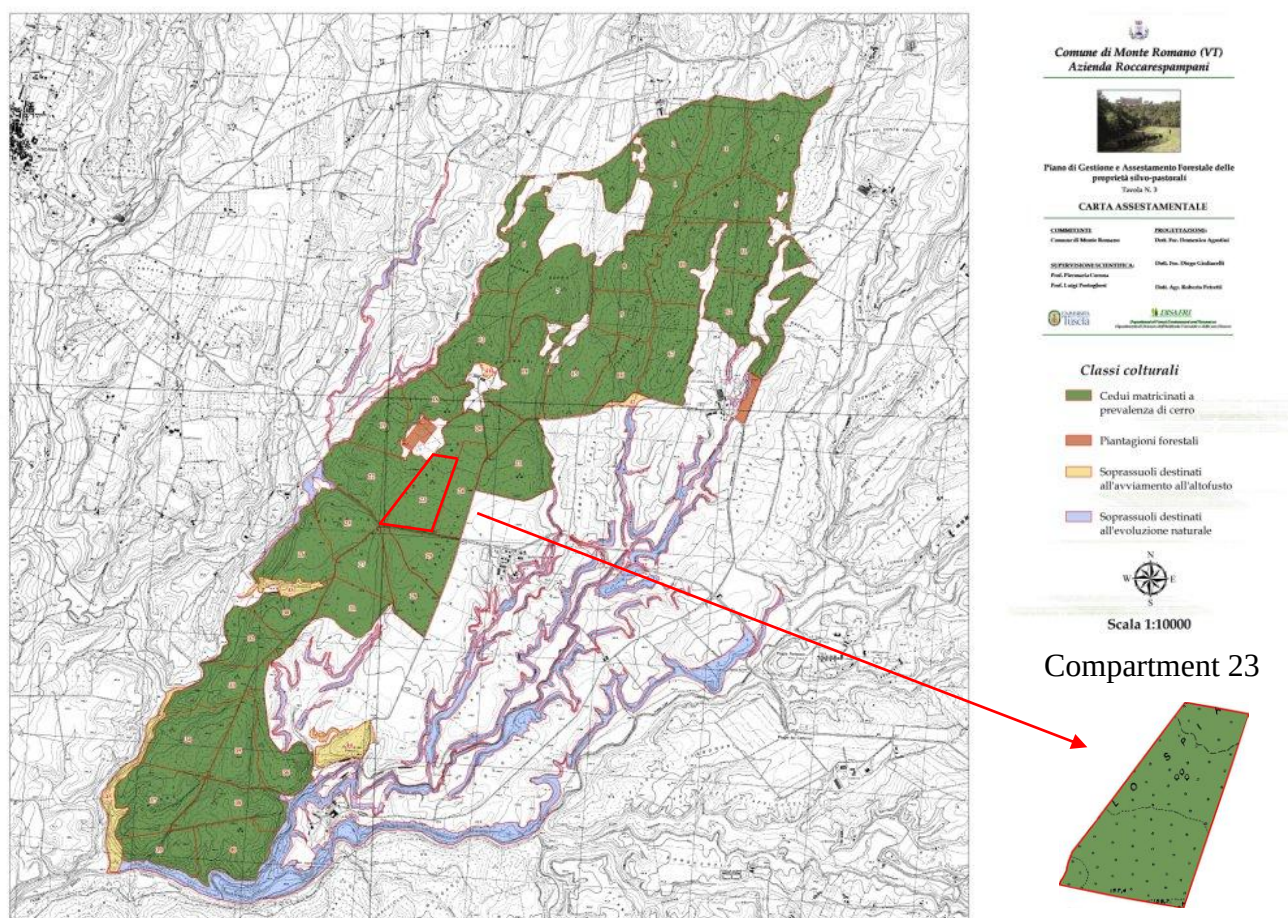


**Fig. 2.2 - Map of the Mediterranean forest of Roccarespampani. The highlighted polygon indicates the compartment 23 in which it was carried out this study and where an eddy covariance system has been running since 1998.**

## 2.2 Field respiration measurements: experimental layout

The main respiration components, stem CO<sub>2</sub> efflux ( $R_{st}$ ), soil respiration ( $R_s$ ) and leaf respiration ( $R_l$ ), were measured and the measurements were carried out between June 2010 and December 2012. All the measurements were done into an area consists of a rectangular plot of about 4 ha (400 x 100 m), was chosen to be always within the flux footprint of the eddy covariance tower, according to the prevailing wind direction (Fig. 2.5). The flux footprint is an upwind area where

the atmospheric flux is generated, namely an upwind area “seen” by the instruments measuring vertical turbulent fluxes.

### **2.2.1 Stem CO<sub>2</sub> efflux**

In the plot of 4 ha, in the vicinity of the tower, according to the diameters distribution, 9 trees, 4 standards and 5 coppice shoots, were selected to measure stem CO<sub>2</sub> efflux, as shown in Fig. 2.3. The CO<sub>2</sub> efflux were measured at the breast height (1.30 m) using a temporary clamp-on chambers made of a transparent, hard plastic Acrylic resin. We called this efflux “stem respiration”, keeping in mind that the CO<sub>2</sub> released in the chamber could also come from CO<sub>2</sub> transported by the xylem, as suggested in several studies (Levy et al., 1999; Teskey & Mcguire, 2002). The chambers (Fig. 2.4) were made up of two parts: a fixed collar on the stem to 1.30 and a removable lid connected to a portable infrared gas analyzer (Li-8100; Li-cor Inc., Lincoln, NE, USA), operating in closed mode. We used nine collars 20-cm-long, 4.5 cm depth and 2 – 5 cm wide for smaller and larger diameters, respectively. During the measurements the cover was placed and fixed on collars that were permanently installed at breast height on the south-facing side of each tree stem. The edges of the chambers in contact with the bark, were covered by neoprene and sealed to the tree bark with Terostat (Henkel KgaA, Germany). A neoprene gasket was used also on the external edge of the collars and on the borders of the lids. The seals were tested by blowing along the joints and measuring the CO<sub>2</sub> evolution in the chamber. The chambers were connected to the IRGA (InfraRed Gas Analyzer) by flexible tubing. Before installing the chambers, the trunk was gently scrubbed in order to remove algae and lichens present on the bark. At the time of first measurement, the chamber was covered with a black cloth to evaluate CO<sub>2</sub> re-fixation by the bark and no stem photosynthesis was found.

The measurements were performed at breast height because it provide an acceptable estimation of CO<sub>2</sub> efflux of the whole stem (J Stockfors, 2000).

The stem CO<sub>2</sub> effluxes were measured over the growing season until the beginning of the winter 2012 (April - December). We measured  $R_{\text{stem}}$  every 15 days, five times per day starting just after dawn and ending at the time of maximum air temperature. The time interval between a measurement and the other was about an hour and a half. The measurement time was 90 seconds. Between measurements sets, the lids were removed from the chambers to allow air ventilation and avoid CO<sub>2</sub> accumulation in the chambers. The stem temperature is the more biologically

relevant reference, so it was measured close to the chamber by an infrared thermometer (MINOLTA-LAND-CYCLOPS-COMPAC).

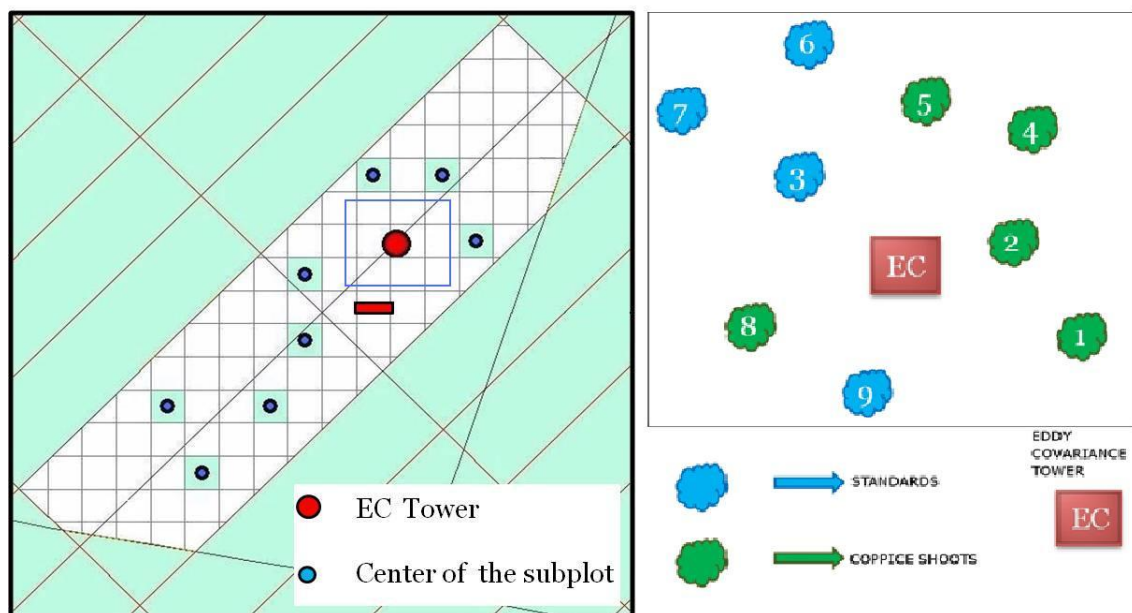


**Fig. 2.3 – Experimental layout of stem CO<sub>2</sub> efflux. Four standards and five coppice shoots were chosen representative the diameter distribution in the compartment.**



**Fig. 2.4 – Chamber with a fixed collar on the stem to 1.30 and a removable lid connected to a portable infrared gas analyzer by flexible tubing.**

### 2.2.2 Soil respiration

In 2010, within the plot of 4 ha, eight rectangular subplots were randomly chosen within a regular grid of mesh 20 x 20 m. In each subplot, 5 PVC collars of 5 cm high and 20 cm in diameter (a total of 40 points) were fixed in the ground to measure soil respiration between August 2010 and August 2011 (Fig. 2.5). In 2012, a transect of 16 m in length was traced and 8 PVC collars of 5 cm height and 20 cm in diameter were fixed in the ground to measure soil respiration from January to December (Fig. 2.5). The collars had two stainless steel legs to facilitate the insertion into the ground leaving 2 cm above the soil surface.

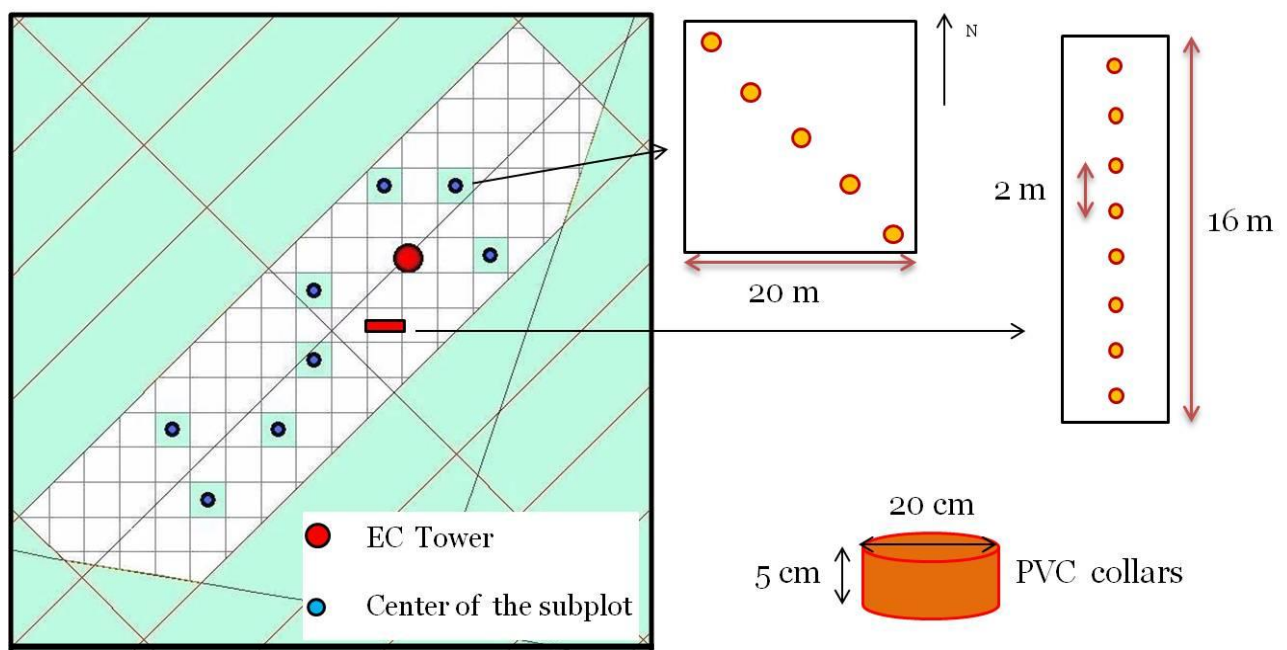


**Fig. 2.5 – Experimental layout of soil respiration. Eight subplots randomly chosen in a 4 ha area falling in the eddy covariance footprint estimated according to the prevailing wind direction.**

Soil respiration was measured with a closed soil CO<sub>2</sub> flux system (Li-8100; Li-cor Inc., Lincoln, NE, USA) connected to 20 cm chamber. The system measures the change in CO<sub>2</sub> concentration inside the chamber within 90s interval.

During the Rs measurements, soil temperature at 5 cm depth (Ts) was measured with a soil temperature probe (HD 9216, DELTA OHM). Soil water content (SWC) over 5 cm depth, was measured with a soil moisture probe (Delta-T ML2). A total of 40 measurement campaigns were done; one every two weeks.

### 2.2.3 Leaf respiration

Leaf respiration was measured on four trees (Fig. 2.6), two standards and two coppice shoots, located near the tower so as to be easily accessed and collected. Four field campaigns were carried out, once a month, from June to September 2010. Three leaves per plant were collected at the same position in the canopy; as found by Hymus et al. (2005), in the same site, on the same species, the leaf respiration measured during the night was unaffected by leaf position in the canopy. The samples were collected at two different moments, pre-dawn and after sunset. The leaves were detached with petiole, placed in water and maintained at the dark while the measurement took place. The dark leaf respiration rate was measured using a portable gas exchange system (Li-6400, Li-cor Inc., Lincoln, NE, USA), fitted with a broadleaf chamber (2cm by 3cm). Respiration rates were recorded when flux readings had stabilized, typically within 3-10 min. Temperatures were manipulated at four different degrees to determine the relationship between respiration and temperature: 15, 20, 25, and 30 °C. Despite we collected three subsample leaf discs and immediately frozen them in liquid nitrogen to estimate the total non-structural carbohydrates (TNC), some technical problems prevented leaf biochemical determinations. In 2012, during the growing season, the leaf area index (LAI) was measured, every 15 days, with a plant canopy analyzer (Li-2000, Li-cor Inc., Lincoln, NE, USA). We traced a transect of about 200 m and we marked 10 fix points, one every 20 m in which LAI was measured just before sunset under diffused light conditions.

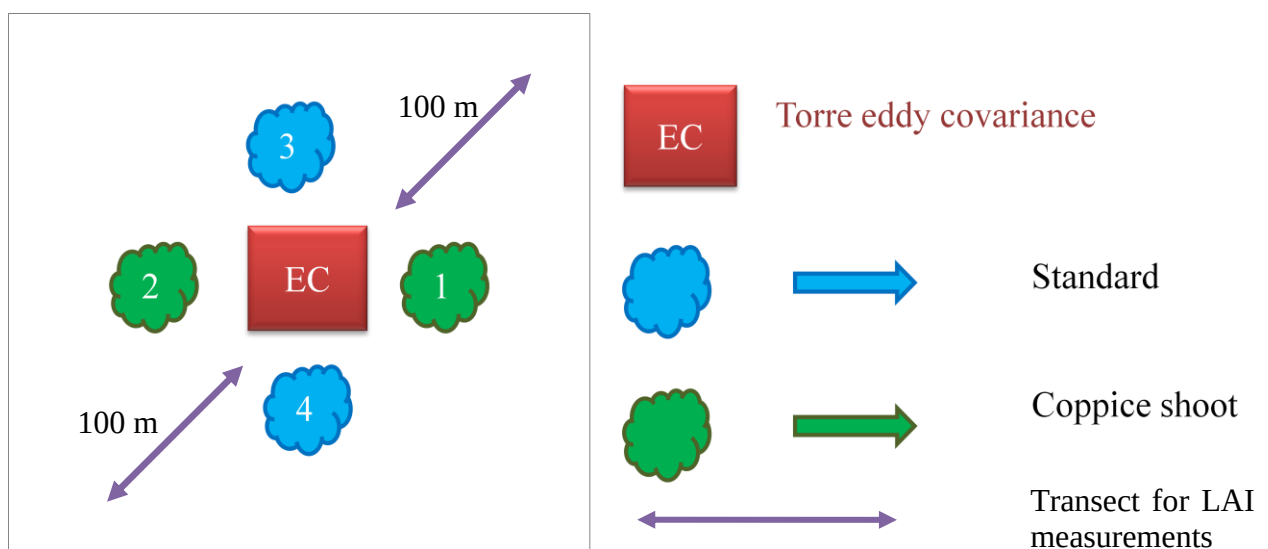


**Fig. 2.6 – Experimental layout of leaf respiration. Four plants, 2 coppice shoots and 2 standards were chosen near the tower to reach the attached leaves.**

#### **2.2.4 Ecosystem respiration**

Net ecosystem CO<sub>2</sub> exchange, in the compartment 23 of the forest of Roccarespampani, was measured from the meteorological tower, using the eddy covariance method (Valentini et al., 1996), since 1998. The eddy covariance system and data processing were as described by Aubinet et al. (2000). The instrumentation consisted of a sonic anemometer (Metek USA-1 standard, Germany) which measures the wind vector and air temperature, and a closed-path infrared gas analyzer sampling with 10 Hz (IRGA Li-7000, Li-cor, USA). The sonic was mounted at a height of 1.60 m above the canopy; the sample intake for the IRGA was located immediately below the sonic anemometer (distance of 20 cm). Air was sampled at a rate of 7 l min<sup>-1</sup> into a 4 m Teflon tube of 4 mm (inner diameter). Fluxes were computed based on a 30 min averaging period.

The local meteorological conditions were recorded continuously along with the eddy covariance data. These data were measured and averaged over a 30-min period using a data logger (CR10X-TD, Campbell Inc., USA). Air temperature and relative humidity were measured using a thermo-hygrometer (TTU 600, Tecno.el s.r.l., Rome, Italy) mounted at height of 16 m above the ground. Continuous soil temperatures were measured using thermistor sensors CS107 (Campbell Inc.) at depths of 0.05, 0.15 and 0.3 m. Soil moisture was measured in one vertical soil profile using the water content reflectometers (CS615-L, Campbell Inc.) installed at depth of 0.1 and 0.3 m. Photosynthetic Active Radiation (PAR) was measured using a net radiometer (SKP215, Skye instruments Ltd) at a height of 19.1 m and eight net radiometers (SQ110 APOGEE, USA) at a height of 1.3 m above the ground. Soil heat flux (G) was determined using two REBS Soil Heat Flux Plates (HFP01-L, Campbell Inc.) installed near the tower at depth of 0.1 and 0.3 m.

### **2.3 Respiration data analysis**

All the data collected during the field campaign were analyzed in order to evaluate the seasonal trend of the respiration components ( $R_{stem}$ ,  $R_s$  and  $R_l$ ) and of the ecosystem respiration estimated by eddy covariance ( $Reco_{eddy}$ ), to scale up the spot respiration measurements to annual bases, and to quantify the uncertainty resulting from the application of predictive models, different methods of estimation.

All the statistical analysis and estimations of parameters by models were performed using R language (R Core Team (2012) with the support of the “car” package (Fox & Weisberg, 2010) for the validation of the models and “qualV” package (Jachner et al. , 2007) for the quantification of the accuracy.

### 2.3.1 Stem CO<sub>2</sub> efflux

The Mediterranean climate is characterized by a typical drought during the summer with a consequent decrease of the Gross Primary Production (GPP). GPP values of this period are comparable with those of the winter. Following the GPP trend, the study period of stem respiration, was divided into two different periods: the growing period from April to June and from September to the end of October and the maintenance period from July to the end of August and from November to December.

The temperature dependency of  $R_{stem}$  was described separately for the two different periods, using a simple exponential equation:

Eqn. 2.1 
$$R_{stem} = ae^{kT_{stem}}$$

where  $a$  e  $k$  are coefficients estimated by the model and  $T_{stem}$  is the stem temperature (°C).

To raise the scale of chamber measurements of stem respiration to the stand level for the year 2012, respiration fluxes per unit of sapwood volume were calculated based on the field measurements and with the biomass values found in the forest management plan drawn up for the forest of Roccarespampani in 2008 by (Agostini, Giuliarelli, & Petretti, 2008) and adding to the value of the biomass of 2008, the average annual growth rate ( $m^3 ha^{-1} y^{-1}$ ) of four years. The resulting value of biomass was used to estimate stem respiration per unit ground area. Stem sapwood volume ( $S_a$ ) was calculated based by the allometric equation (Eqn. 2.2) developed by Bréda, N. et al. (1993) for *Quercus petraea*:

Eqn. 2.2 
$$S_a = 2.49 \pi DBH - 34.098$$

where DBH is the diameter of the tree at the breast height.

The temperature used to scale up the spot  $R_{\text{stem}}$  measurements to annual bases was the air temperature continuously measured by the thermo-hygrometer installed on the eddy tower.

### 2.3.2 Soil respiration

Despite the strong relationship between soil respiration and temperature, the Eqn. 2.3 (Reichstein et al., 2003) was used in order to take into account also the relationship with water availability. The modelling of soil respiration at the daily time step follows the logic that the main abiotic drivers that determine  $R_s$  are soil temperature ( $T_s$ ) and soil water content (SWC) (Reichstein et al., 2003).

$$\text{Eqn. 2.3} \quad R_s = R_{ref} \cdot f(T_{soil}, SWC) \cdot g(SWC),$$

$$\text{Eqn. 2.4} \quad f(T_{soil}, SWC) = e^{E_0(SWC) \cdot \left( \frac{1}{T_{ref}-T_0} - \frac{1}{T_{soil}-T_0} \right)},$$

$$\text{Eqn. 2.5} \quad g(SWC) = \frac{SWC}{SWC_{1/2} + SWC},$$

$$\text{Eqn. 2.6} \quad E_0(SWC) = a_{REW} + b_{REW} \cdot SWC.$$

As explained in Reichstein et al., (2003), in these equations,  $R_{ref}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) is the soil respiration under standard conditions (at  $T_{ref} = 18^\circ\text{C}$ ; non-limiting water),  $E_0$  ( $\text{K}^{-1}$ ) is the

activation-energy-type parameter of Lloyd & Taylor (1994),  $T_{ref}$  (°C) is the reference temperature,  $T_0$  (°C) is the lower temperature limit for the soil respiration  $R$ , and  $SWC_{1/2}$  (fraction) is the soil water content where half-maximal respiration (at a given temperature) occurs. In Eqn. 2.6, the temperature sensitivity of soil respiration is dependent on the soil water status of the soil, where as a first approximation  $E_0$  is linearly dependent on SWC.

Reichstein et al. (2002) corroborated the same hypothesis for ecosystem respiration.  $T_0$  was fixed at -46 °C as in the original model of Lloyd & Taylor, (1994), and  $T_{ref}$  was set to 18 °C, which approximates the mean soil temperature at the study sites.

### 2.3.3 Leaf respiration

Leaf respiration measured at 4 different temperature (15, 20, 25 and 30 °C), allowed us to estimate the temperature sensitivity of  $R_l$ . A  $Q_{10}$  function (Eqn. 2.7) was used to describe the temperature dependency of  $R_l$ , and the Eqn. 2.8 to estimate the leaf respiration.

The  $Q_{10}$  is the temperature sensitivity of  $R_l$  (fractional change in rate with a 10 °C increase in temperature) and  $k$  is a parameter to be estimated.

Eqn. 2.7 
$$Q_{10} = e^{10 \cdot k},$$

Eqn. 2.8 
$$R_l = R_{lTb} \cdot Q_{10}^{(T_{air}-T_b)/10}$$

$R_{lTb}$  is the basal respiration rate. In our case, a basal temperature ( $T_b$ ) of 20°C ( $R_{lTb} = R_{l20}$ ) was chosen. Air temperature were used for the variable  $T_{air}$ .

As reported in Tjoelker et al. 2001, models using a constant  $Q_{10}$  are biased, and use of a temperature-corrected  $Q_{10}$  may improve the accuracy of modeled respiratory CO<sub>2</sub> efflux, hence, the vegetative period was divided and the model was parameterized (Eqn. 2.8) separately for each subset.  $R_l$  was estimates using the found parameters,  $Q_{10}$  and  $R_{20}$ , and the air temperature

continuously measured by the thermo-hygrometer (TTU 600, Tecno.el s.r.l., Rome, Italy) installed on the eddy tower. The integration at canopy level was obtained by using the leaf area index (LAI) estimated by MOD15A2 that gives an 8-day-composite LAI ( $\text{m}^2 \text{m}^{-2}$ ) with 1 km resolution (Oak Ridge National Laboratory Distributed Active Archive Center [ORNL DAAC]). A smoothed function based on the MOD15A2 data integrated with the data measured in the field by LI-2000 was used to interpolate the LAI on a daily scale. This smoothing function performs the computations using a locally-weighted polynomial regression. The partition of the LAI into sun and shaded leaves wasn't performed.

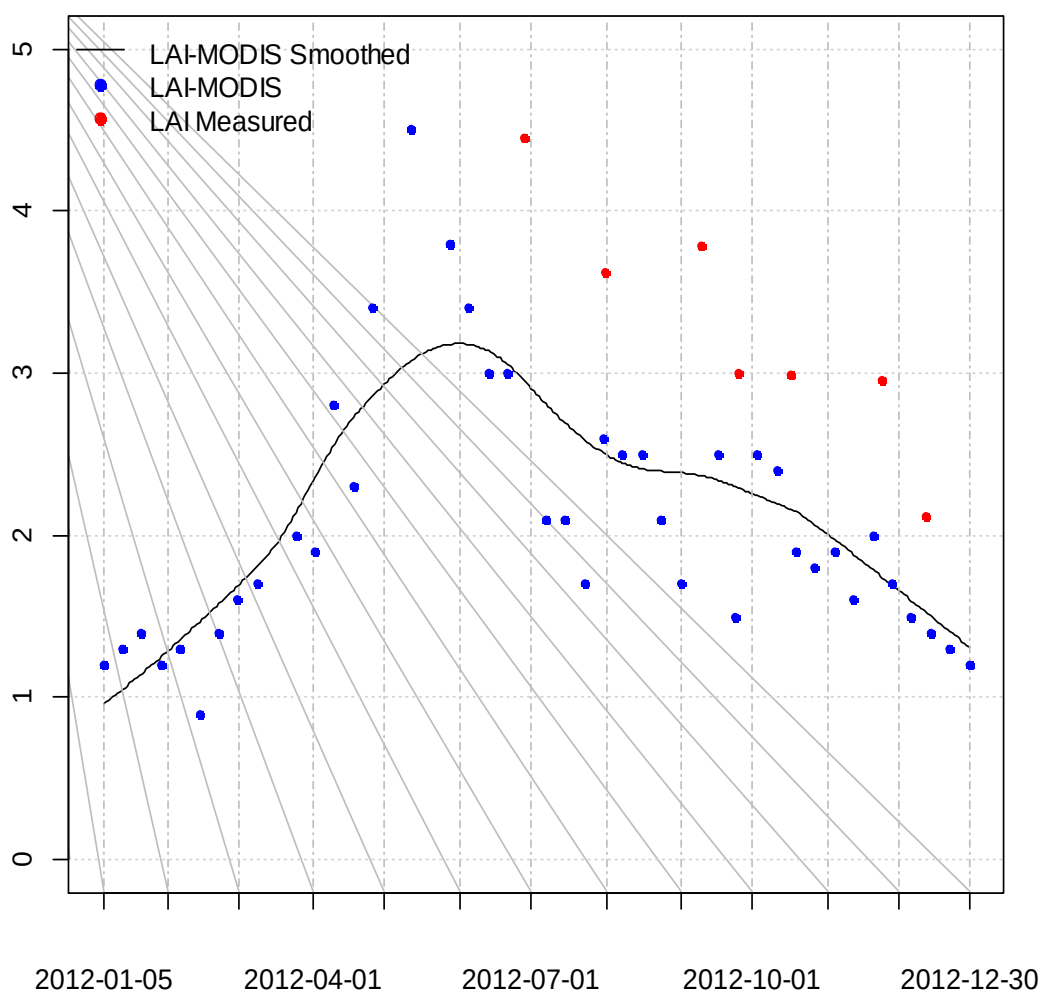


**Fig. 2.7 – Graphical representation of the smoothing function used to interpolate data of the LAI from MOD15A2 and LAI measured, on a daily scale.**

### 2.3.4 Ecosystem respiration

To estimate Reco from eddy covariance data, two conventional approaches were used:

- 1) Respiration measurements made at night are extrapolated to the daytime; this is the method described in Reichstein et al. (2005) that introduced a new generic algorithm which derives a short-term temperature sensitivity of Reco from eddy covariance data that applies this to the extrapolation from night to daytime, and that further performs a filling of data gaps that exploits both, the covariance between fluxes and meteorological drivers and the temporal structure of the fluxes. This algorithm should give less biased estimates of gross ecosystem carbon uptake and Reco.
- 2) Light-response curves are fit to daytime NEE measurements and respiration is estimated from the intercept of the ordinate, which avoids the use of potentially problematic night time data. This method developed by Lasslop et al. (2010), introduced an algorithm for NEE partitioning that uses a hyperbolic light response curve fit to daytime NEE, modified to account for the temperature sensitivity of respiration and the VPD limitation of photosynthesis.

### 2.3.5 Statistical analysis

Repeated- measures ANOVA and Fisher's post hoc test were used to test the seasonal variation of  $R_{stem}$  and to test the tree treatment (standards and coppice shoots). The Cox-Stuart test for trend analysis and the Student's  $t$ -test for comparison between groups of variables were used. Overall differences were considered significant with a  $p$ -value of  $< 0.05$ .

MAE (mean absolute error), MAPE (mean absolute percentage error), RMSE (root mean squared error), and  $r^2$  (coefficient of determination), were used as measures of model evaluation as defined by Janssen & Heuberger, (1995).

#### 2.3.5.1 Model validation of $R_{stem}$ and $R_s$

Uncertainty quantification was conducted through two different methods:  $k$ -fold cross validation and bootstrap.

In  $k$ -fold cross-validation method, the original sample is partitioned into  $k$  equal size subsamples. Of the  $k$  subsamples, a single subsample is retained as the validation data for testing the model,

and the remaining  $k - 1$  subsamples are used as training data. The cross-validation process is then repeated  $k$  times (the *folds*), with each of the  $k$  subsamples used exactly once as the validation data. The advantage of this method over repeated random sub-sampling is that all observations are used for both training and validation, and each observation is used for validation exactly once. 10-fold cross-validation is commonly used, but in this study  $k$  was fixed equal to the number of the plants for  $R_{\text{stem}}$  ( $k = 7$ ) and the number of the plots for  $R_s$  ( $k = 8$ ). Because of some technical problems the data of two plants were not considered.

In the bootstrap method, given a sample of size  $n$ , a bootstrap sample is created by re-sampling  $n$  cases from the data (with replacement). This method was used to evaluate the stability of the model prediction associated to different sample size. Bootstrap was then performed:

- data of stem  $\text{CO}_2$  efflux were split in subsets containing an increasing number of plants, from 1 to 7. All the possible combinations between the plants measured, were considered and within these combinations a non-linear regression model (nls in R Core Team (2012)) was run. The original data set, the one with only one possible combination (7 plants),  $R_{\text{stem}}$  and  $T_{\text{stem}}$  were randomly resampled (with replacement) 200 times and a non-linear regression model, was run for each resample, resulting in 200 parameter estimates;
- data of soil respiration, the whole dataset of the year 2012 was split in subsets corresponding to data of 10, 15, 20, 25, 30, 35 and 40 collars. For each subset, soil respiration, soil water content and temperature were randomly resampled (with replacement) 200 times, where each resample was made up to the same number of data points as the original data subset. The non-linear regression was run for each re-sample, resulting in 200 parameter estimates.

The results of the application of the bootstrap method, were graphically analyzed, both for  $R_{\text{stem}}$  and  $R_s$ , using a box-and-whisker plots.

### **2.3.5.2 *Reco<sub>eddy</sub>: Model Efficiency selection***

Concerning the Reco estimation, a source of uncertainty was evaluated due to the  $u^*$  filtering.

The starting dataset is NEE already corrected by storage and de-spiked (method described in Papale et al., (2006)). The  $u^*$  filtering has been based on thresholds calculated using the method reported in Reichstein et al. (2005) and using 100 bootstrapped datasets.

Two different methods has been used to extract the  $u^*$  thresholds:

- **yearly** (identified by the variables names with ref\_y): the thresholds were found for each year and the years before; then have been put together and from this join population the final threshold was extracted (thresholds different between years).

- **common** (identified by the variables names with ref\_c): all the thresholds found in the different years have been put together and final threshold extracted from this dataset (each year filtered with the same threshold).

In both the NEE\_ref\_y and NEE\_ref\_c, 40 NEE datasets have been created filtering the original NEE using 40 different  $u^*$  values extracted from the thresholds datasets at percentiles 5, 16, 25, 50, 75, 84, 95. These 40 NEE versions have been used as basis for all the derived variables.

The reference NEE was selected on the basis of the Model Efficiency. Starting from the 40 different NEE estimations it was calculated the Model Efficiency between each version and the others 39. The reference NEE was selected as the one with higher Model Efficiency sum (so the most similar to the others 39). As reference, in the 2012, were selected:

1) for the estimation of Reco by the method of Lasslop (2010)

NEE\_ref\_c filtered using the  $u^*$  percentile 36.25

NEE\_ref\_y filtered using the  $u^*$  percentile 38.75

2) for the estimation of Reco by the method of Reichstein (2005)

NEE\_ref\_c filtered using the  $u^*$  percentile 48.75

NEE\_ref\_y filtered using the  $u^*$  percentile 46.25

### **3. RESULTS**



## 3.1 Stem CO<sub>2</sub> efflux

### 3.1.1 Daily variation

On most days, the relationship between stem temperature and stem respiration was well described by the exponential Eqn. 2.1. The temporal variation in  $R_{\text{stem}}$  rates were explained by stem surface temperature on daily scale. It reached the maximum when stem and air temperature were highest, while the minimum values in the early hours of the morning, when the temperature was lower. The relationships between stem CO<sub>2</sub> efflux and stem temperature on daily scale, were strong with almost always a value of  $R^2 > 0.70$ . In

Fig. 3.1 are showed, the data of all plants for each date of measurement. Each curve is represented by the fit of the 5 points corresponding to the measurements of the 5 moments of the day, from just after dawn at the time of maximum daily temperature.

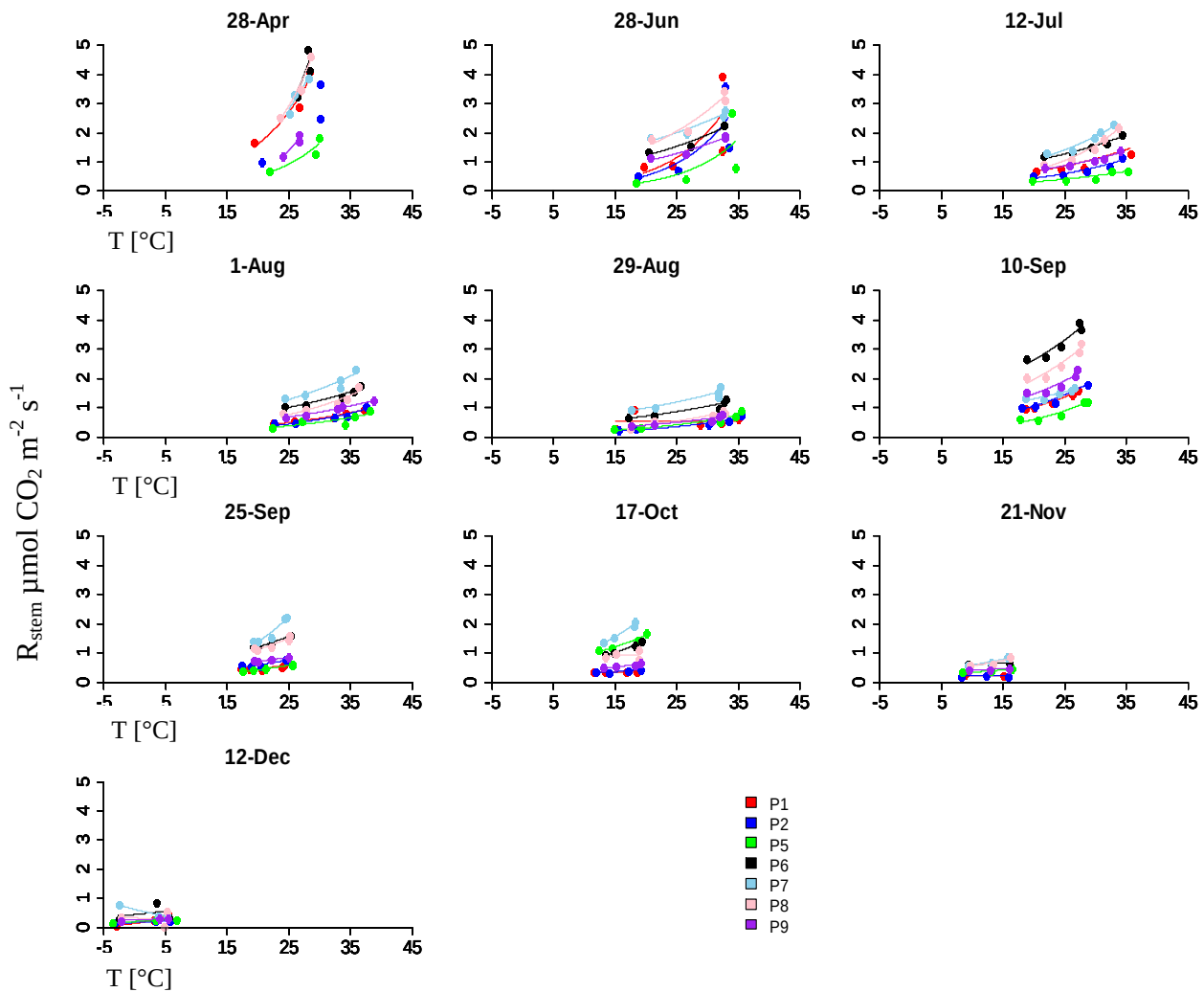


Fig. 3.1 – Relation between stem CO<sub>2</sub> efflux and temperature on daily scale.

In Tab. 3.1 are shown the values of the parameters  $a$  and  $k$  and the coefficients of correlation ( $r^2$ ) of each curve. While the slope of the curve ( $k$ ), on most days, for each plant, is very similar, the value of the intercept ( $a$ ), during the growing period (spring and autumn), varied from 0.18 to  $0.92 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  representing the high spatial variability between individuals.

| Coppice shoots |        |            |            |       | Standards |        |            |            |       |
|----------------|--------|------------|------------|-------|-----------|--------|------------|------------|-------|
| Sample         | Date   | Coeff. $a$ | Coeff. $k$ | $R_2$ | Sample    | Date   | Coeff. $A$ | Coeff. $k$ | $R_2$ |
| 1              | Apr 28 | 0.21       | 0.10       | 0.94  | 3         | Apr 28 | 0.10       | 0.11       | 0.77  |
| 1              | Jun 28 | 0.07       | 0.11       | 0.49  | 3         | Jun 28 | 0.50       | 0.05       | 0.89  |
| 1              | Jul 12 | 0.25       | 0.05       | 0.57  | 6         | Apr 28 | 0.08       | 0.14       | 0.61  |
| 1              | Aug 1  | 0.13       | 0.05       | 0.97  | 6         | Jun 28 | 0.49       | 0.05       | 0.92  |
| 1              | Sep 10 | 0.31       | 0.06       | 0.98  | 6         | Jul 12 | 0.46       | 0.04       | 0.95  |
| 1              | Sep 25 | 0.19       | 0.04       | 0.67  | 6         | Aug 1  | 0.35       | 0.04       | 0.94  |
| 2              | Apr 28 | 0.08       | 0.12       | 0.81  | 6         | Aug 29 | 0.32       | 0.04       | 0.87  |
| 2              | Jun 28 | 0.05       | 0.12       | 0.56  | 6         | Sep 10 | 1.04       | 0.05       | 0.90  |
| 2              | Jul 12 | 0.13       | 0.06       | 0.88  | 6         | Sep 25 | 0.42       | 0.05       | 0.97  |
| 2              | Aug 1  | 0.09       | 0.06       | 0.85  | 6         | Oct 17 | 0.36       | 0.07       | 0.98  |
| 2              | Aug 29 | 0.08       | 0.06       | 0.92  | 6         | Nov 21 | 0.55       | 0.01       | 0.82  |
| 2              | Sep 10 | 0.30       | 0.06       | 0.95  | 7         | Apr 28 | 0.21       | 0.10       | 0.88  |
| 2              | Sep 25 | 0.20       | 0.05       | 0.78  | 7         | Jun 28 | 0.81       | 0.04       | 0.93  |
| 2              | Oct 17 | 0.19       | 0.04       | 0.70  | 7         | Jul 12 | 0.34       | 0.06       | 0.95  |
| 2              | Dec 12 | 0.17       | 0.07       | 0.94  | 7         | Aug 1  | 0.38       | 0.05       | 0.88  |
| 5              | Apr 28 | 0.05       | 0.11       | 0.86  | 7         | Aug 29 | 0.46       | 0.04       | 0.86  |
| 5              | Jun 28 | 0.03       | 0.11       | 0.41  | 7         | Sep 10 | 0.65       | 0.03       | 0.90  |
| 5              | Jul 12 | 0.12       | 0.05       | 0.77  | 7         | Sep 25 | 0.20       | 0.10       | 0.93  |
| 5              | Aug 1  | 0.09       | 0.06       | 0.70  | 7         | Oct 17 | 0.47       | 0.08       | 0.97  |
| 5              | Aug 29 | 0.09       | 0.06       | 0.86  | 7         | Nov 21 | 0.33       | 0.06       | 0.95  |
| 5              | Sep 10 | 0.12       | 0.08       | 0.91  | 9         | Apr 28 | 0.03       | 0.15       | 0.90  |
| 5              | Sep 25 | 0.12       | 0.06       | 0.99  | 9         | Jun 28 | 0.42       | 0.04       | 0.96  |
| 5              | Oct 17 | 0.52       | 0.06       | 0.94  | 9         | Jul 12 | 0.28       | 0.05       | 0.92  |
| 5              | Nov 21 | 0.23       | 0.04       | 0.89  | 9         | Aug 1  | 0.22       | 0.04       | 0.98  |
| 5              | Dec 12 | 0.20       | 0.05       | 0.66  | 9         | Aug 29 | 0.16       | 0.04       | 0.87  |
| 8              | Apr 28 | 0.14       | 0.12       | 0.97  | 9         | Sep 10 | 0.50       | 0.05       | 0.84  |
| 8              | Jun 28 | 0.47       | 0.06       | 0.93  | 9         | Sep 25 | 0.36       | 0.03       | 0.94  |
| 8              | Jul 12 | 0.14       | 0.08       | 0.96  | 9         | Oct 17 | 0.28       | 0.04       | 0.85  |
| 8              | Aug 1  | 0.16       | 0.06       | 0.88  | 9         | Nov 21 | 0.31       | 0.03       | 0.93  |
| 8              | Aug 29 | 0.12       | 0.06       | 0.89  | 9         | Dec 12 | 0.26       | 0.03       | 0.99  |
| 8              | Sep 10 | 0.63       | 0.06       | 0.90  |           |        |            |            |       |
| 8              | Sep 25 | 0.36       | 0.06       | 0.89  |           |        |            |            |       |
| 8              | Nov 21 | 0.32       | 0.06       | 0.80  |           |        |            |            |       |

Tab. 3.1 - Values of the parameters  $a$  and  $k$  and the coefficients of correlation ( $R^2$ ) of each plant divided per day.

### 3.1.2 Seasonal variation of stem CO<sub>2</sub> efflux

Seasonal trend in stem respiration followed the same pattern in all trees, with the greatest rates occurring during the growing season.

The total average ( $\pm$ SE) of the 362 measurements of stem respiration ( $R_{\text{stem}}$ ), carried out from April to December 2012, was  $1.23 \pm 0.05 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . On the end of the year, the lowest CO<sub>2</sub> efflux rates were probably caused by a cessation of growth processes and a decrease in temperature. The highest rates of CO<sub>2</sub> efflux were reached in spring as a result of active woody tissue growth, high temperature and transpiration.

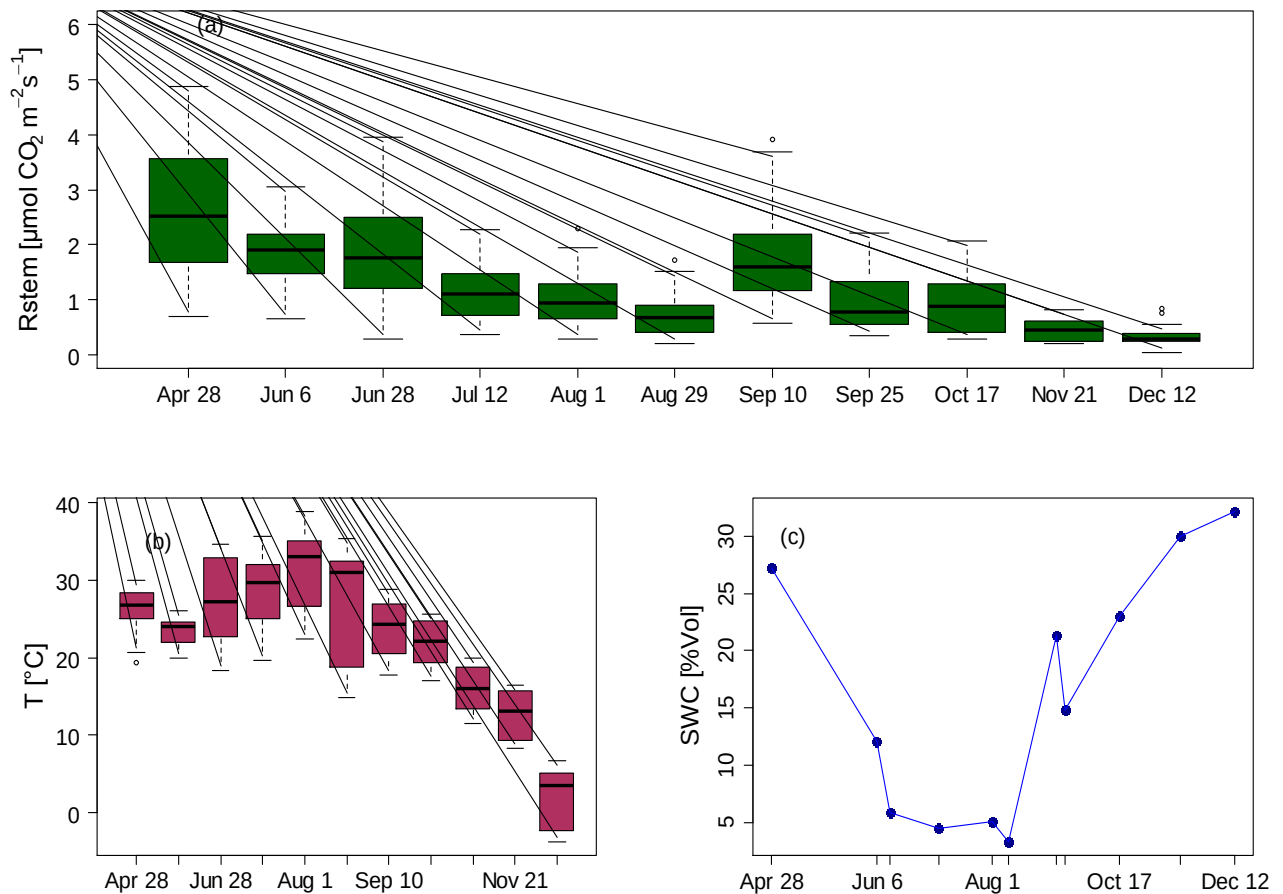


**Fig. 3.2 – (a) Trend of seasonal CO<sub>2</sub> efflux from stem surface from April to December 2012. The vertical bars indicate the minimum and maximum values, the bottom and top of the box are the 25<sup>th</sup> and 75<sup>th</sup> percentile, the black band near the middle of the box is the median. (b) Variations of temperature during the study period. There is a marked temperature range from the early hours of the morning until shortly before midday, both in August and December. (c) Seasonal trend of soil water content over 5 cm depth.**

During the whole period of study all the trees shown the same trend apart plant 4 that started, on August 29, to have a huge efflux of CO<sub>2</sub> from the stem. This plant suffered because of the strong period of drought until get to death. For this reason was chosen to treat it separately from the other plants.

Stem respiration varied through the season, starting from  $2.64 \pm 0.24 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  on April and reaching  $0.33 \pm 0.04 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  on December. This last value represents the minimum of the measurement period. If we considered only the growing season, the mean value of  $R_{\text{stem}}$  was equal to  $1.36 \pm 0.05 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and the minimum was reached in August 29 ( $0.70 \pm 0.06 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), in fact, during summer the efflux was low due to a strong period of drought.

Fluxes are declined basically during the whole period (Cox-Stuart test for trend analysis - downward trend; p-value < 0.05) with a slight increase on the end of June and a substantial variation on the beginning of September. On this day, 10 September, the flux reached the maximum peak of the summer, equal to  $1.78 \pm 0.14 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , after rain events.

### 3.1.3 Effect of environmental factors

Seasonal variation in stem CO<sub>2</sub> efflux rates for the study period was only partially explained by stem temperature. The simple exponential dependency of all data of stem respiration on stem temperature was heavily weaker ( $r^2 = 0.17$ ). However, dividing the data in two subsets, using a threshold of Gross Primary Productivity (GPP) of  $2 \text{ g C m}^{-2} \text{ d}^{-1}$ , was possible to obtain two fitting curves representing different sensitivities to temperature. The first subset corresponded to data of the days with high GPP namely the period in which the main part of CO<sub>2</sub> efflux was due to the growing stem respiration; the second one, corresponded to data of the days with low GPP namely the period in which the main part of CO<sub>2</sub> efflux is due to maintenance stem respiration. The close correlations between stem surface temperature and respiration rates (Fig. 3.3) ( $r^2 = 0.38$  for “growing” respiration and  $r^2 = 0.55$  for the “maintenance” respiration) permitted the calculation of two  $Q_{10}$  values: 2.01 and 1.49 respectively.

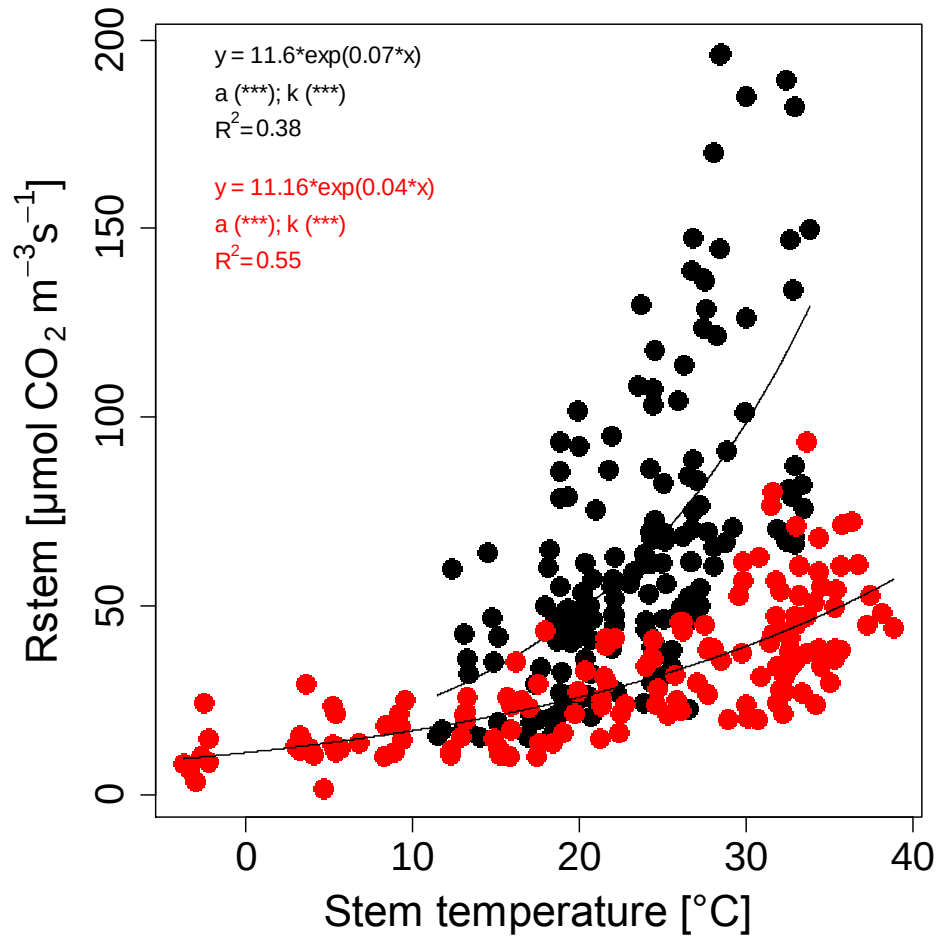


Fig. 3.3 - Black circles show  $R_{\text{stem}}$  measured at  $\text{GPP} > 2 \text{ gC m}^{-2} \text{ d}^{-1}$ . Red circles show  $R_{\text{stem}}$  measured at  $\text{GPP} < 2 \text{ gC m}^{-2} \text{ d}^{-1}$ , corresponding basically to the summer and winter periods. The black lines represent the exponential regressions between stem respiration and stem surface temperature.  $R_{\text{stem}}$  is expressed on volume basis ( $\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$ ).

### 3.1.4 Effect of diameter

Expressing stem  $\text{CO}_2$  efflux on a surface basis ( $R_{\text{sup}}$ ) and plotting it versus DBH (Fig. 3.4), a significant positive linear relationship ( $R^2 = 0.65$ ;  $p < 0.05$ ), was found.  $R_{\text{sup}}$  showed a pronounced increase with an increasing tree diameter. On a volume basis, the respiration rate ( $R_{\text{vol}}$ ) was not related with diameter. This indicates that the major respiratory source is volume related because sapwood xylem parenchyma cells are a more important source.

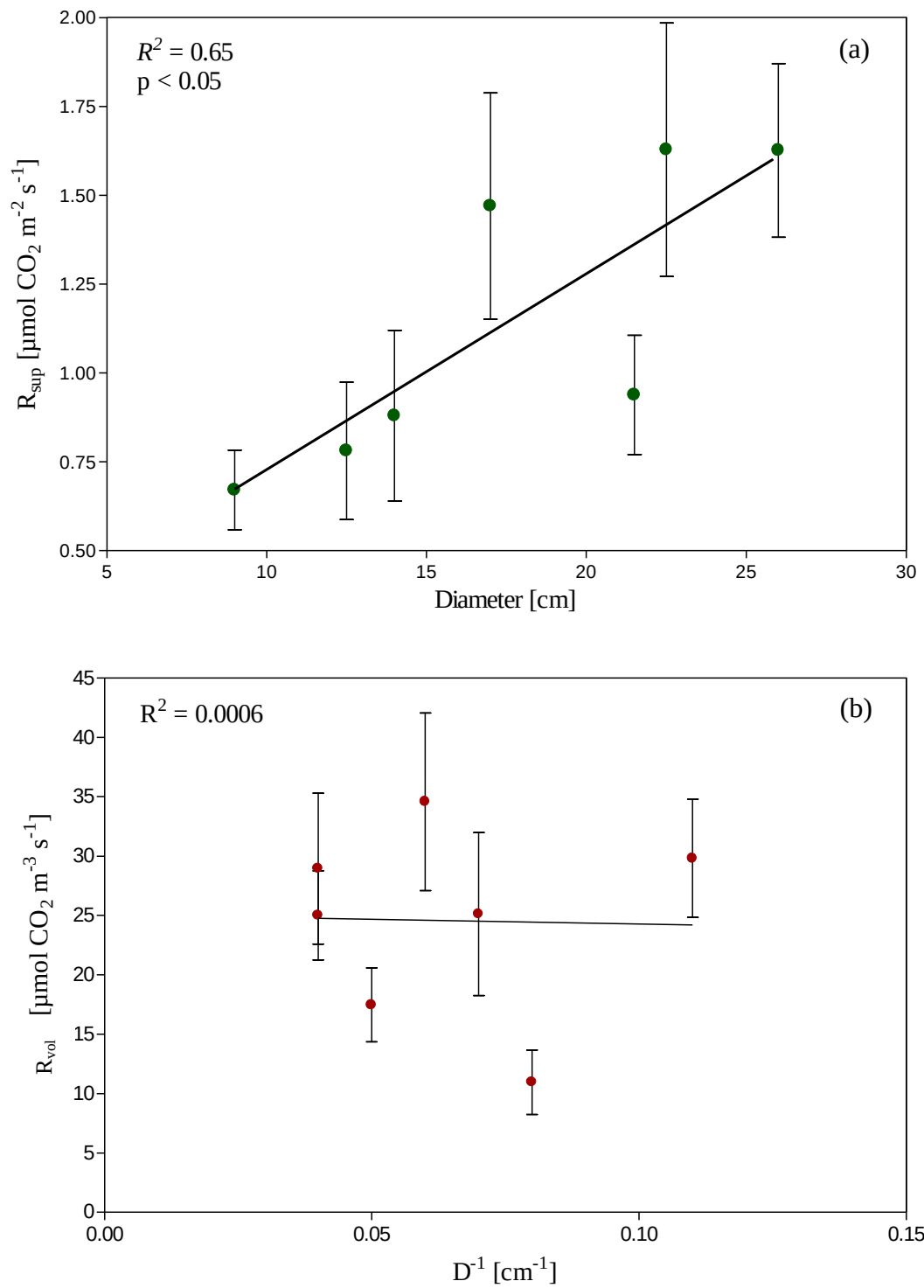


**Fig. 3.4 – Respiration rate,  $R_{stem}$ , expressed on surface (a) and on a volume basis (b). Graphs (a) and (b) show the expected relationship if the respiratory source is proportional to stem surface area or stem volume. The respiration rate,  $R_{stem}$ , is related to the diameter.; for  $R_{stem}$  expressed on a surface basis ( $R_{sup}$ ) there is a significant positive linear relationship ( $R^2 = 0.65$ ;  $p < 0.05$ ); on a volume basis, the respiration rate ( $R_{vol}$ ) was not related with diameter. It indicates that the major respiratory source is volume related.**

Comparing the  $Q_{10}$  calculated for each plant in the growing and maintenance period, two different relationships were observed. A decrease in the  $Q_{10}$  with increasing stem diameter and a strong non-linear relation ( $R^2 = 0.92$ ) was found for the growing period (Fig. 3.5), while no relationship was found during the maintenance period, as shown in Fig. 3.6.

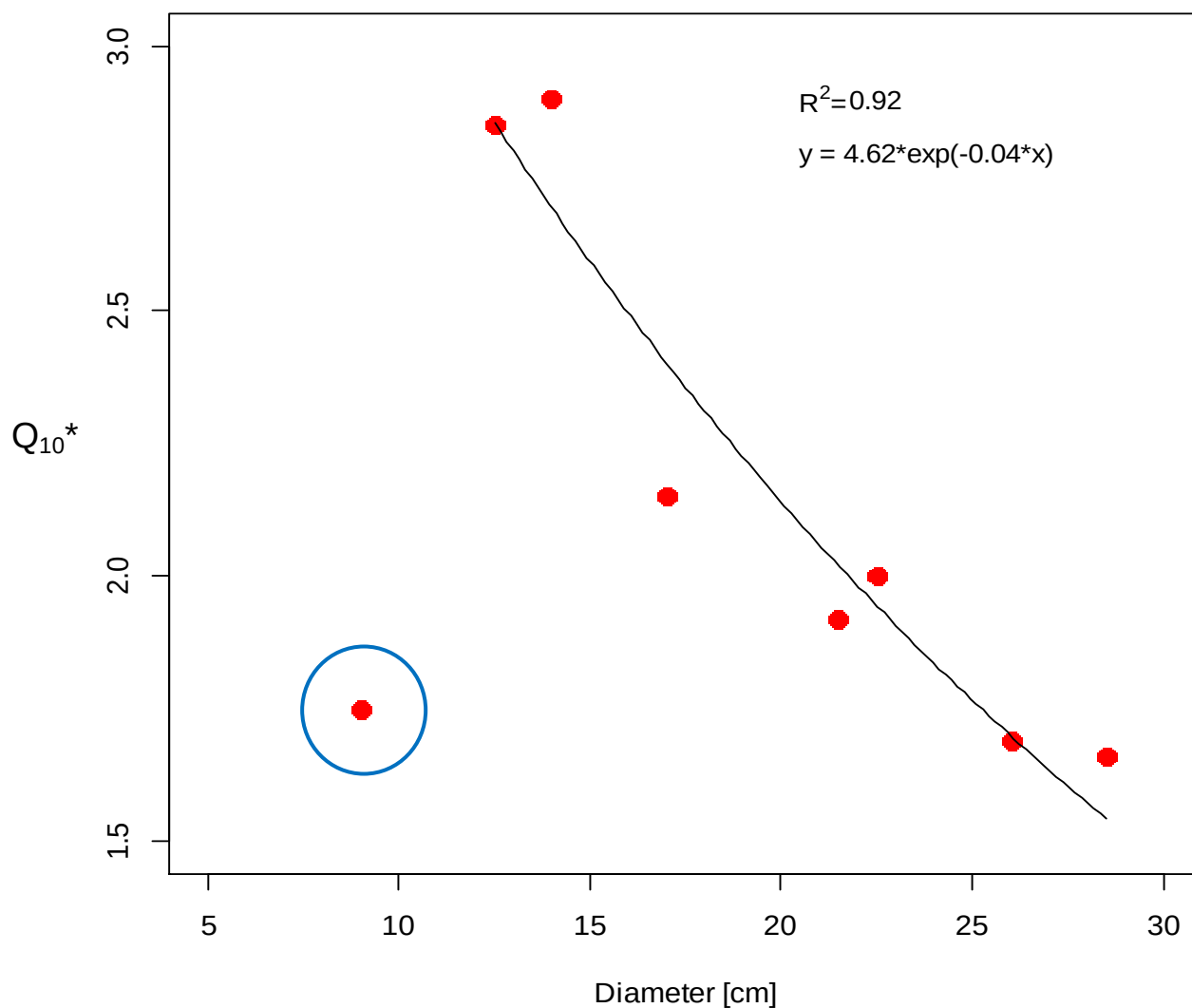


**Fig. 3.5 – The apparent  $Q_{10}^*$  decreased with increasing diameter with a strong non linear relationship. The circled point was considered as an outline probably due at the age of the stand, with the smaller plants that suffered shading of the larger plants and had a growing smaller than the others.**

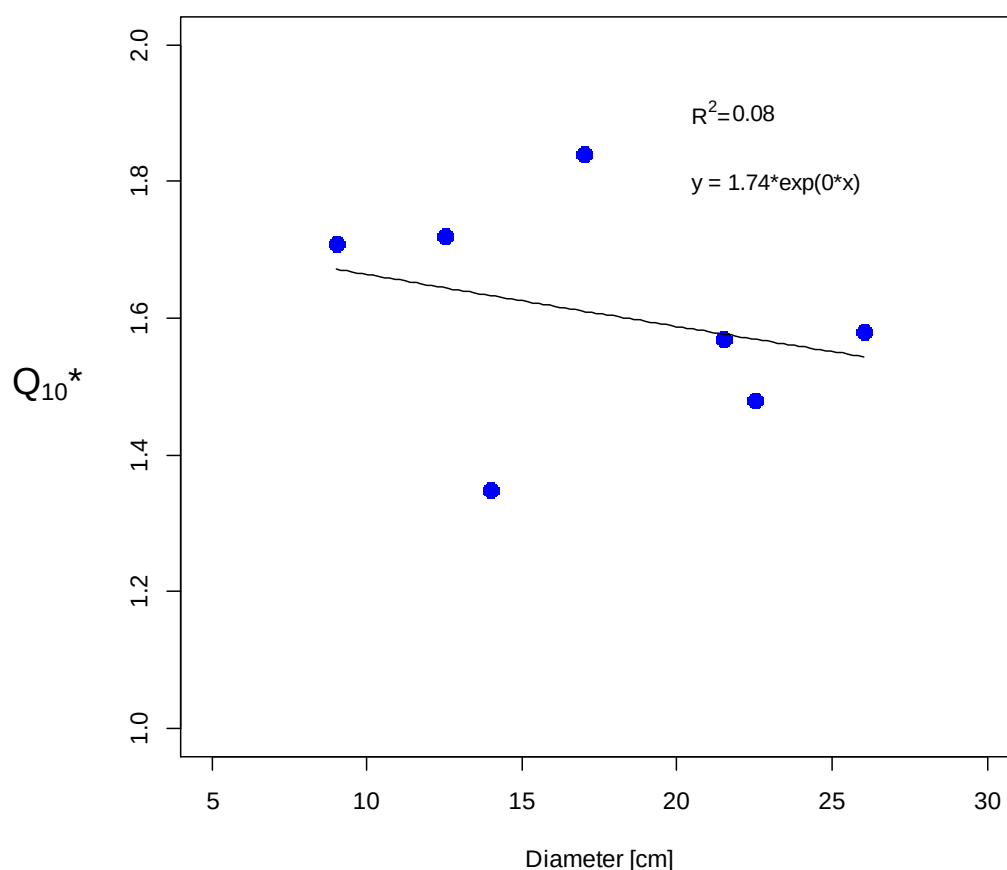


**Fig. 3.6 – During winter and summer (maintenance period) the relationship between apparent  $Q_{10}$  and diameter wasn't found. It ranged between 1.35 – 1.84 without a clear trend.**

### 3.1.5 Standards and coppice shoots

Separating the fluxes attributable to different structures, was obtained a significant difference between the mean value ( $\pm$  SE) of  $\text{CO}_2$  efflux from the stems of standards ( $1.49 \pm 0.14 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) and the stems of coppice shoots ( $1.01 \pm 0.07 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), ( $t$ -test,  $p < 0.001$ ). Considering the mean values of  $R_{\text{stem}}$  calculated on volume basis was found a significance of the difference clearly lower ( $t$ -test,  $p < 0.1$ ); the average of standards was equal to  $25.32 \pm 2.33 \mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$  and that of coppice  $32.80 \pm 3.36 \mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$ .  $R_{\text{stem}}$  shown a significant seasonal trend (Repeated Anova;  $p < 0.001$ ) for the two separated kind of structure but the differences in respiration rates between standards and coppice shoots were significant only on some days, as shown in Fig. 3.7.

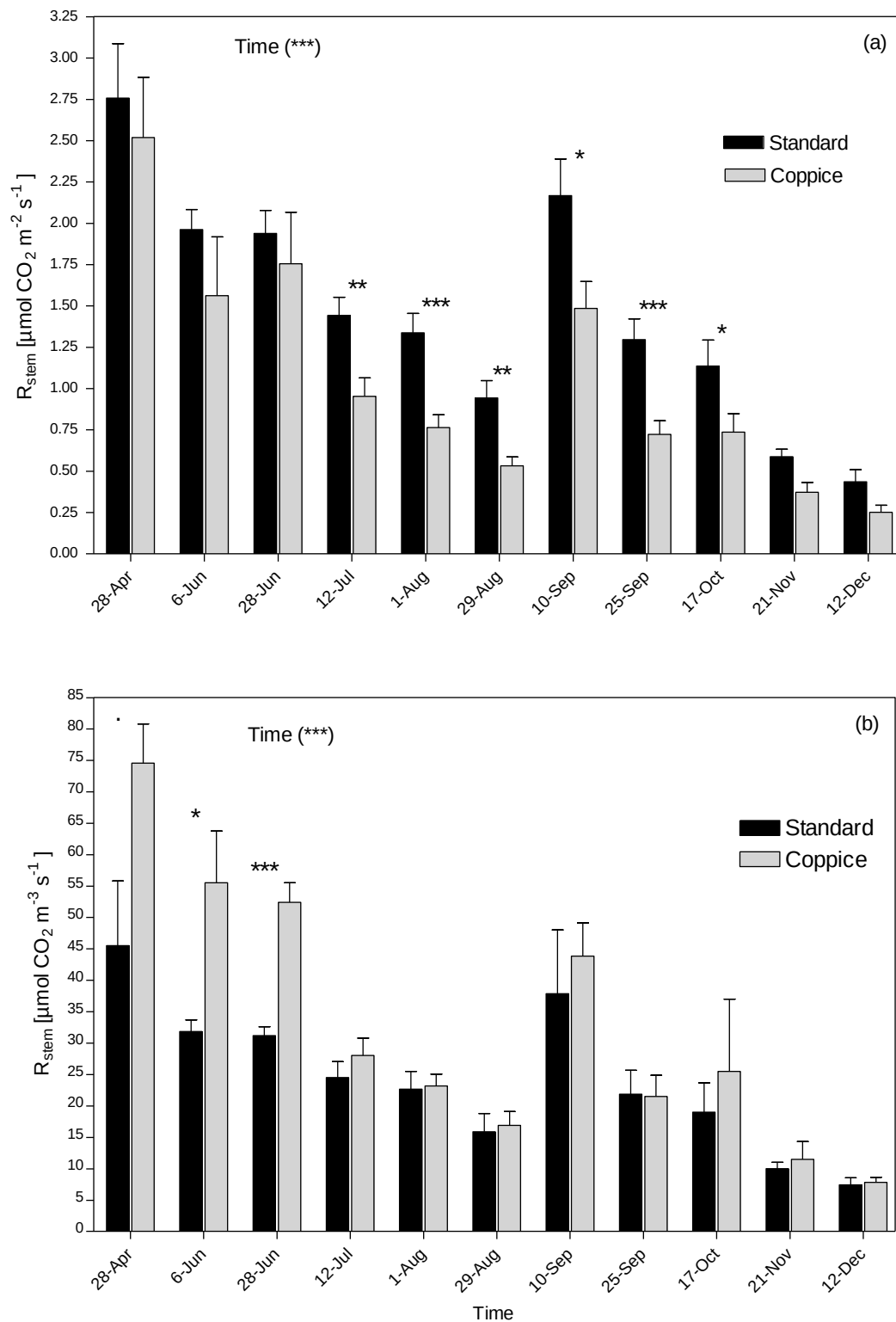
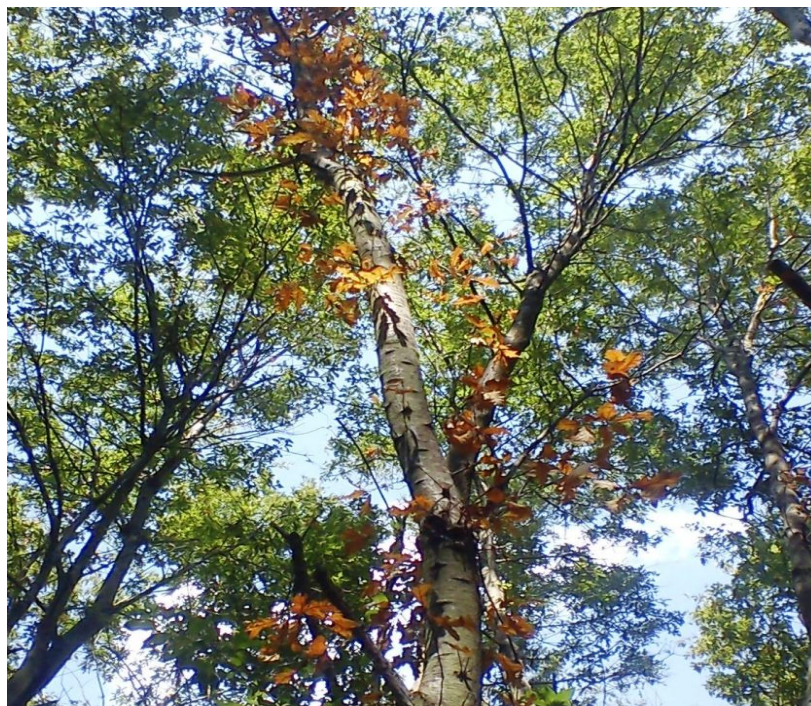


**Fig. 3.7 – Seasonal trend of stem respiration calculated on surface basis (a) and on volume basis (b) of stems of standards and stems of coppice shoots. The time had a significant effect on the seasonal variation in both of cases. The significance of the differences between groups of standard and coppice shoots are signed with the notation “\*\*”.**

### 3.1.6 Water stress and susceptibility to weakness parasites

A really different behavior had the plant 4; it is a coppice shoot of 11.5 cm in diameter. As shown in Fig. 3.8 this plant started to emit a huge amount of CO<sub>2</sub> from the stem since the end of August, as a consequence of a strong period of drought. This plant shown the total and sudden die back of the crown (Fig. 3.8) between the beginning and the end of August. The association of water stress and susceptibility to a weakness parasites led to the rupture of cortical tissue and the complete death of the plant. The sudden emission increase was probably due to the synergistic action of both attack of parasites of weakness and the attempt to reaction of the plant. In October the high CO<sub>2</sub> efflux started to decrease until up to return to normal values, due to both health conditions and low temperatures. The mean value of the whole period of study was equal to  $3.70 \pm 0.57 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ .  $R_{\text{stem4}}$  ranged from  $0.52 \pm 0.08 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  on July 12 to  $10.04 \pm 1.12 \text{ CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  on September 25.

To verify if this was an isolated case, was measured the CO<sub>2</sub> efflux from the stems of other plants that exhibited the same symptoms. We estimated that the density of these suffering plants, in the population, was equal to 75 plants per hectare with mean diameter measured at the breast height equal to  $8.4 \text{ cm} \pm 0.36$ . On September 10 the average of  $R_{\text{stem}}$  of the 18 dying plants measured was  $6.89 \pm 0.86 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  against  $1.78 \pm 0.14 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  of the healthy plants in the same day. The contribution to the total efflux, over the year, has been less than 3%.



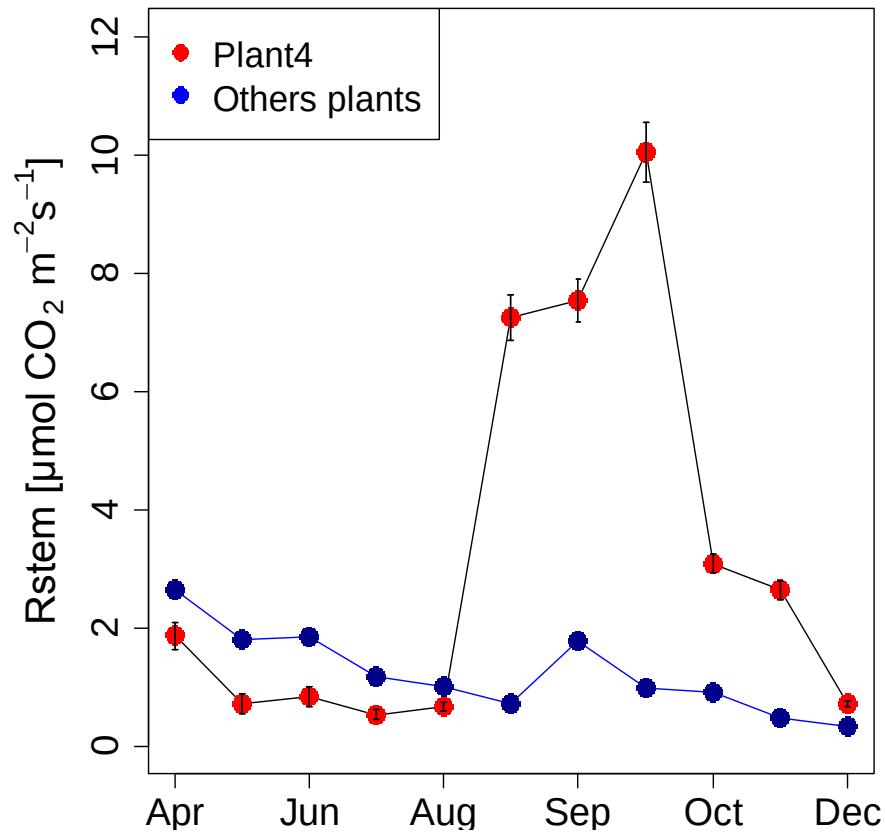


Fig. 3.8 – The picture on the top shows the die back of the crown, while the graph shows the seasonal trend of the plant 4 (red circles with SE) compared with the others plants (blue circles; SE was omitted for a better readability and is shown in fig 3.2). From August 29 a sudden increase in stem CO<sub>2</sub> efflux rate occurred and returned at normal values only on December when the plant was dying.

### 3.1.7 Scaling-up and model validation of $R_{\text{stem}}$

The model (Eqn. 2.1) used to scale-up the chamber measurements explained 38% of  $R_{\text{stem}}$  during the growing period and 55% during the maintenance period. The model didn't fit the data very well because of the high variability between individuals. Furthermore, temperature alone explained less 40% of the temporal variation, which relates to the high incidence of severe water stress at the site. The period when the model did not correctly simulated the temporal variation in stem CO<sub>2</sub> efflux, was mainly Spring and Autumn, when flux rates peaked. The plants had different behavior because not all recovered after the water stress. In table Tab. 3.2 – is shown the percentage of recovery per plant normalized for his own maximum reached in spring.

Comparing the data estimated by the model with the data measured, a correlation coefficient equal to 0.51 was found. It is clear a general underestimation of the highest and lowest values and an overestimation of the average values (Fig. 3.9). The statistical distributions of the residuals of the modeled  $R_{\text{stem}}$  was very dissimilar during spring and autumn respect to summer and winter (Fig. 3.10).

| Plant | DBH (cm) | Recovery(%) |
|-------|----------|-------------|
| 1     | 14       | 17          |
| 2     | 12.5     | 22          |
| 5     | 9        | 47          |
| 6     | 22.5     | 40          |
| 7     | 26       | 42          |
| 8     | 17       | 35          |
| 9     | 21.5     | 56          |

Tab. 3.2 – Percentage of recovery per plant normalized for the maximum reached in spring.

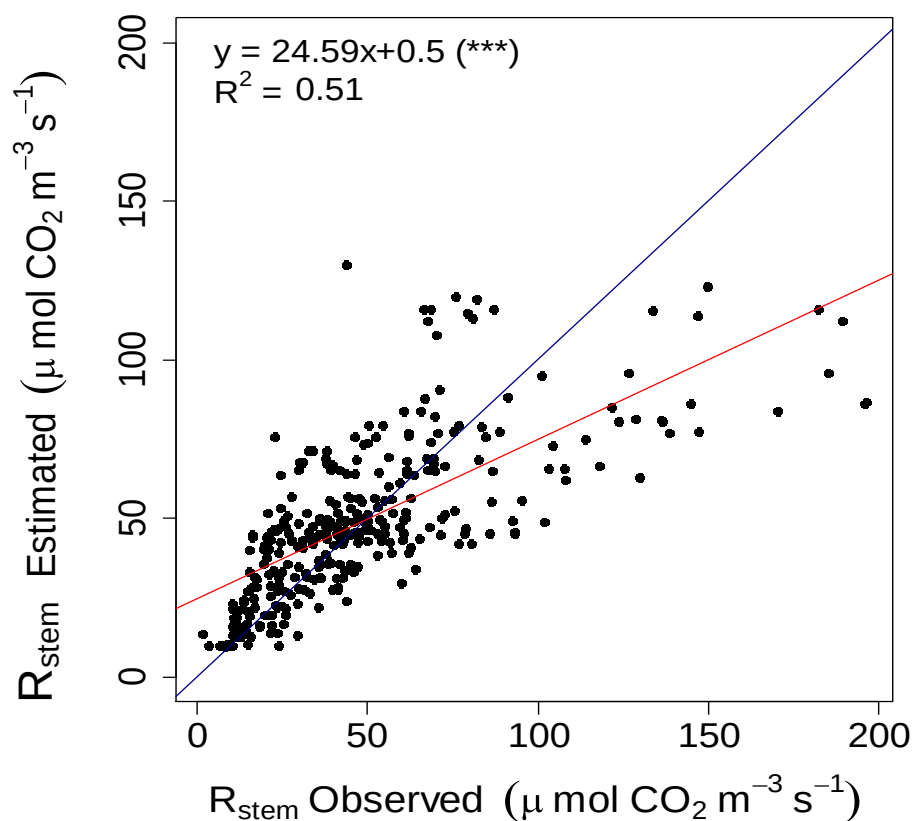


Fig. 3.9 – Comparison of model prediction with observed data of stem  $\text{CO}_2$  efflux during the whole period of measurements.

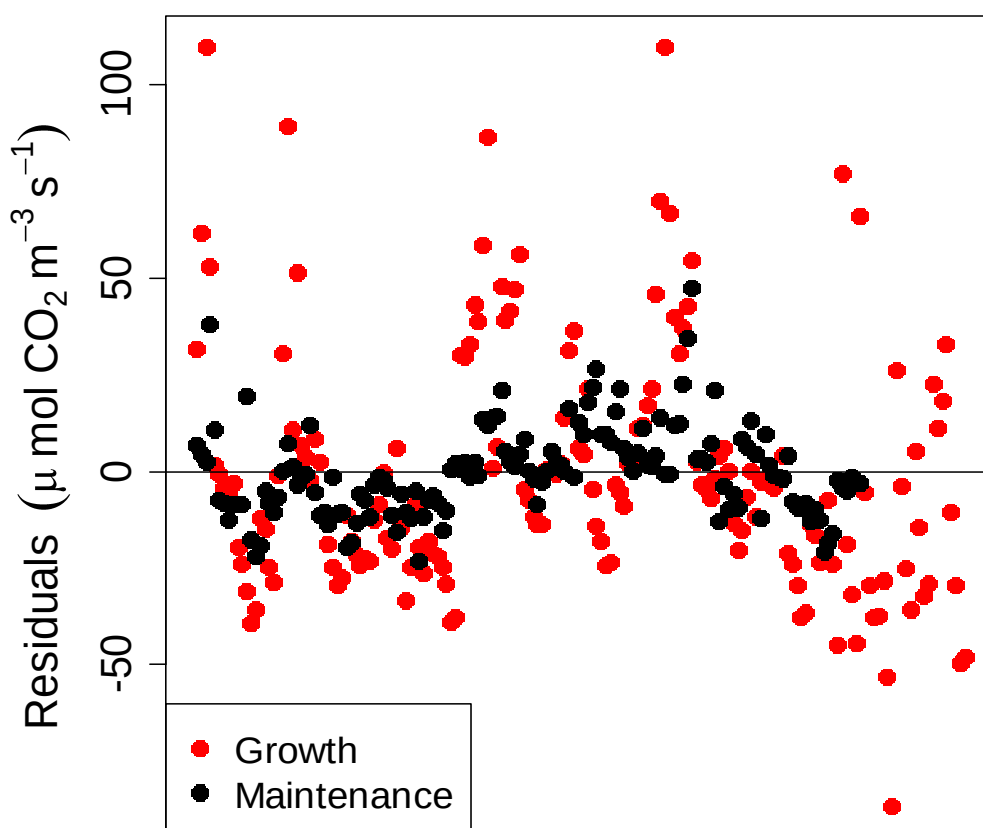


Fig. 3.10 – Residuals distribution: spread of the difference between predicted and measured data.

The measures of mean absolute errors (MAE), mean absolute percentage errors (MAPE), root mean square errors (RMSE) and coefficient of correlation ( $R^2$ ) were used to express quantitatively the deviation between model predictions and observations; the results in Tab. 3.3 show how the prediction errors are higher for the growing period compared to the maintenance period, with MAE 23.46 and 8.91  $\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$ , MAPE 44.89% and 36.83%, and RMSE 31.05 and 11.73  $\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$ ,  $R^2$  0.38 and 0.55, respectively.

| Period      | MAE<br>$\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$ | MAPE<br>% | RMSE<br>$\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$ | $R^2$ |
|-------------|-----------------------------------------------------------|-----------|------------------------------------------------------------|-------|
| Growing     | 23.46                                                     | 44.89     | 31.05                                                      | 0.38  |
| Maintenance | 8.91                                                      | 36.83     | 11.73                                                      | 0.55  |

Tab. 3.3 – Quantification of the deviation between model predictions and observation by MAE, MAPE, RMSE and  $R^2$ .

*K*-fold cross validation was used to evaluate the performance measures on the data set which is different or independent from the data set used for calibrating the model. Based on up-scaled chamber measurements, the cumulate value of the whole year, was 1.77 t C ha<sup>-1</sup> y<sup>-1</sup> while the range of the cumulative estimations obtained by the *k*-fold cross validation, varied from 1.66 to 1.85 t C ha<sup>-1</sup> y<sup>-1</sup> (Fig. 3.11).

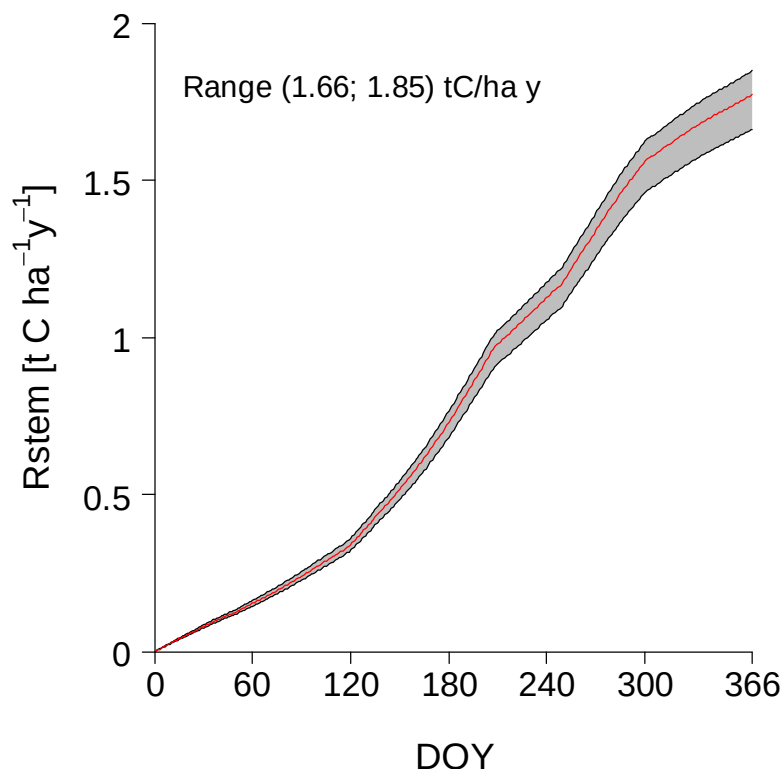


Fig. 3.11 – Cumulates of the up-scaled chamber measurements for the year 2012. Red line represents the cumulate obtained using the whole data set for calibrating the model. The grey area represents the range of the cumulates estimated by *k*-fold cross validation analysis.

|                                                                    | Growing          | Maintenance      |
|--------------------------------------------------------------------|------------------|------------------|
| <b>MAE</b> ( $\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$ )  | $36.32 \pm 5.54$ | $26.6 \pm 1.23$  |
| <b>MAPE</b> (%)                                                    | $45.37 \pm 4.33$ | $52.77 \pm 8.94$ |
| <b>RMSE</b> ( $\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$ ) | $48.54 \pm 6.47$ | $34.28 \pm 1.98$ |
| <b>R<sup>2</sup></b>                                               | $0.22 \pm 0.03$  | $0.39 \pm 0.07$  |

Tab. 3.4 - Quantification of the deviation between observation and model predictions by MAE, MAPE, RMSE and R<sup>2</sup>  $\pm$  SE of the *k* results.

By bootstrap analysis was verified that increasing the sample size for the estimation of the model parameters, the variability of the estimation of the total annual  $R_{\text{stem}}$  decreases. The difference shifts from 0.93 to 0.41  $\text{t C ha}^{-1} \text{y}^{-1}$  (Fig. 3.12).

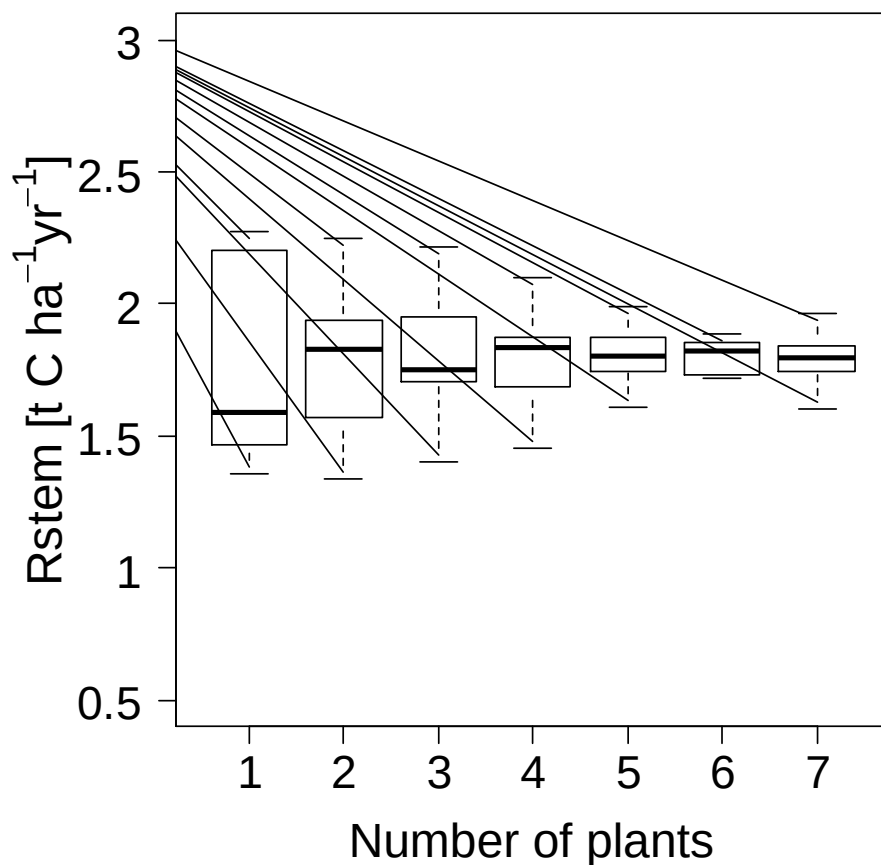


Fig. 3.12 - Representation of the variability of the estimated total  $R_{\text{stem}}$  calculated by estimating the model parameters with increasing number of plants. The greater the number of plants the lower the variability of the result and the greater is its reliability.

## 3.2 Soil respiration

### 3.2.1 Annual variations of soil respiration

Soil respiration ( $R_s$ ) was measured from August 2010 to August 2011 ( $R_{s1}$ ) and from January to December 2012 ( $R_{s2}$ ). The general trend of  $R_s$  of the two years considered, was the same with the lowest values in winter and summer and the highest, in autumn and spring. The total average ( $\pm$ SE) of the 1360 measurements of  $R_s$ , carried out during the two years, was  $2.60 \pm 0.04 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ .

As shown in Fig. 3.13 and Fig. 3.14 soil respiration varied markedly through the seasons following the changes in soil temperature and in soil moisture, although with a different pattern along the two years considered. There is not significantly difference between the means of  $R_s$  of the two years of measurements; its resulted equal to 2.79 and 2.36  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , for the first and for the second year respectively. The maximum peaks of  $R_s$  have the same value but occurred in different periods, on July 6 for the first year and on September 6 for the second year.

In the year 2010 the measurements started on August, with a slight drought that ended between September and October. During the year 2011 occurred a drought period, on June and on August, interrupted by a rain event on July. The 2012 was characterized by a strong and large drought period occurred from May and September and by another one, quite atypical, on spring, between March and April. In both years, the maximum temperatures coincided with minimum water contents in summer, while minimum temperatures coincided with highest soil water content in winter. Soil temperature increased steadily until mid-summer reaching a maximum in August, and then declined smoothly through autumn and reaching the minimum in January and February in first and second year, respectively.

In Tab. 3.5 and Tab. 3.6, are shown the summary results of soil respiration ( $R_s$ ), soil temperature ( $T_s$ ) and soil water content (SWC) of the two years considered. In 2010 – 2011, the annual mean temperature of the soil at 5 cm depth was  $15.20 \pm 1.04 ^\circ\text{C}$ , while SWC over 5 cm depth ranged from  $7.58 \pm 0.16 \text{ \%vol}$  (July) to  $40.97 \pm 0.82 \text{ \%vol}$  (February). In 2012, the annual mean temperature of the soil at 5 cm depth was  $16.88 \pm 1.44 ^\circ\text{C}$  while the SWC ranged from  $4.28 \pm 0.54 \text{ \%vol}$  (July) to  $36.89 \pm 0.95 \text{ \%vol}$  (February). The strong drought is shown by the high difference of the mean SWC of the two years, 27.35 %vol in 2010- 2011 and 17.92 in 2012 %vol.

| 2010-11              | Mean $\pm$ SE    | Min $\pm$ SE    | Max $\pm$ SE     |
|----------------------|------------------|-----------------|------------------|
| <b>R<sub>s</sub></b> | 2.79 $\pm$ 0.056 | 0.88 $\pm$ 0.05 | 6.36 $\pm$ 0.26  |
| <b>T<sub>s</sub></b> | 15.20 $\pm$ 1.04 | 8.18 $\pm$ 0.08 | 22.19 $\pm$ 0.07 |
| <b>SWC</b>           | 27.35 $\pm$ 0.41 | 7.58 $\pm$ 0.16 | 40.97 $\pm$ 0.82 |

Tab. 3.5 - Summary results of soil respiration (R<sub>s</sub>), soil temperature (T<sub>s</sub>) and soil water content (SWC) of the year 2010-2011.

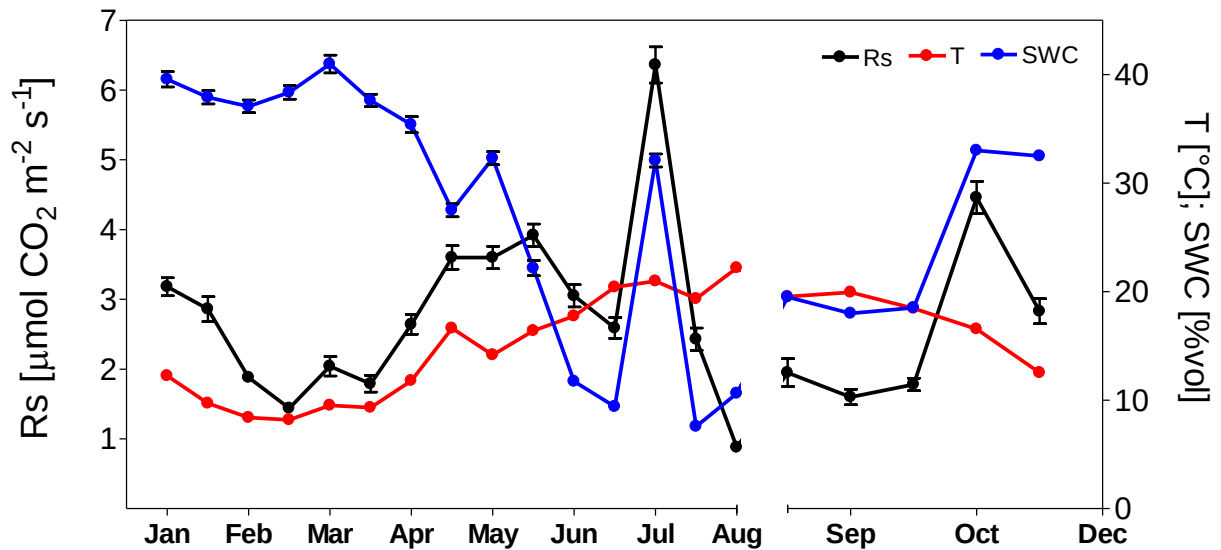


Fig. 3.13 - Seasonal trend of soil respiration, temperature and soil water content from August 2010 to August 2011.

| 2012                 | Mean $\pm$ SE    | Min $\pm$ SE    | Max $\pm$ SE     |
|----------------------|------------------|-----------------|------------------|
| <b>R<sub>s</sub></b> | 2.36 $\pm$ 0.30  | 0.88 $\pm$ 0.05 | 6.36 $\pm$ 0.26  |
| <b>T<sub>s</sub></b> | 16.88 $\pm$ 1.44 | 8.18 $\pm$ 0.08 | 22.19 $\pm$ 0.07 |
| <b>SWC</b>           | 17.92 $\pm$ 2.28 | 4.28 $\pm$ 0.54 | 36.89 $\pm$ 0.95 |

Tab. 3.6 - Summary results of soil respiration (R<sub>s</sub>), soil temperature (T<sub>s</sub>) and soil water content (SWC) of the year 2012.

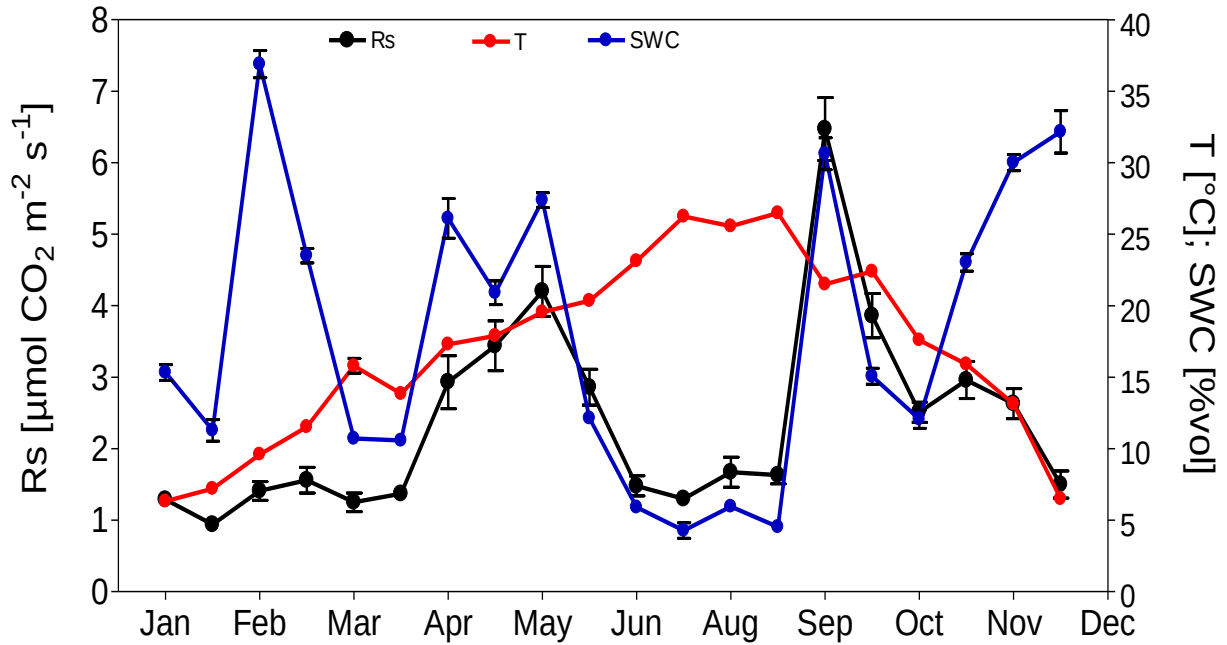


Fig. 3.14 - Seasonal trend of soil respiration, temperature and soil water content from January to December 2012

### 3.2.2 Effect of environmental factors on soil respiration

Seasonal variation in soil respiration rates was partially explained by soil temperature. The best fit between  $R_s$  and  $T_s$  was found by binning the data for different values of SWC and the thresholds of  $0.20 \text{ m}^3 \text{ m}^{-3}$  and  $0.18 \text{ m}^3 \text{ m}^{-3}$  were found for the first and the second year respectively. Temperature was the main controlling factor over  $R_s$  during most of the two years, when volumetric soil water content was not limiting. The data of the no drought period resulted in a good relationship between temperature and soil respiration, with  $R^2 = 0.58$  (Fig. 3.15a) and  $R^2 = 0.73$  (Fig. 3.15b).

Excluding the drought-affected data, the temperature sensitivity represented as “apparent”  $Q_{10}$  values (Eric A Davidson & Janssens, 2006) were similar in both years, 2.46 on 2010 -2011 and 2.22 on 2012. No clear relationship were found with the solely SWC, during the drought.

From June to December 2012,  $R_s$  was measured every two weeks, 5 times per day. The daily variation of soil respiration, was studied in relation to the soil temperature at 5 cm depth and not

significantly differences were found between the average values of all plots measured five per day. The small daily range in soil temperature may justify this low variability.

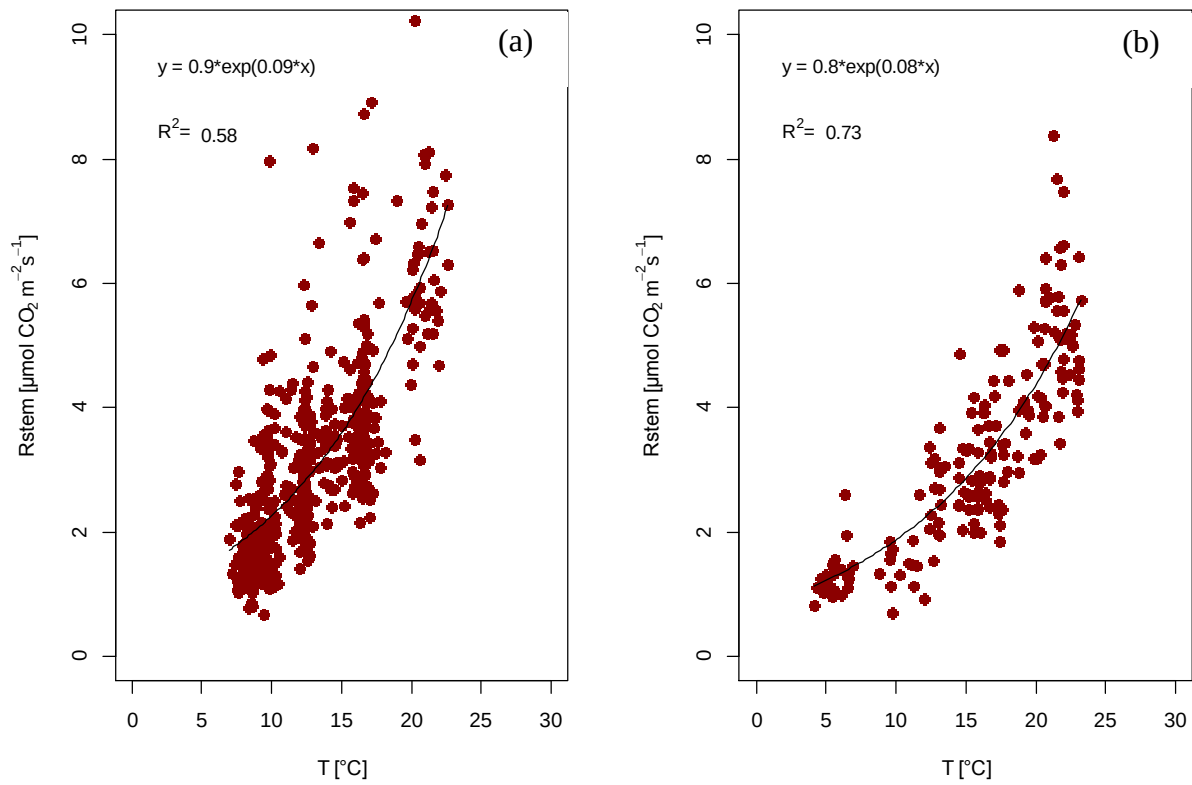


**Fig. 3.15 - CO<sub>2</sub> efflux from the soil (Rs) in dependence of the temperature (T) at 5 cm depth. (a) Rs from August 2010 to August 2011; (b) Rs from January to December 2012. Because of the drought, the data were filtered for a threshold of volumetric soil moisture of 0.20 m<sup>3</sup> m<sup>-3</sup> in the first year and of 18 m<sup>3</sup> m<sup>-3</sup> in the second one.**

### 3.2.3 Spatial variability

During the year 2010 – 2011 we measured Rs in 8 plots on 40 collars. Not statistically significant differences were observed on the average values of Rs between the plots (One-way Anova Analysis). A different result was obtained comparing the annual mean of each collar: by the one-way analysis of variance; a  $p$ -value  $< 0.0001$  was found and, by a Tukey's Multiple Comparison Test, 55 pairs were found significantly different. The difference ranged from -3.35 to 3.12  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  with an average equal to 0.50  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (Fig. 3.16).

Significant seasonal spatial variability in Rs, along the 8 plots measured, was observed but didn't strictly followed the general seasonal trend of mean Rs: decreasing throughout the winter,

increasing with the onset of the summer months. The largest degree of variability, indicated by the coefficient of variation (%CV) was observed in August 2010 (42%) but an opposite situation was found August 2011 (22%). The minimum degree of spatial variability was observed during winter, on December 2010 (16%).

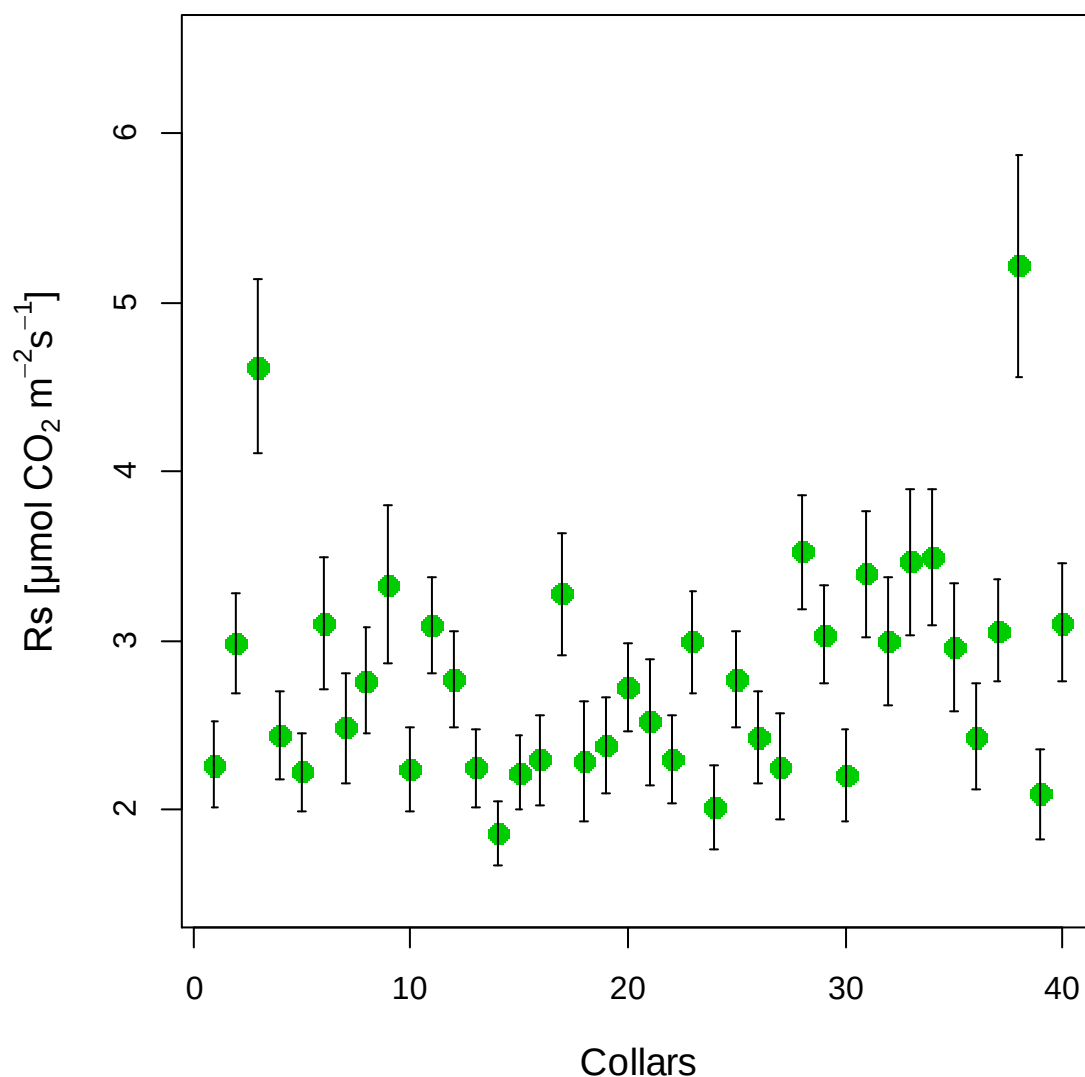


Fig. 3.16 – Annual mean of soil respiration of the 40 points of measurements. The bars indicate the standard error.

### 3.2.4 Scaling-up and model validation of $R_s$

The model (Eqn. 2.3) used to scale-up the chamber measurements of the year 2012 fits the data well but did not correctly simulated the temporal variation in soil CO<sub>2</sub> efflux during Spring and

Winter. Comparing the data estimated by the model with the data measured, a correlation coefficient equal to 0.75 was found (Fig. 3.17). The measures of mean absolute errors (MAE), mean absolute percentage errors (MAPE), root mean square errors (RMSE) and coefficient of correlation ( $R^2$ ) were used to express quantitatively the deviation between model predictions and observations for the year 2012 (Tab. 3.7). The modeled  $R_s$  plotted with measured data (Fig. 3.18) show a clear underestimation of the values corresponding to the period from December to January and an overestimation of the values corresponding to the period from March to June.

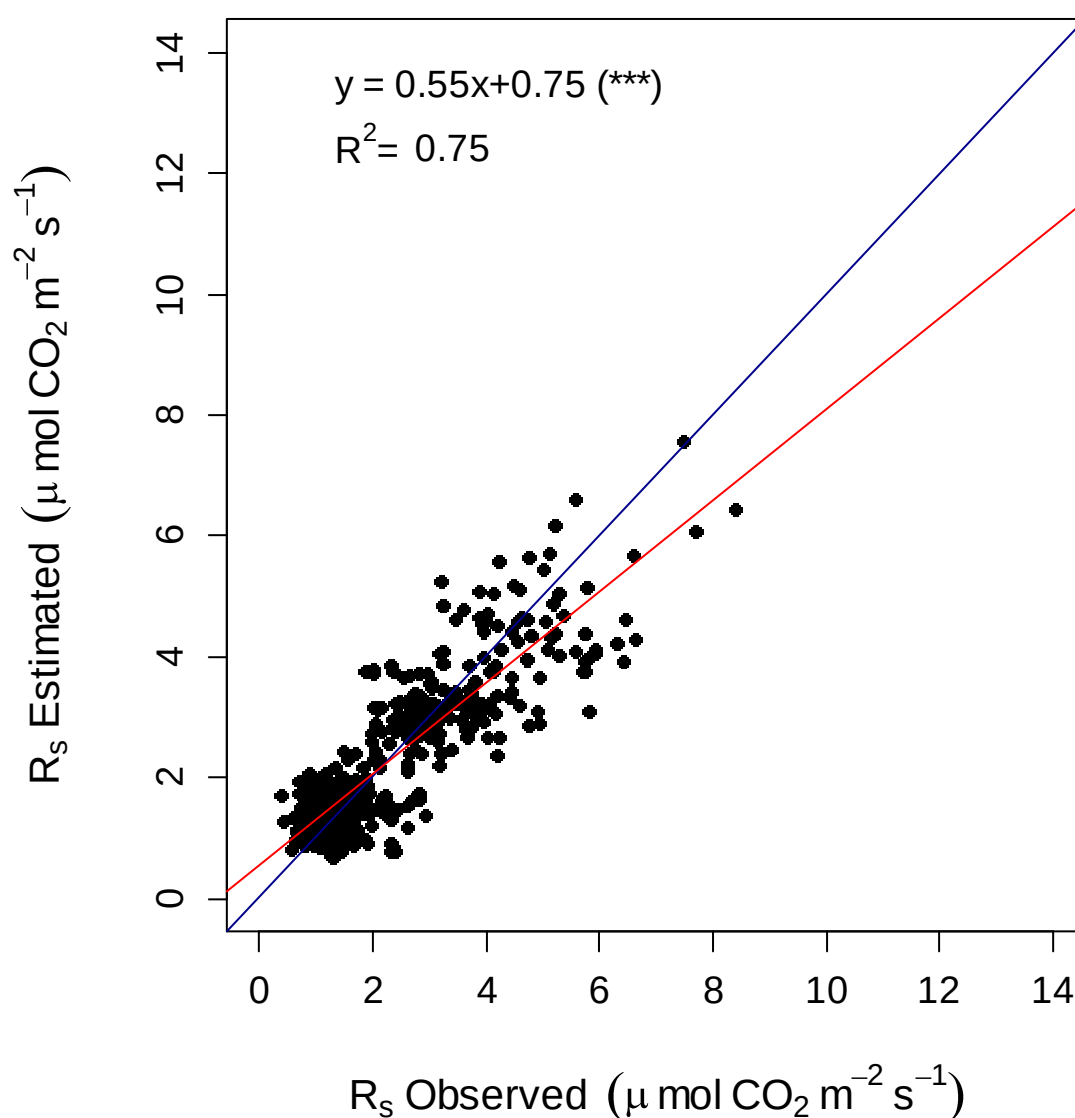


**Fig. 3.17 – Comparison of model prediction with observed data of soil respiration. The model prediction was good and a correlation coefficient equal to 0.75 was found.**

| MAE<br>$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ | MAPE<br>% | RMSE<br>$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ | $R^2$ |
|-----------------------------------------------------------|-----------|------------------------------------------------------------|-------|
| 0.52                                                      | 26.49     | 0.70                                                       | 0.75  |

Tab. 3.7 – Quantification of the deviation between model predictions and observations by MAE, MAPE, RMSE and  $R^2$ .

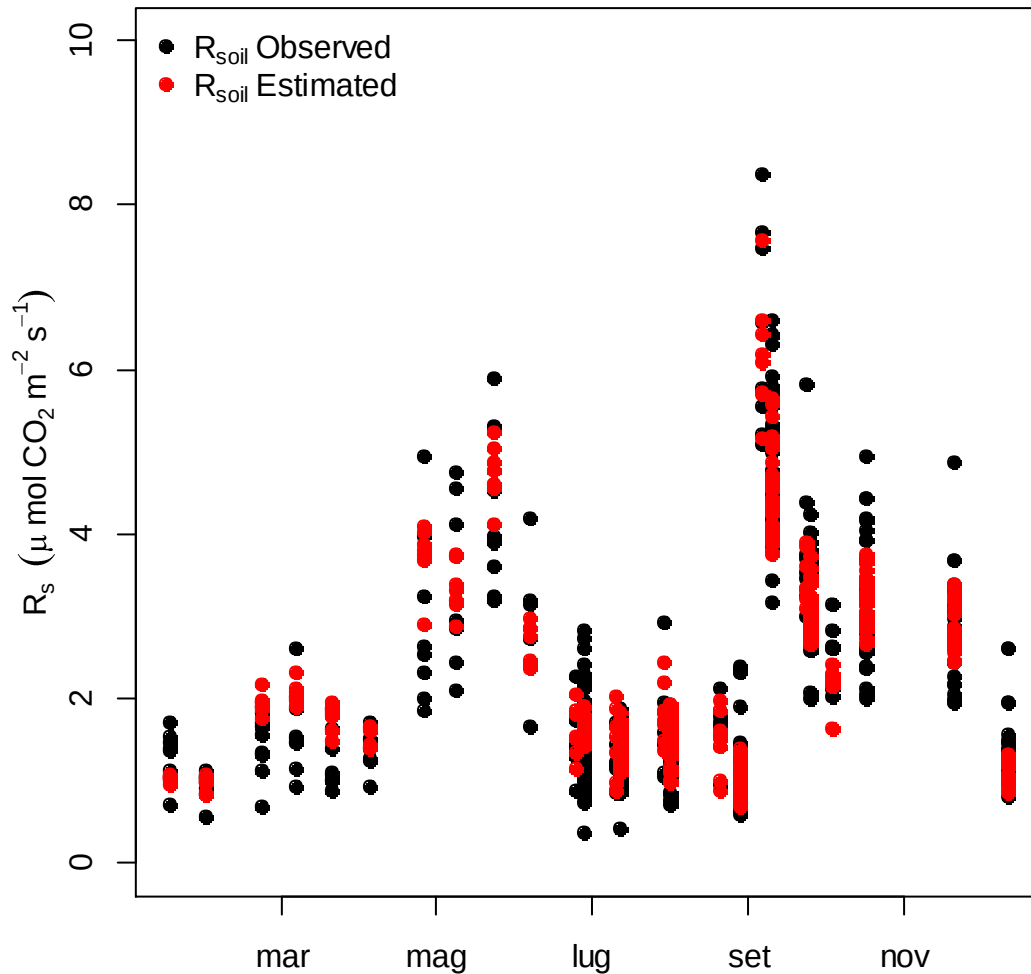


Fig. 3.18 – Differences between predicted and measured data shows a general underestimation of the values corresponding to the period from December to January and an overestimation of the values corresponding to the spring.

$K$ -fold cross validation was used to evaluate the performance measures on the data set which is different or independent from the data set used for calibrating the model. Based on up-scaled chamber measurements, the cumulate value of the whole year, was  $6.78 \text{ t C ha}^{-1} \text{ y}^{-1}$  while the range of the cumulative estimations obtained by the  $k$ -fold cross validation, varied from  $6.41$  to  $7.33 \text{ t C ha}^{-1} \text{ y}^{-1}$  (Fig. 3.19). The measures of mean absolute errors (MAE), mean absolute

percentage errors (MAPE), root mean square errors (RMSE) and coefficient of correlation ( $R^2$ ) were used to express quantitatively the deviation between model predictions and observations; the results are shown in Tab. 3.8. The resulted uncertainty was equal to 7% of the mean.

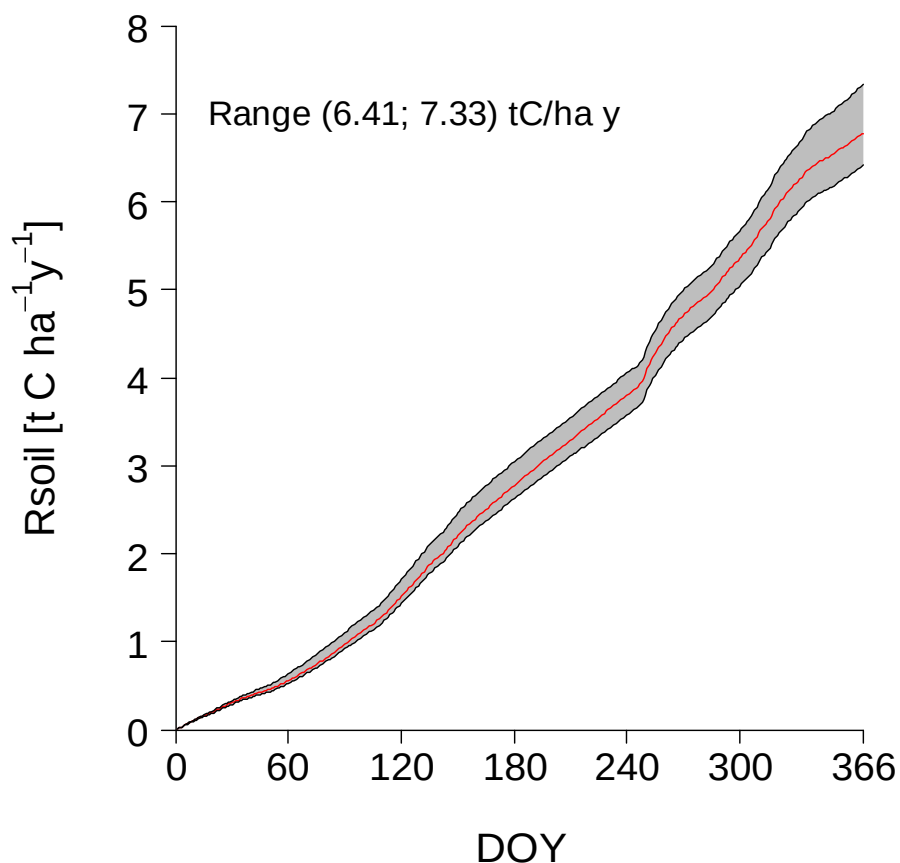


Fig. 3.19 – Cumulates of the up-scaled chamber measurements of the year 2012. Red line represents the cumulate obtained using the whole data set for calibrating the model. The grey area represents the range of the cumulate estimated by  $k$ -fold cross validation analysis.

| $K$ | MAE<br>$\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$ | MAPE<br>% | RMSE<br>$\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$ | $R^2$ |
|-----|-----------------------------------------------------------|-----------|------------------------------------------------------------|-------|
| 1   | 0.98                                                      | 72.68     | 1.08                                                       | 0.52  |
| 2   | 0.47                                                      | 29.47     | 0.56                                                       | 0.86  |
| 3   | 0.56                                                      | 28.54     | 0.69                                                       | 0.64  |
| 4   | 0.43                                                      | 25.23     | 0.52                                                       | 0.89  |
| 5   | 0.37                                                      | 15.21     | 0.52                                                       | 0.83  |
| 6   | 0.41                                                      | 22.21     | 0.48                                                       | 0.88  |
| 7   | 0.72                                                      | 21.86     | 1.02                                                       | 0.80  |
| 8   | 0.99                                                      | 27.26     | 1.29                                                       | 0.80  |

Tab. 3.8 – Quantification of the deviation between model predictions and observations by MAE, MAPE, RMSE and  $R^2$ , of the different  $k$  estimations.

Not statistically significant differences were observed on the average values of  $R_s$  between the plots (One-way Anova Analysis). It was also investigated indirectly by the an unusual  $k$ -fold cross validation with the training set smaller than the test set. The cross validation with a training set of 5 collars (1 plot) for the year 2011 was performed as to simulate a sample similar to the one measured in 2012 (8 collars in a transect). The estimation of the test set (35 collars) gave an uncertainty higher than the previous  $k$ -fold cross validation (errors are showed in Tab. 3.9) with a variability of 13.2% respect the mean.

By bootstrap analysis was verified that increasing the sample size for the estimation of the model parameters, the variability of the estimation of the total annual  $R_s$  decreases. The quantification of the variability shifts from 8.8 to 1.05 t C ha<sup>-1</sup> y<sup>-1</sup>. In Fig. 3.21, each box plot represents the distribution of the sample of 200 total respiration estimated from 200 bootstrap samples for the growing number of collars.

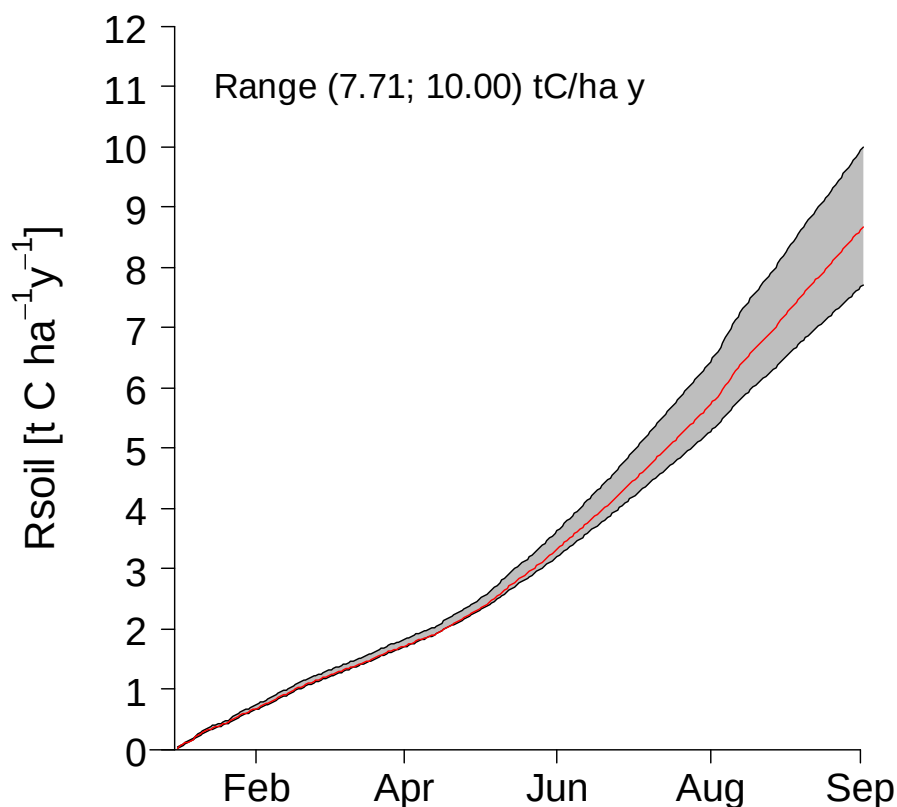


**Fig. 3.20** – Cumulates of the up-scaled chamber measurements of the year 2011 on 40 collars. Red line represents the cumulate obtained using the whole data set for calibrating the model. The grey area represents the range of the cumulate estimated by  $k$ -fold cross validation analysis ( $k = 8$ ; train set = 5 collars and test set = 35 collars)

| $K$ | MAE<br>$\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$ | MAPE<br>% | RMSE<br>$\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$ | $R^2$ |
|-----|-----------------------------------------------------------|-----------|------------------------------------------------------------|-------|
| 1   | 0.92                                                      | 49.89     | 1.19                                                       | 0.48  |
| 2   | 0.88                                                      | 41.10     | 1.20                                                       | 0.43  |
| 3   | 0.83                                                      | 36.03     | 1.21                                                       | 0.46  |
| 4   | 0.85                                                      | 37.87     | 1.23                                                       | 0.39  |
| 5   | 0.84                                                      | 36.50     | 1.22                                                       | 0.45  |
| 6   | 0.94                                                      | 41.92     | 1.44                                                       | 0.22  |
| 7   | 0.97                                                      | 49.92     | 1.30                                                       | 0.39  |

Tab. 3.9 - Quantification of the deviation between model predictions and observations by MAE, MAPE, RMSE and  $R^2$ , of the different  $k$  estimations.

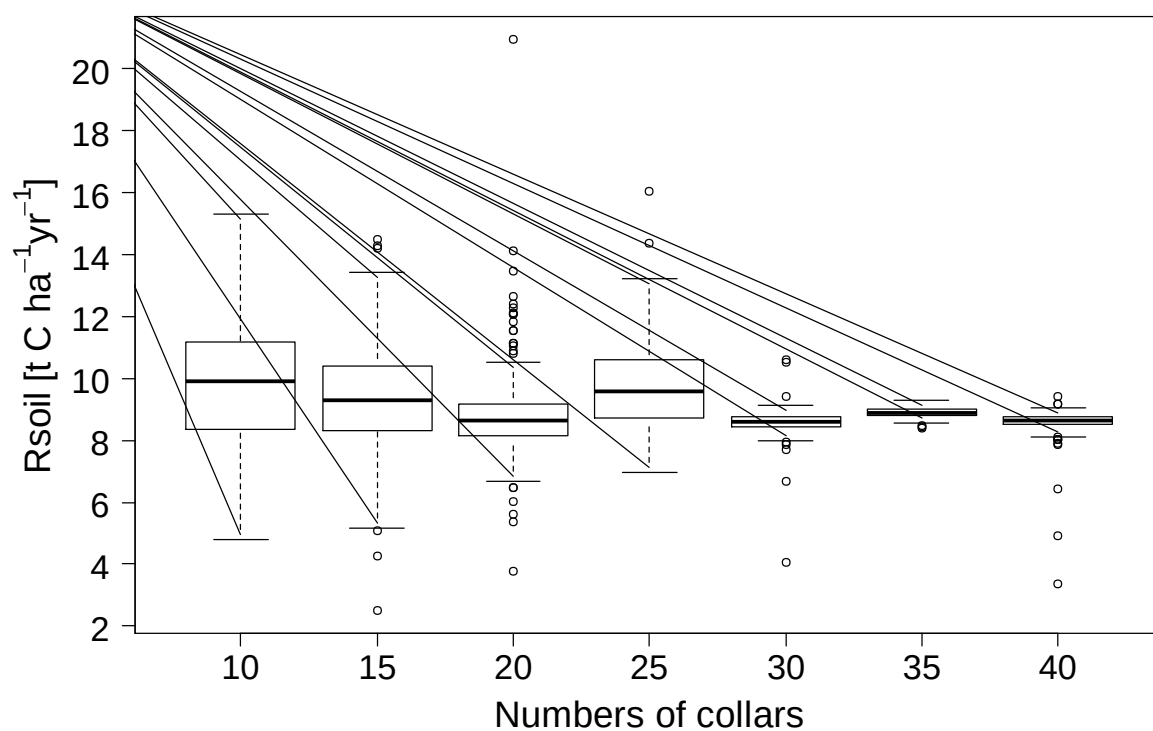


Fig. 3.21 – Median, quartiles, and data range of cumulated soil respiration, are represented in box and whisker plots as a function of sample size. The estimated total soil respiration were calculated by estimating the model parameters 200 times after bootstrap resampling of each dataset with different sample size.

### 3.3 Leaf respiration

For the four measurement periods (June, July, August and September), the rates of leaf dark respiration ( $R_l$ ) at ambient temperature (Fig. 3.22) show no significant differences (One-way analysis of variance,  $p$ -value  $> 0.05$ ). The average value of dark respiration  $\pm$  SE of the growing season was equal to  $1.32 \pm 0.10 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and ranged from the minimum of  $0.13 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in July, to the maximum of  $3.00 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in August.

The mean respiration rate  $\pm$  SE, measured at ambient temperatures, at pre-dawn and after sunset, was equal to  $2.07 \pm 0.14 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and  $1.05 \pm 0.09 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , respectively. The two fluxes varied markedly, through time and between the moments of the day.  $R_l$  at pre-dawn was significantly higher than  $R_l$  after sunset ( $t$ -test;  $p$ -value  $< 0.001$ ) but the two rates of respiratory  $\text{CO}_2$  release show a similar trend, increasing from July to August and decreasing in September following the same trend of the air temperature (Fig. 3.23). This year the typical summer drought of the Mediterranean ecosystems was absent.

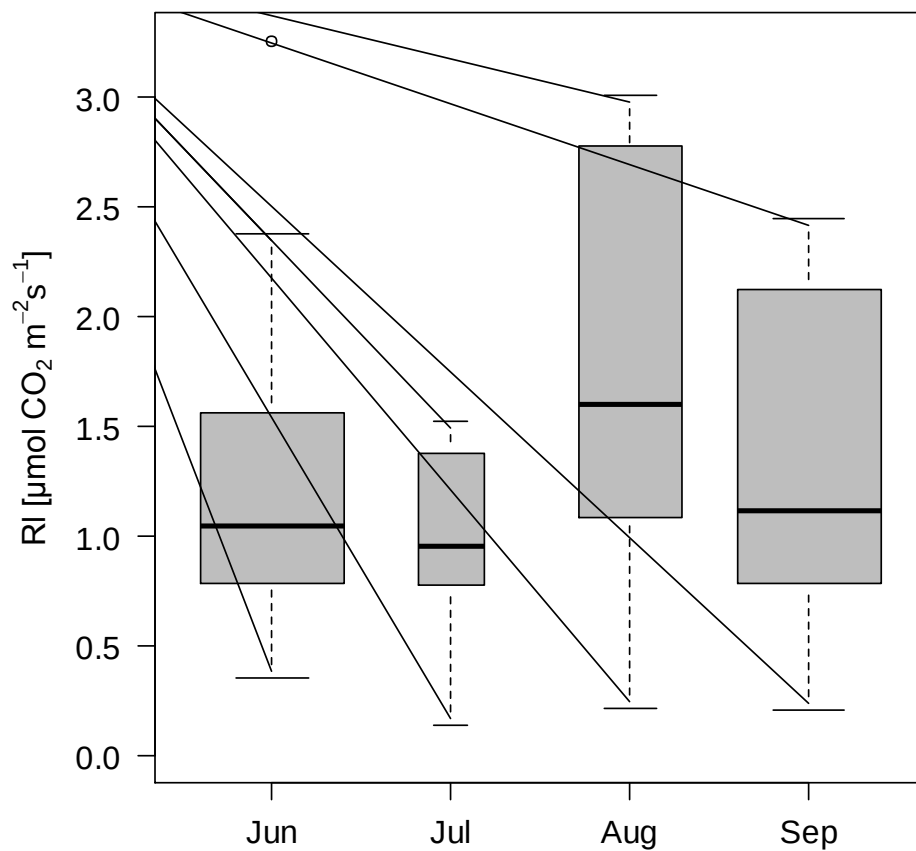


Fig. 3.22 – Leaf respiration rate of the growing season at ambient temperature. The width of the box represents the sample size.

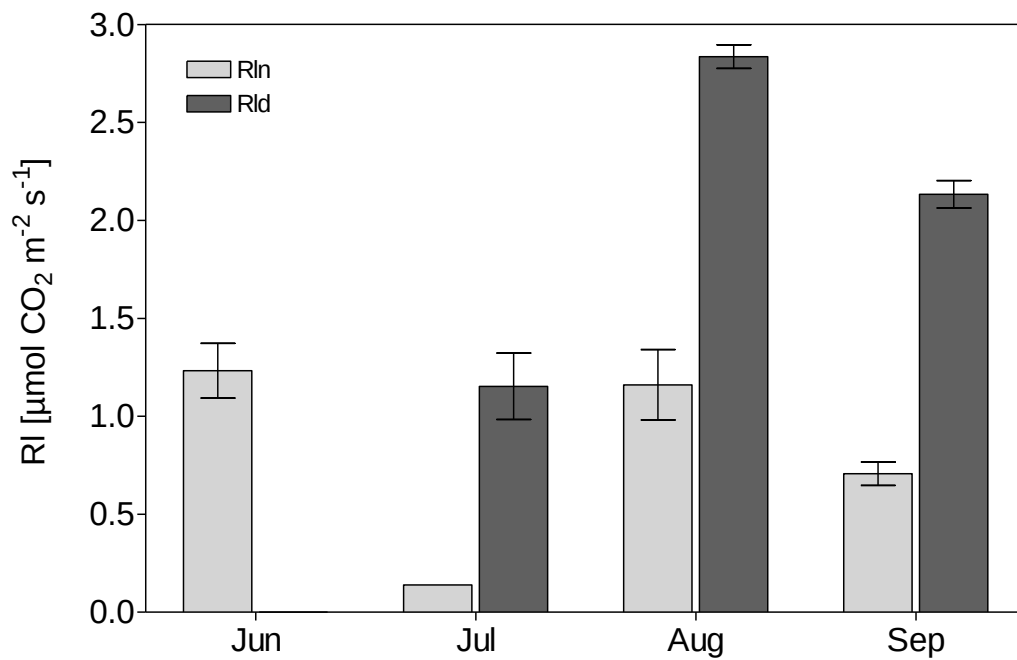
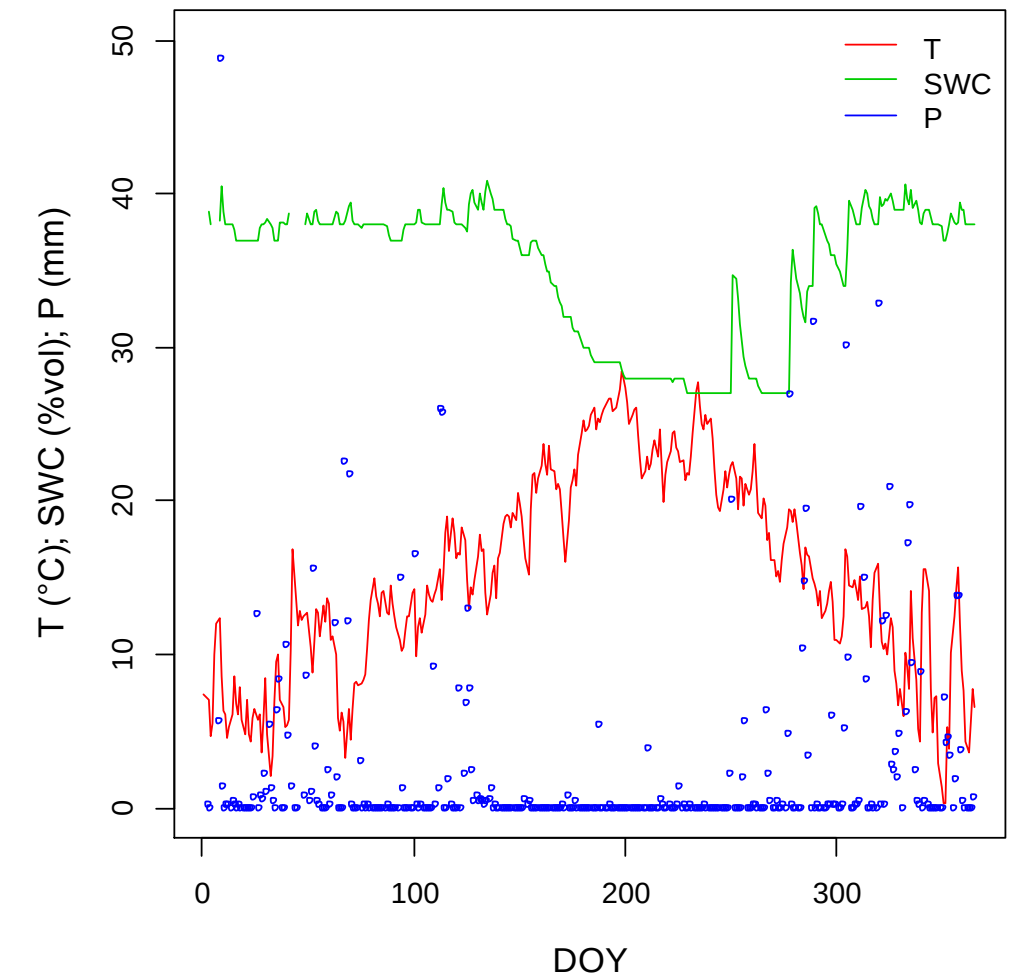


Fig. 3.23 – On the top, the meteorological variables in 2010. Below, mean respiration rate, measured at ambient temperatures, at pre-dawn and after sunset. The bars represent the standard error. The respiration rate at pre-dawn (Rld) was significantly higher than the respiration rate after sunset (Rln) (*t*-test; *p*-value < 0.001).

The leaf dark respiration was driven primarily by air temperature.  $R_l$  as a function of air temperature, for each month, reported in Fig. 3.24, shows that the sensitivity to temperature was lower in September than the others months, while in July and August the slope was similar. In Tab. 3.10 are reported the values of the estimated parameters ( $a$ ;  $k$ ), of the coefficient of correlation ( $r^2$ ) and of the  $Q_{10}$ . On average, leaf respiration rate measured at the standard temperature of 20 °C was  $1.19 \pm 0.09 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and the apparent  $Q_{10}$  was 1.27.

$R_{l20}$ ,  $Q_{10}$  and LAI varied during the growing season and the estimation of carbon released via  $R_l$  integrated for the whole canopy was  $4.74 \text{ t C ha}^{-1} \text{ y}^{-1}$  and the foliage  $\text{CO}_2$  efflux rate was bell shaped with some little inflections on summer (Fig. 3.25).

|            | <b>a</b> | <b>k</b> | <b><math>r^2</math></b> | <b><math>Q_{10}</math></b> |
|------------|----------|----------|-------------------------|----------------------------|
| <b>Jul</b> | 0.21     | 0.06     | 0.94                    | 1.86                       |
| <b>Aug</b> | 0.51     | 0.04     | 0.95                    | 1.61                       |
| <b>Sep</b> | 1.28     | 0.001    | 0.27                    | 1.01                       |

Tab. 3.10 -  $R_l$  as a function of air temperature. Values of the estimated parameters ( $a$ ;  $k$ ), of the coefficient of correlation ( $r^2$ ) and of the  $Q_{10}$

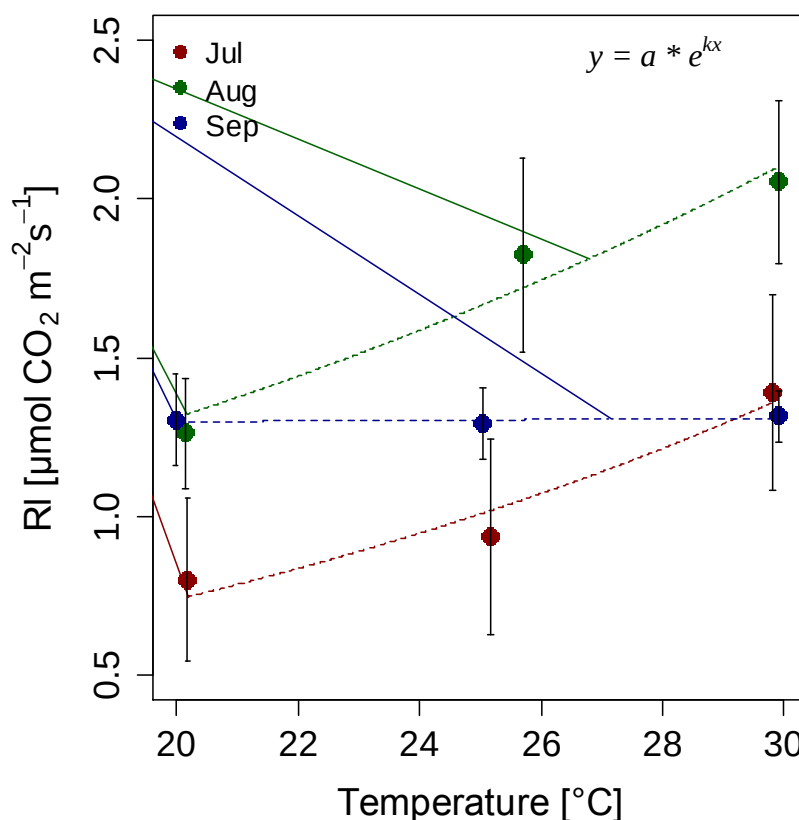


Fig. 3.24 – Leaf dark respiration as a function of air temperature. The bars represent the standard error.

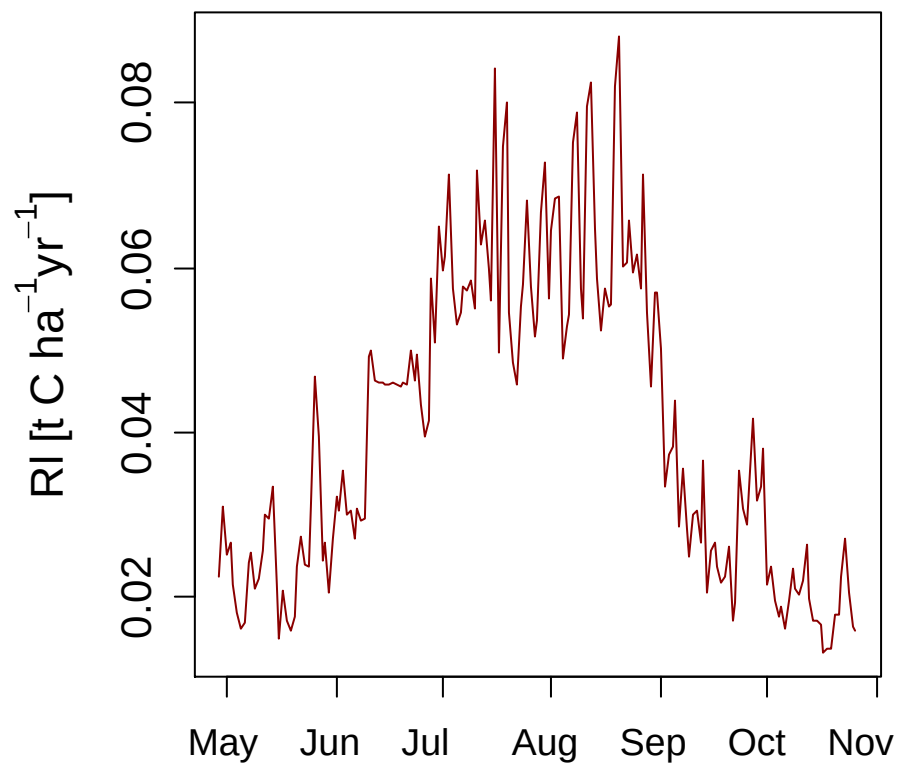


**Fig. 3.25 - Estimation of carbon released via  $R_i$  integrated for the whole canopy.**

## 3.4 Ecosystem respiration

### 3.4.1 Ecosystem respiration from up-scaled chamber measurements

Based on up-scaled chamber measurements, Reco showed a significant temporal variation over the study period.  $R_s$  and  $R_{stem}$  followed the same trend, increasing from winter to spring, decreasing in summer and increasing again in autumn. A different situation is showed by leaf respiration that increased in spring, peaked in August and decreased in autumn (Fig. 3.28). Leaf respiration was higher than the sum of stem and soil respiration in June, July, and August. Total ecosystem respiration from up-scaled chamber measurements, was  $13.31 \text{ t ha}^{-1} \text{ y}^{-1}$  in 2012. Cumulative stem  $\text{CO}_2$  efflux, soil respiration and leaf respiration were 1.77, 6.79 and  $4.74 \text{ t ha}^{-1} \text{ y}^{-1}$  respectively, accounting for 13%, 51% and 36% of total ecosystem respiration. In Tab. 3.11 are shown the percentages of the components of ecosystem respiration during the seasons.  $R_s$  was almost always the component that contributes most to the total flux of respiration, except in summer when the main contribution is given by the respiration of leaves.

|               | Soil % | Stem % | Leaf % |
|---------------|--------|--------|--------|
| <b>Winter</b> | 84     | 17     | 0      |
| <b>Spring</b> | 48     | 13     | 39     |
| <b>Summer</b> | 31     | 12     | 57     |
| <b>Autumn</b> | 48     | 13     | 39     |

Tab. 3.11 – Percentage contribution of each component to the total ecosystem respiration in the different seasons of 2012.

### 3.4.2 Eddy covariance ecosystem respiration

Fig. 3.26 shows the seasonal patterns of daily mean Reco, NEE (Net Ecosystem Exchange) and GPP (Gross Primary Production) from January to December 2012. As is typical in Mediterranean ecosystems, seasonal changes in Reco were characterized by small fluxes in winter and summer and large fluxes in spring and in autumn, after rain events. Reco peaked in

May,  $5.10 \text{ g C m}^{-2} \text{ d}^{-1}$  (DOY 142), and the minimum was reached at the end of June with  $0.41 \text{ g C m}^{-2} \text{ d}^{-1}$  (DOY 177). The annual average of Reco was  $2.27 \text{ g C m}^{-2} \text{ d}^{-1}$ .

Net Ecosystem Exchange (NEE), was partitioned with two different methods (Lasslop et al., 2010; Reichstein et al., 2005) and the cumulative annual totals of  $9.11$  and  $6.98 \text{ t ha}^{-1} \text{ y}^{-1}$  were estimated respectively, in 2012.

Concerning the Reco estimation, a source of uncertainty was evaluated due to the  $u^*$  filtering and the resulted range of cumulative annual respiration varied from  $5.38$  to  $9.44 \text{ t ha}^{-1} \text{ y}^{-1}$  for the method of Reichstein 2005 (Fig. 3.27a) and from  $5.88$  to  $12.08 \text{ t ha}^{-1} \text{ y}^{-1}$  for the method of Lasslop 2010 (Fig. 3.27b).

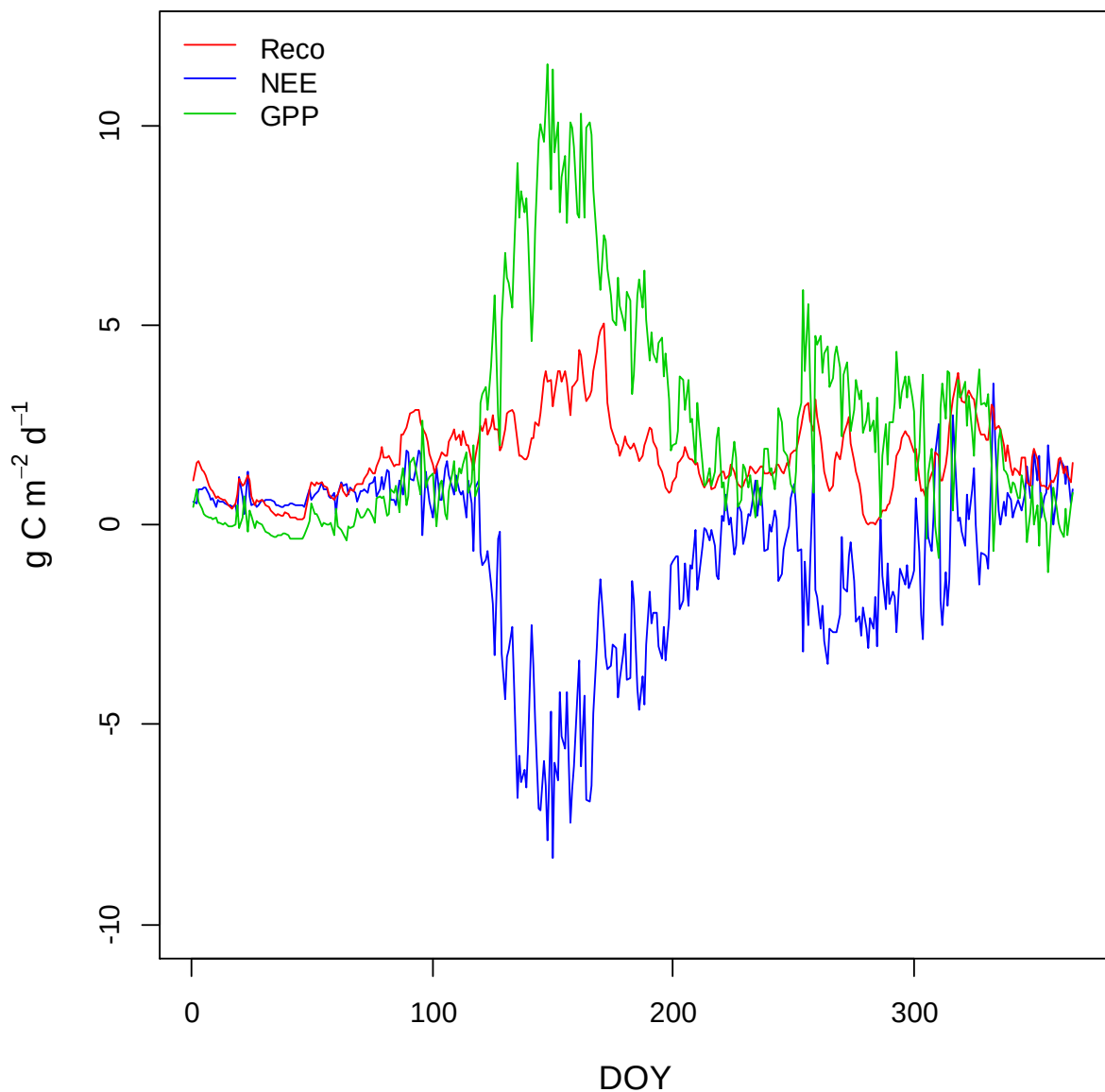


**Fig. 3.26 – Seasonal trend of Reco, NEE and GPP in 2012. Is evident the crucial role of the strong aridity that occurred in summer, on these fluxes, with a clear reduction from mid-July to mid-September.**

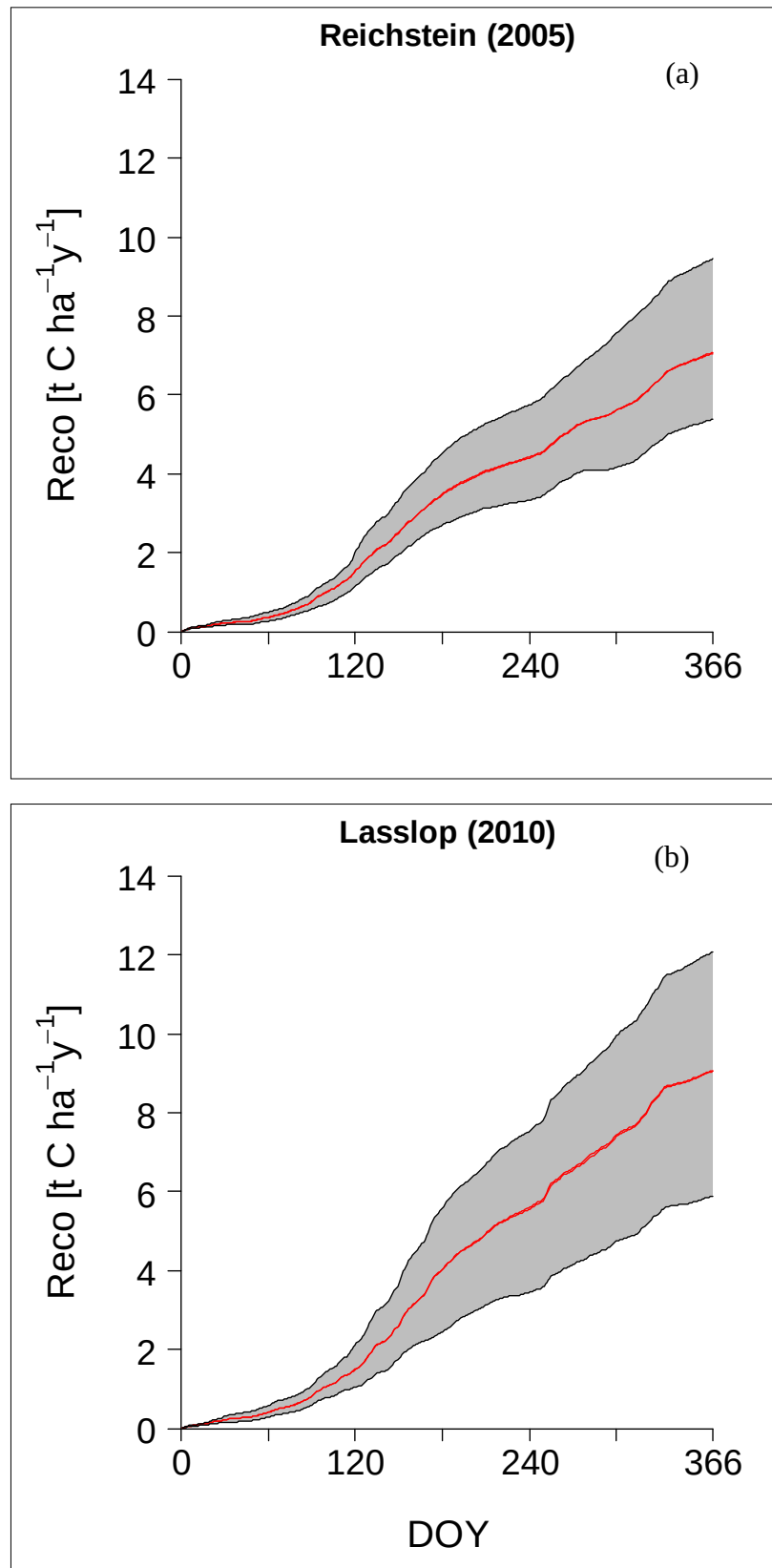


Fig. 3.27 - Cumulative annual ecosystem respiration estimated by the method described in Reichstein 2005 (a) and by the method described in Lasslop 2010. Red line represents the cumulate curve of respiration calculated from the reference NEE. The grey area represents the range of cumulative annual respiration calculated starting from forty  $u^*$  thresholds.

### 3.4.3 Comparison of $\text{Reco}_{\text{cuv}}$ with $\text{Reco}_{\text{eddy}}$

Eddy covariance flux data followed similar variations during winter to those produced by the summed chamber-based method. A different situation occurred during the growing season, mostly due to leaf respiration. Up-scaled  $R_l$  peaked in August when  $\text{Reco}_{\text{eddy}}$  reached the minimum of the period. If are considered only  $R_s$  and  $R_{\text{stem}}$  the trend of the two components is similar to that of  $\text{Reco}_{\text{eddy}}$ , with lower fluxes of respiration in winter and summer and the greater fluxes in spring and autumn. However the increase in respiration as the season developed, was much greater for the chamber estimate than the eddy covariance estimate (Fig. 3.28). There was a significant correlation between the chamber and eddy covariance flux estimates for the entire period with  $R^2 = 0.54$  and  $p\text{-value} < 0.01$  (Fig. 3.29a). The  $R^2$  value increases significantly ( $R^2 = 0.97$  and  $p\text{-value} < 0.001$ ) if solely the winter period is considered (Fig. 3.29b), while a completely opposite situation occurs during the growth period ( $R^2 = 0.08$ ) (Fig. 3.29c). In the growing season, chamber estimate fluxes had values 38% higher than estimates obtained from the eddy covariance method, while in winter chamber estimates were 12% higher.

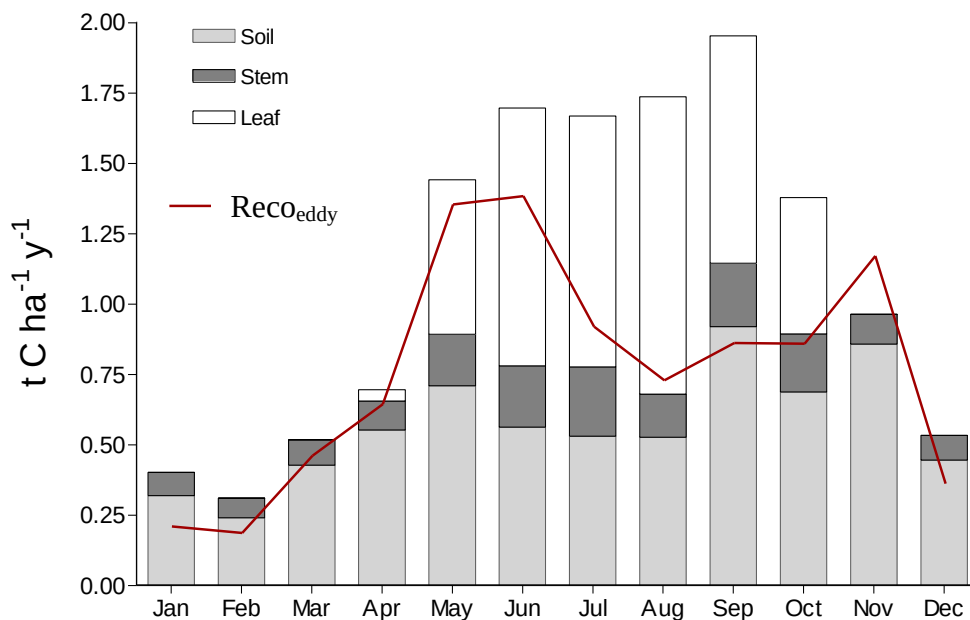


Fig. 3.28 – Estimated monthly  $R_s$  (light grey bars),  $R_{\text{stem}}$  (dark grey bars) and  $R_l$  (white bars) in 2012. The red line is the total  $\text{Reco}_{\text{eddy}}$  of the same period.

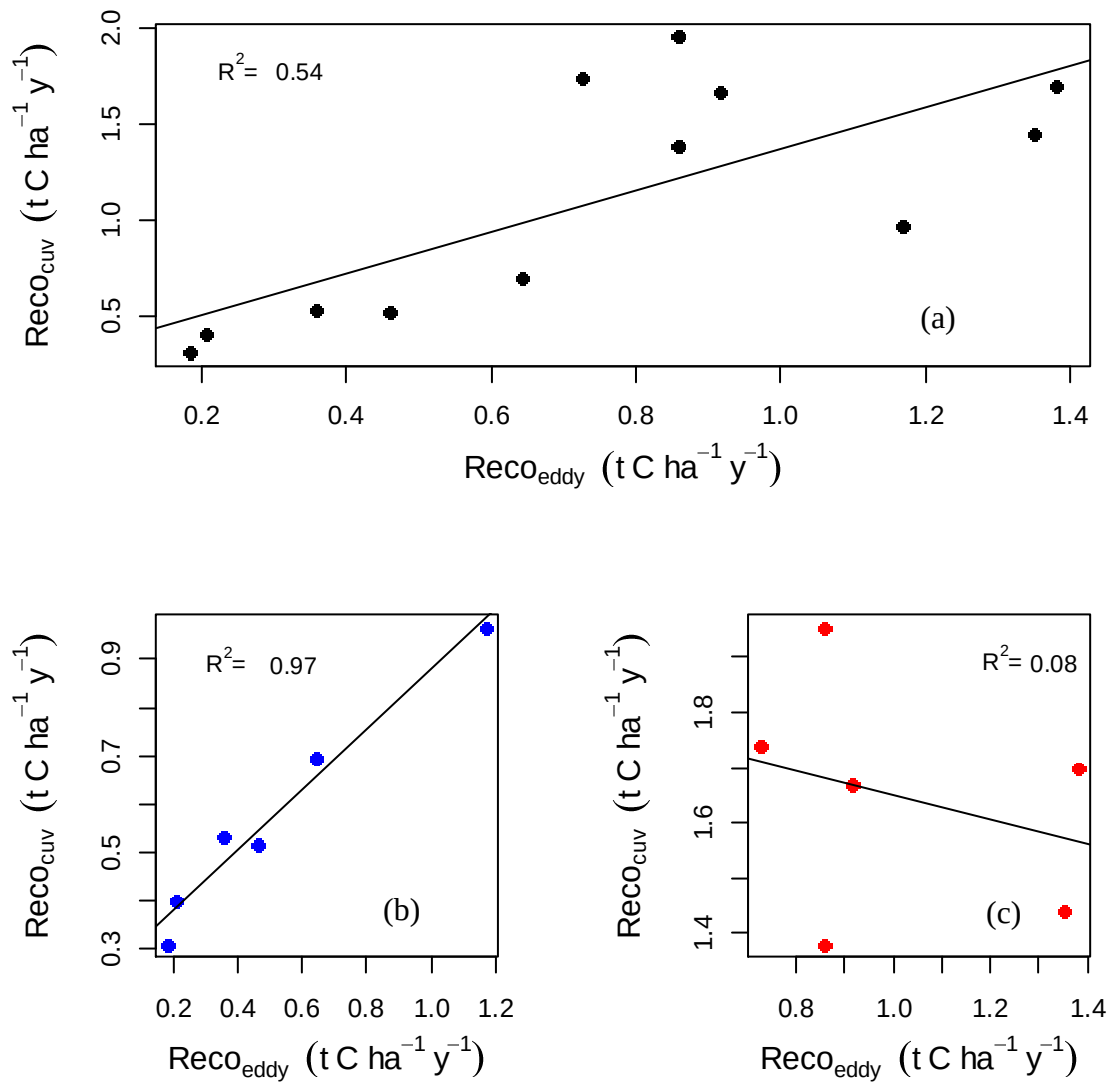


**Fig. 3.29 – (a) Total Reco estimated by the sum of  $R_s$ ,  $R_{\text{stem}}$  and  $R_l$ , in comparison with total  $\text{Reco}_{\text{eddy}}$ , of the entire year. Data comparison of the winter period (b) and of the growing period (c) of the same year.**

An uncertainty assessment of the estimations of  $\text{Reco}_{\text{eddy}}$  and  $R_s - R_{\text{stem}}$  was made and the results are summarized in

Fig. 3.30. Considering every source of uncertainty the range of variation of the resulting estimations is very high. Regarding the eddy covariance Reco estimation, the range starts from a minimum value of  $4.3 \text{ t C ha}^{-1} \text{ y}^{-1}$  to a maximum of  $12.1 \text{ t C ha}^{-1} \text{ y}^{-1}$  with the mean  $\pm$  SD equal to  $8.03 \pm 1.74 \text{ t C ha}^{-1} \text{ y}^{-1}$ . The summarized uncertainty of  $R_s$  and  $R_{\text{st}}$ , derived from  $k$ -fold cross validation was (mean  $\pm$  SD)  $8.74 \pm 0.33 \text{ t C ha}^{-1} \text{ y}^{-1}$  and the one due to prediction (RSME) was

$8.53 \pm 5.46 \text{ t C ha}^{-1} \text{ y}^{-1}$ . The estimated errors may lead to both underestimation and overestimation higher than 50%.

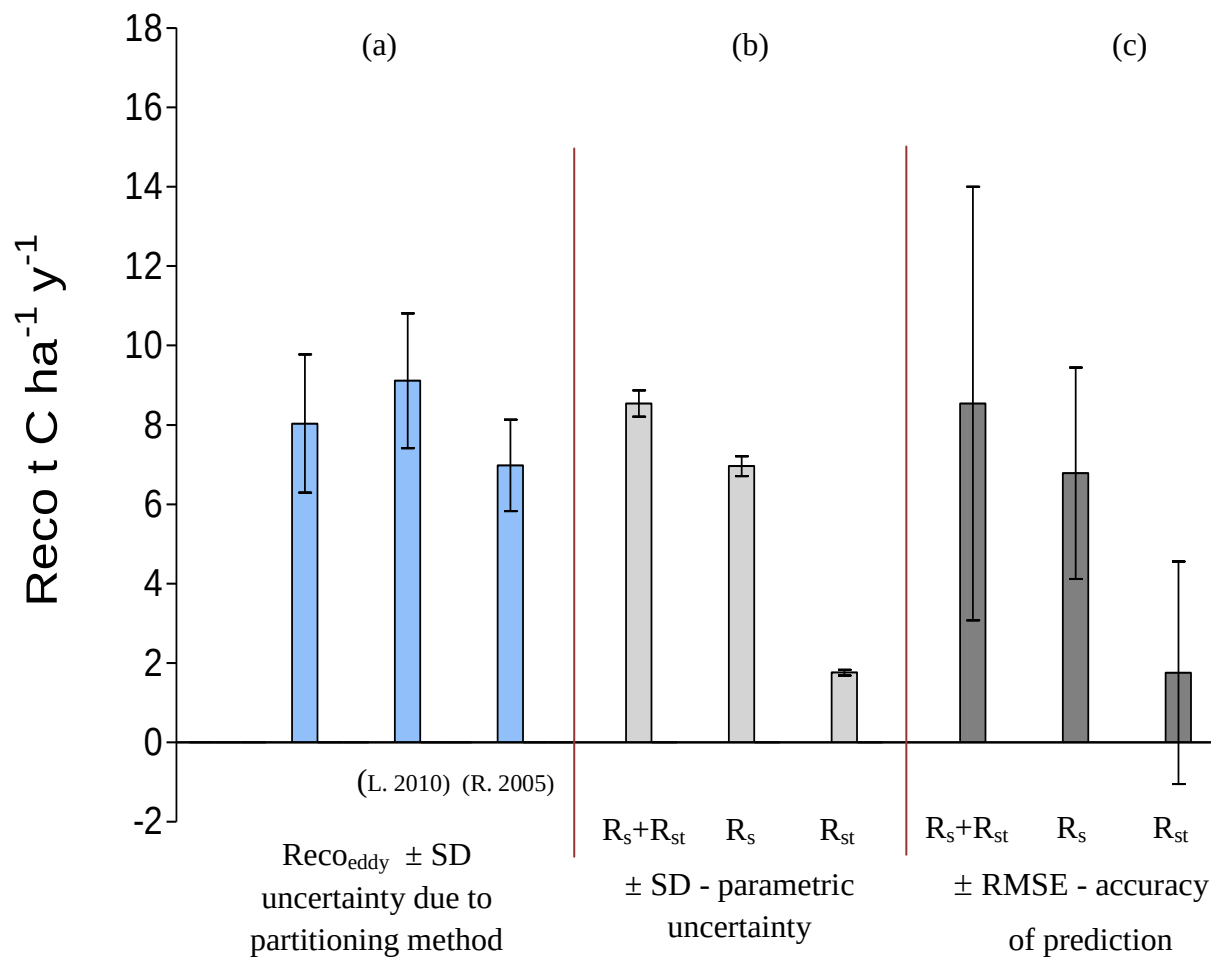


**Fig. 3.30 – Summarization of the total uncertainty due to the partitioning method for  $\text{Reco}_{\text{eddy}}$  (a) and due to the parametric uncertainty estimated by  $k$ -fold cross validation (b) and due to the accuracy of the model prediction (c) for  $R_s$  and  $R_{\text{stem}}$ .**



## **4. Discussion**



## 4.1 Stem CO<sub>2</sub> efflux

Daily stem CO<sub>2</sub> efflux at the breast height changed in response to the temperature of the stem surface, with the highest rates corresponding to the hotter hours of the day.

The exponential relationship between respiration and temperature reflects the importance as a factor regulating respiration. Stem CO<sub>2</sub> efflux measurements using the chamber-based method indicate that diurnal fluctuations were very small in the winter and summer periods while, were high in April, June and September. This last result reflects the response to a combination of high temperatures and fast growth that occurred during spring and autumn. In summer the high temperatures were not accompanied by growth because of strong aridity that characterized the year 2012. Because of limited soil water availability the stem growth rate may became very low. The reduction in stem CO<sub>2</sub> efflux results from the reduced rates of metabolic activity, which is in turn caused by the decrease in stem water status (Saveyn et al., 2007b).

Zha, et al. (2004) showed that diurnal changes in stem respiration were in response to a combination of temperature and assimilation. The response to temperature, on daily scale, was substantially similar between individuals, but the main difference was expressed in terms of respiration, mostly during spring and autumn. The sample trees were chosen in a large range of diameters (9 - 27 cm) and the different rate of respiration between the sample trees probably reflects the different growth rate of each individual.

The resulted  $R_{\text{stem}}$  for the measurement period is well in the range reported for temperate forest trees in China (Wang et al., 2010) but the range is larger than the one found by Yang et al. (2012) in the same site. Total stem respiration varied throughout the study period with maximum rates during spring and minimum rate during winter.  $R_{\text{stem}}$  decreased from spring to summer until the beginning of September. During spring the tree growth rate is high and growth respiration is the dominant contributor to total stem respiration (Stockfors & Linder, 1998). Growth processes are very sensitive to drought stress (Hsiao, 1973) and so very probably depend on the dynamics of the water status in the living stem tissues (Saveyn et al., 2007). During summer the reduction of stem CO<sub>2</sub> efflux is really high but as indicate in Saveyn et al. (2007), in contrast with growth, maintenance metabolism always occurs, even under stress conditions. Saveyn et al. (2007) in this study on daytime CO<sub>2</sub> efflux rates of young beech and oak stems, demonstrates that the loss of turgor in the living stem tissues is quantitatively consistent with the slowing, or even cessation, of growth processes in these tissues. However, when conditions become more favorable (e.g. an

enhanced water status in the living stem tissues), the rate of maintenance metabolism, and hence the stem CO<sub>2</sub> efflux, will be enhanced. In autumn, after rain events, the conditions for growth were restored, and a new rise in respiration processes occurred with a return at the emission levels, albeit lower, of spring. This increment was probably due to the increase of both maintenance and growth respiration.

In this study, a threshold of GPP was fixed and two different periods were individuated and assimilated to a dormant season (mainly summer and winter when GPP was lower than 2 gC m<sup>-2</sup> d<sup>-1</sup>) and a growing season (mainly spring and autumn when GPP was higher than 2 gC m<sup>-2</sup> d<sup>-1</sup>). The resulted two exponential relationships between R<sub>stem</sub> and T<sub>stem</sub> showed as stem temperature was well correlated with R<sub>stem</sub> during the dormant season but not in the growing season. Stem temperature explained 55% of the variation in R<sub>stem</sub> during the dormant season, but only 38% in the growing season. Among the factors that influence R<sub>stem</sub> during the growing season, but are not present in the dormant season, are growth respiration, which is considered temperature independent (Thornley & Johnson, 1990), the flux of transported CO<sub>2</sub> in xylem sap (Aubrey & Teskey, 2009; Teskey et al., 2008), current photosynthate supply (Wang et al., 2006; Christiane Wittmann & Pfanz, 2008). Zach et al. (2009) found that for trees in tropical montane forest, R<sub>stem</sub> was independent from T<sub>stem</sub> in the wet season, but was well correlated with T<sub>stem</sub> in the dry season. Higher rates of physiological activity in the wet season than the dry season, including higher rates of substrate supply to the stem and xylem sap CO<sub>2</sub> imported via transpiration were individuated as responsible for the seasonal difference. Edwards & Hanson, (1996) measured stem respiration on 56 mature trees of *Quercus spp.* and *Acer rubrum*. In this study, respiration rates during the growing season tracked growth rate increments, except during a drought when growth dropped to zero and respiration increased to its highest rate. Before and after the growing season, respiration rates correlated well with stem temperatures. In other studies were observed different relationships between R<sub>stem</sub> and T<sub>stem</sub> with better relationship in the growing season than in dormant season (Brito et al., 2010; Gruber et al., 2009) and the differences were attributed to different rates of stem diameter growth.

The apparent Q<sub>10</sub> values derived from the measurements performed over time, so including temporal phenological changes, were inside the Q<sub>10</sub> range of the database for R<sub>stem</sub> rates reported in Damesin et al., (2002). Q<sub>10</sub> values estimated by Edwards & Hanson (1996) were 2.4 for two oak species and 1.7 for red maple while, in Saveyn (2007b), the Q<sub>10</sub> value for *Quercus robur* L. was 2.0. For temperate forest trees in China, Wang et al., (2010), found a Q<sub>10</sub> value varied from 1.86 to 2.41 among trees, and Yang et al. (2012) found a Q<sub>10</sub> value ranged from 1.87 to 2.61.

The  $Q_{10}$  values calculated for each plant during the growing season, showed a strong negative relationship with DBH.  $Q_{10}$  decreased, with increasing DBH but the same relationship was not found during the dormant season. The observation that  $Q_{10}$  decreased with increasing tree DBH has been previously reported (Damesin et al., 2002; Kim et al., 2007; Yang et al., 2012; Ceschia et al., 2002). Explanations for this effect include differences in diffusion resistance due to tree size and bark thickness (Hölttä & Kolari, 2009) and differences in the gain and loss of heat energy in small and large trees (Kim et al., 2007). As was expected, the relationship between  $Q_{10}$  and DBH was not found during the dormant season because of the small differences between individuals in stem  $CO_2$  efflux and between the temperature dependence of each one during the dormant season.

Stem  $CO_2$  efflux expressed on a surface basis showed a significant positive relationship with DBH; on the other hand, the relationship was not found if  $R_{\text{stem}}$  was expressed on a volume basis and plotted against the reciprocal of stem diameter ( $D^{-1}$ ). As reported in (Levy & Jarvis, 1998) if sapwood xylem parenchyma cells are a more important source of  $CO_2$ , the volume of wood will be the most important factor and if  $R_{\text{stem}}$  is proportional to volume, then the ratio between  $R_{\text{stem}}$  and surface area is proportional to the ratio between volume and surface area. The relationships found in our study suggest that the flux is volume dependent. This may be because a higher portion of the xylem cells are alive or the cambium and phloem make up a significant part of the stem volume, mainly in the thinnest stems. Several studies (Ryan, 2011; Ryan et al., 1995; Ryan et al., 1994) have found that sapwood volume was the major component in stems of various coniferous species. (Sprugel et al., 1995) reviewed results of  $R_{\text{stem}}$  measurements of trees with diameter from 8 to 41 cm and they state that when construction respiration was absent, phloem and cambium respiration were insignificant compared with sapwood maintenance respiration and concluded that area-averaged rates will not be generally useful.

Many factors may account for the relationship between DBH and  $R_{\text{stem}}$ . As indicate in Teskey et al. (2008) respiring cells of the periderm, phloem, cambium, and rays, all contribute to  $R_{\text{stem}}$ .

In McGuire et al. (2007) and in Moore et al. (2008), a close correlation between DBH and sapwood indices (sapwood area, width, volume, increment, and relative growth rate) indicates that and the proportion of living cells of these tissues changes with tree size. Moore et al. (2008) reported that annual stem diameter increment explained 42–74% of the variation in  $R_{\text{stem}}$  for *P. taeda*. Wang et al. (2010) reported that sapwood area and sapwood width were positively correlated with DBH of seven tree species. In addition, Aubrey & Teskey (2009) found that a large proportion of the  $CO_2$  present in stem xylem sap can originate in the root system. Larger

stems have larger root systems and could potentially transport more CO<sub>2</sub> from their root systems upwards in the xylem into the main stem (Aubrey & Teskey, 2009; Teskey & McGuire, 2007). Several studies indicated that the corticular photosynthesis is generally a factor that influence  $R_{\text{stem}}$ . Photosynthesis rates were generally higher in young stems than in older stems (Wittmann et al., 2001; Wittmann & Pfanz, 2007, 2008; Wittmann et al., 2006). In our study, corticular photosynthesis was excluded by testing the difference between measures made in light conditions and measurements made in dark condition. No difference was found between the two sets of data due to the thickness of the bark of *Quercus cerris* L. trees in a mature coppice at the point of measurement (DBH).

Dividing the data of  $R_{\text{stem}}$  between coppice shoots and standards and observing the seasonal trend of  $R_{\text{stem}}$  calculated on surface basis and on volume basis, differences in the rates of  $R_{\text{stem}}$  were found. If  $R_{\text{stem}}$  was calculated on surface basis, the mean CO<sub>2</sub> efflux rate was significantly higher in standards than in coppice shoots while, analyzing the rate of each day of measurement, the difference was significantly only in summer and autumn. If  $R_{\text{stem}}$  was calculated on volume basis the mean CO<sub>2</sub> efflux rate was significantly higher in coppice shoots than in standards while, analyzing the rate of each day of measurement, the difference was significantly only in spring. In the first case, with  $R_{\text{stem}}$  expressed on surface basis, Edwards & Hanson, (1996) found that during the dormant season, rates of total stem respiration tended to be greater in large trees with thick sapwood but no such trend was observed during the growing season. Standards are larger than coppice shoots and in summer, when the main source of  $R_{\text{stem}}$  is due to maintenance respiration because construction respiration was absent, phloem and cambium respiration were insignificant compared with sapwood maintenance respiration (Sprugel et al, 1995). Thin stems have a high surface/volume ratio, so the volume component of respiration will be relatively small, but at some point as diameter increases, the volume of living cells in the sapwood will surpass that of the cambium and phloem (Levy & Jarvis, 1998). In oak, a ring porous species, trees achieve a large part of the annual radial stem growth (including the entire early wood with large vessels) before leaf expansion in spring (Bréda & Granier, 1996; Dougherty et.al, 1979). In autumn the significantly difference was maintained but it isn't attributable only to the recovery of the plants after rain events, because this phenomena is probably related to the previously discussed about the positive relationship between  $R_{\text{stem}}$  and DBH. In the same date of measurements stem respiration followed the same trend of soil respiration; a sudden increase in soil respiration due to the "birch effect" was registered. CO<sub>2</sub> in the rhizosphere, originating from microbial or root respiration, dissolves in soil water and can be absorbed by roots and

transported into the stem in flowing sap (Teskey et al., 2008). As indicated in Aubrey & Teskey, (2009) and in Teskey & McGuire, (2007), larger stems could potentially transport more CO<sub>2</sub> from their root systems upwards in the xylem into the main stem. In the second case, with R<sub>stem</sub> expressed on volume basis, the major CO<sub>2</sub> efflux from the stems of coppice shoots in spring, may be due to the fact that in the thinnest stems the cambium and phloem make up a significant part of the stem volume (Levy & Jarvis, 1998).

In 2012, a severe period of drought occurred and some immediate consequences were registered during the field campaign of measurements on some plants. Drought induces short term physiological disorders, like decreased carbon and nutrient assimilation, and sometimes even a breakdown of the photosynthetic machinery itself (McDowell, 2011). The damages have to be repaired before normal processes can resume. In the meantime, the amount of stored carbohydrates is reduced and the storage compartments are not fully refilled at the end of the growing season. The tree must allocate existing stored reserves among the demands for repair, maintenance, growth and defense. Any additional demand on already limited reserves may delay, if not inhibit, recovery of the growth potential. Irreversible drought damage leads to organ dysfunction, but it only seldom results in direct and immediate tree decline and mortality (McDowell, 2011). However, physiological disorders increase tree vulnerability to secondary stresses like insect damage (Rouault et al., 2006), frost or another drought. Jenkins & Pallardy (1995) emphasize the role of severe droughts in predisposing trees to eventual death. The implication of drought in oak stand decline was demonstrated in all Central Europe wide (Thomas et al., 2002). Fungi may invade weakened trees (Desprez-Loustau et al., 2006). Such cumulated processes may lead to a decline and eventual death. In our measurements, the high increase of CO<sub>2</sub> efflux from the stem of the suffering plants of *Q. cerris*, registered since the end of August, was probably due to the synergistic action of both attack of parasites of weakness and the attempt to repair of the plant. Moreover, a consequence of drought is the risk of hydraulic failure or desiccation and subsequent cessation of cellular metabolism if the entire water column becomes irreparably cavitated. All these factors have a consequences for carbon uptake by photosynthesis and release by stem and total ecosystem respiration. In a study on *Q. petraea* and *Q. cerris*, Tognetti et al. (1996) found that the higher stem water reserves in Turkey oak, respect to Sessile oak, appeared to ameliorate water deficits under natural conditions, promoting greater water flow and only slightly higher transpiration rates in this species. Lo Gullo et al. (1995) found Turkey oak to be very resistant to cavitation. Vannini & Scarascia Mugnozza (1991) found a positive relationship between water stress and the decline syndrome in *Q. cerris* L.. Symptoms

include dieback of the crown, yellowing of leaves, and the occurrence of stem cankers with abundant black exudation (EPPO, 1990). Vannini & Valentini (1994) observed increased fungal growth in the xylem of seedlings in response to water stress. They found a close relationship between the susceptibility to the fungus and the loss of hydraulic conductivity. They hypothesized that, after penetration of the vascular system, fungus increases the extent of xylem embolism, in which case the decline of infected trees may be caused, entirely or in part, by lack of xylem functionally and, hence, transport of water to the crown.

By monitoring a wide number of plants with the same symptoms of the plant that started to emit a huge amount of CO<sub>2</sub> since the end of August, we found that only the coppice shoots with thinnest diameter had suffered irreversible drought effects and, at the end of the growing season they presented the total rupture of the bark and the complete death. This suggests that despite the adaptation of the Turkey oak to periods of summer drought, competition between shoots could be the further factor of selection.

The exponentially relationship between stem CO<sub>2</sub> efflux and stem temperature was used to estimate  $R_{\text{stem}}$  and to scale-up the measurements at the breast height. Despite good overall model performance during the dormant season (the model provided estimates of stem respiration with a small mean absolute error), larger model errors occurred during the growing period. Besides, the model did not accurately describes the extreme data and the mean absolute error is less sensitive to outlier than the root mean square error, thus, RMSE is lower.  $R_{\text{stem}}$  is a complex process with different sources of CO<sub>2</sub> and many controlling factors (Maier et al., 2010). Therefore, the model didn't account all the factors previous discussed, that play a crucial role in  $R_{\text{stem}}$  during the growing period.

To scale-up the stem CO<sub>2</sub> efflux of the whole year 2012, sapwood volume was used. The annual amount accounted in this study for the year 2012 is in the range of other studies carried out in broadleaved forests (Edwards & Hanson, 1996; Tang et al., 2008) but is smaller compared with the ones reported by Damesin et al. (2002) and by Wang et al. (2010). Yang et al. (2014), found that  $R_{\text{stem}}$  is more sensitive to night than day warming, and temperature responses of  $R_{\text{stem}}$ , estimated by only daytime measurement, can lead to underestimated stem respiration. Overall, comparison between different studies is difficult as climate, tree density, age and scaling up method can vary largely (Damesin et al., 2002).

For a long time, surface area was the most common basis for scaling up, but in several studies sapwood volume has proved to be a better scaling factor for maintenance respiration in some species (Ryan, 2011a; Sprugel, 1990; Kim et al., 2007). The reason for this is probably that

sapwood volume is proportional to the amount of living cells in the xylem (ray parenchyma) (Stockfors & Linder, 1998) and in thick stems there are more living cells in the xylem than in the phloem and cambium (Michael G. Ryan, 2011b). For the trees studied, respiration at the breast height was considered useful for an acceptable estimate of respiration of the whole stem. As in several studies (Guidolotti et al., 2013; Lavigne, et al., 1996; Ryan et al., 1995; Stockfors, 1997) the implicit assumptions for scaling stem respiration from small sample measurements to whole stems was that the temperature-respiration relationship is constant for the entire stem, and that stem temperature, at a given time, is the same throughout the stem. However as indicate in Stockfors, (2000), for tree with an even distribution of the living cells in the stem, scaling up whole year respiration by sapwood volume causes only small errors.

Additional source of error has been detected by methods of cross validation to assess the parametric uncertainty and avoid over-fitting bias. The substantial increase of the errors demonstrate that the simple discrepancy of difference between a predicted value and the measured value, may give a measure of the error smallest than is really the case (Starkweather, 2013). Another factor that greatly influences the estimation of the respiration of the stems through the chamber method, is the sample size. The bootstrap analysis performed on the data of this study showed that as the number of trees for the estimation of the parameters increases, the variability of the estimates decreases. With the number of trees sampled in this study was not possible to evaluate a decrease in the variability up to a constant value. This suggests that in order to well represent all diameter classes of this coppice, more replicates are required of every diameter.

## 4.2 Soil respiration

The rates of soil respiration of this study were comparable to those measured in previous studies on sites exposed to drought (Epron et al., 1999; Rey et al., 2002; Valentini et al., 2000). The range of the rates of CO<sub>2</sub> efflux from the soil was lower than those measured in the same site at a different development stages after coppice by Tedeschi et al. (2006); they found a linear relationship between soil respiration and time after coppicing and they estimated a reduction of 24% over the usual 20-years-rotation cycle. Moreover, they used a different instrument for measurements (closed dynamic chamber - SRC model, PP – Systems Ltd) which tends to overestimates soil respiration rate, as a consequence of a different pressure at the soil surface caused by the fan (Pumpanen et al., 2004).

In agreement with other studies carried out in the Mediterranean ecosystems (Guidolotti et al., 2013; Reichstein et al., 2002; Rey et al., 2002; Tedeschi et al., 2006; Janssens & Pilegaard, 2003), the seasonal pattern of soil respiration in the study site followed soil temperature for only part of the year. In general, the seasonal course of soil respiration followed the seasonal cycle of temperature but moderated by the availability of soil water. Reichstein et al.(2003) found a strong dependency of soil respiration on soil water content with a reduction of  $R_s$  of 24%, 62% and 76% at 50%, 10% and 5% of relative soil water content, respectively.

The respiration rate was characterized by peaks in spring, before the onset of drought and again in early autumn after rewetting of the soil, indicating that availability of soil moisture was also a strong determinant. In September of both years,  $R_s$  increased suddenly after substantial rain events. This increase was probably the result of a stimulative effects, on the microbiological activity, of rewetting to the upper soil layers (Birch, 1958; Curiel Yuste et al., 2003; Jarvis et al., 2007; Rey et al., 2002), of the high availability of organic matter accumulated during the drought period due to the fine roots mortality (Konôpka et al., 2005), and of the displacement of CO<sub>2</sub>-rich air from within the soil (Rey et al., 2002).

The estimated  $Q_{10}$  was, well within the range found for European forests (Curiel Yuste, 2003). This value was estimated with data corresponding to the period when water availability was not limiting but not avoiding the confounding effects of rain as a result of rewetting of the upper soil layers (Jarvis et al., 2007). However, as already observed in another study (Curiel Yuste et al., 2003), inclusion of drought-affected data, can decrease significantly the  $Q_{10}$ . As found in Konôpka et al. (2005) for a forest of Penduculate oak, after a strong period of drought high fine

root mortality may occur. Moreover, low decomposition rates and low microbial activity may affect  $R_s$  with consequent decrease of  $Q_{10}$  (Konôpka et al., 2005; Curiel Yuste, 2005).

An annual  $Q_{10}$  reflects a true response of  $R_s$  to temperature only when no other important variables vary simultaneously (Janssens & Pilegaard, 2003). A short temporal scale would minimize the probability that other factors confound the observed temperature dependence, but are not always realistic because the smaller number of flux measurements increase the uncertainty in the calculated  $Q_{10}$  values as also the occasionally small range in soil temperature (Janssens & Pilegaard, 2003). The annual  $Q_{10}$  estimated in this study was similar to the  $Q_{10}$  estimated by Tedeschi et al. (2006) for the same site. Tedeschi et al. (2006) found that both respiration rates and its temperature sensitivity declined with age, reporting many possible explanations linked to the different canopy covers, to the soil exposition to direct sunlight and to the human activity (harvest). In Tedeschi et al. (2006), the trees in the four compartments where the measurements were carried out, had an age of 1 year, 5 years, 10 years and 17 years while the population of this study was 20-22-year-old. The hypothesis is that when the age is close to the maturity of the coppice, there are not structural differences that may affect the  $Q_{10}$  and all the effects of the harvest are lost.

Soil  $CO_2$  efflux measurements of this study indicated that diurnal fluctuations were very small. This observation was consistent with other studies (e.g. Janssens et al., 2001), and is probably related to the small changes in soil temperature under forest canopies.

The amplitude of the spatial variability varied through the year. The decrease in %CV with the onset of winter, as was found in other studies (e.g. Khomik et al., 2006), is probably reflective of the degree of respiratory activity below ground. During winter, trees become dormant and so root respiration decreases, greatly limiting any spatial variability. Heterotrophic respiration is also reduced during winter months because soil temperature decreases. Thus, the amplitude of the  $CO_2$  emission signal goes down with decreasing temperatures. The same assumption is the basis of the reduction of spatial variability during summer months in 2011. In 2010 the highest result obtained in terms of variation coefficient is probably due to the absence of a strong reduction of the soil moisture in the summer of this year and the contemporary high temperature that is favourable to metabolic activity, as strengthened in other studies (Barba et al., 2013; Khomik et al., 2006).

Value of annual  $R_s$  in 2012 was within the ranges of  $R_s$  reported by Raich & Schlesinger (1992) for temperate mixed forests ( $4.7\text{--}7.3 \text{ t C ha}^{-1} \text{ y}^{-1}$ ) and by Janssens et al. (2001) for European forests ( $3.8\text{--}8.5 \text{ t C ha}^{-1} \text{ y}^{-1}$ ). Curiel Yuste et al. (2005), in mixed temperate forest with selected

plots including the two most representative overstory species (*Pinus sylvestris* L. and *Quercus robur* L.), found that the total annual  $R_s$  in the different vegetation types ranged between 4.1 and 13.6 t C ha<sup>-1</sup> y<sup>-1</sup>. A similar value of the annual  $R_s$  estimated in this study was found by Tang & Baldocchi (2005) in an oak-grass savanna under the trees while, a lower value was estimated in the open area. In a managed oak forest ecosystem, Li et al. (2012) estimated a higher value of  $R_s$  in all the treatments considered and the main reason can be found in the total absence of the reduction of soil respiration during summer drought in the ecosystem considered.

There are several studies in which were used and developed models that relate soil respiration to soil temperature and water content (Reichstein, 2003; Reichstein et al., 2002; Ana Rey & Jarvis, 2006; Yuste et al., 2005). Despite good overall model performance used in this study, with a little mean absolute error and root mean square error, some causes may influence the estimation. The model accounted for the effect of episodic rain events, and the solely soil water and temperature data alone provided an adequate explanation of the mechanism for enhanced CO<sub>2</sub> release during transient rainfall events also if often T and SWC are indicated as insufficient (Jarvis et al., 2007). Nevertheless, the model was used under conditions indicated by Reichstein et al. (2003) as cause of an overestimation of the respiration rate as occurred in spring with high temperature combined with high soil water content. In December and in January the very low temperatures may have influenced the prediction causing an underestimation.

Additional source of error has been detected by methods of cross validation to assess the parametric uncertainty and avoid over-fitting bias. The mean absolute error increased while the root mean square error was overall unchanged. This is probably due to the accuracy with which the model describes the noise-free data (Janssen & Heuberger, 1995). The resulted cumulated values of annual soil respiration by 8 k-fold cross validation varied in a strict range (~ 7%) and it is an indication of the stability of the model with a reduced parametric uncertainty. The cross validation on data of 2011 showed a greater variability (double of the previous analysis) representing the influence of the high spatial variability on the parameter estimation. A factor that may greatly influence the estimation of the soil respiration through the chamber method, is the sample size. By the bootstrap analysis performed on the data of 2010 – 2011 was evident that as the number of trees for the estimation of the parameters increases, the variability of the estimates decreases. The same sample size found to be representative to estimate soil respiration was found by Yim et al., (2003) in a larch plantation. Other studies, conducted in tropical forests, required higher sample size (Adachi et al., 2005), while similar size was found in Alpine ecosystem by Rodeghiero & Cescatti (2008). Anyway, a minimum sampling size might not be a

perfect proxy for heterogeneity because of the lack of a standardized methodology to measure the spatial variability of soil respiration (Keith & Wong, 2006; Rodeghiero & Cescatti, 2008)

### 4.3 Leaf respiration

On average, leaf dark respiration rate expressed on leaf area basis was higher than the one found for a Turkey oak Mediterranean forest. Hymus et al., (2005) in the *Quercus cerris* L. coppice forest of Roccarespampani, by measuring leaf respiration twice during the night found that  $R_l$  was low (less than  $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), did not change between measurement periods and was unaffected by leaf position in the canopy. Values of about half size, at the standard temperature of  $15^\circ\text{C}$ , were also found by Guidolotti et al. (2013) in a Mediterranean forest of *Fagus sylvatica* in Central Italy.

The cause of the significantly difference between pre-dawn and after-sunset leaf respiration rates is unknown. In Atkin et al. (2000) they found that pre-dawn respiration was higher than the one after sunset. Nevertheless, it is clear that leaf respiration does not necessarily decline during the night. This contrasts with previous controlled environment studies in which plants were exposed to constant night temperatures (e.g. Averill & Rees, 1995).

The  $R_l$  increasing along the season with a peak in August was probably due to the lack of the typical summer drought in 2010. The same result was achieved by Catoni et al. (2013) in a study on evergreen species of a Mediterranean ecosystem in Latium between 2010 and 2011. However recent studies on different tree species point out the conclusion that  $R_l$  generally decreases in response to drought; this makes possible that acclimation of  $R_l$  during summer was a composite effect of both heat and drought (Atkin & Macherel, 2009; Crous et al., 2011; Maseyk et al., 2008; Rodríguez-Calcerrada et al., 2010; Rodríguez-Calcerrada et al., 2011).

The resulted  $Q_{10}$  in this study varied through the season but was always less than 2. In other studies on *Quercus* spp. (see table in Tjoelker et al. (2001)) were reported higher values of  $Q_{10}$ . In September the  $Q_{10}$  value was the lowest. Tjoelker et al. (2001) show that a declining  $Q_{10}$  indicates that the temperature sensitivity of respiration is reduced with increasing measurement of temperature, but the factor that contributes to the variation in  $Q_{10}$  value (short and long-term changes in temperature, reaction to drought stress, nutrient supply, and changes in atmospheric  $\text{CO}_2$  concentration) are various and is unclear what has determined this reduction. A simple exponential function using a fixed  $Q_{10}$  value of 2 has gained wide acceptance in modeling leaf-

to ecosystem-scale respiration responses to temperature and global vegetation response to climate change (e.g. Cramer et al., 1999; Ryan & Law, 2005; Schimel et al., 1997). However, biases may result if  $Q_{10}$  is assumed to be constant when estimating respiration over a broad range of temperatures (Tjoelker et al. 2001). Observed respiration rates and derived  $Q_{10}$  values may also depend on whether only the leaf, shoot, or whole plant are exposed to short-term temperature changes (Atkin et al., 2000).

The estimated total amount of  $R_l$  was higher than the one reported in some other forests (Bolstad, et al., 2004; Li et al., 2012; Tang et al., 2008; Wang et al., 2010b). Similar values were found on different species by (Ryan et al., 1997).

#### **4.4 Ecosystem respiration**

Whole ecosystem respiration is dominated by soil respiration (Bolstad et al., 2004; Law et al., 1999; Valentini et al., 2000).  $R_s$  was the largest source of  $Reco_{eddy}$  (51% of  $R_s$  against 13% and 36% of  $R_{stem}$  and  $R_l$ , respectively). Similar size of contribution was found in a temperate mixed forest by Wang et al. (2010b) and in a Mediterranean beech forest by Guidolotti et al. (2013) while Li et al. (2012), in a managed oak forest ecosystem, found a contribution  $R_s$  of 75%-85%. Soil  $CO_2$  efflux has been found to be 30%-90% of total ecosystem respiration in temperate forests (Epron et al., 1999; Valentini et al., 2000) and estimated  $R_s$  in the present study is well in this range. During summer the main source of  $CO_2$  efflux resulted to be the  $R_l$  and the reason are described in the previous discussion of  $R_l$ . The estimated total amount of  $R_l$  was higher than the one reported in some other forests (Bolstad, et al., 2004; Li et al., 2012; Tang et al., 2008; Wang et al., 2010b), but similar values were found on different species by Ryan et al. (1997). Stem respiration is generally the lowest contributing component and, in several studies conducted in Mediterranean forests, varies in the range between 8% -11% (Guidolotti et al., 2013; Maseyk et al., 2008; Wieser et al., 2009). The contribution of  $R_{stem}$  resulted in this study is higher but the up-scaling method, based on the solely temperature, has to be improved to better predict the stem  $CO_2$  efflux rates during the growing period.

The annual amount of carbon released via ecosystem respiration estimated by summing up the different components was higher than the one estimated by eddy covariance. These results are consistent with other comparisons of chamber-based and eddy-covariance respiration data in which the chamber-based flux estimates exceeded the eddy-covariance  $Reco$  estimate (Bolstad et

al., 2004; Drewitt et al., 2002; Guidolotti et al., 2013; Lavigne et al., 1997; Schmid, 2000; Tang et al., 2008; Wang et al., 2010a). Although not universal, ecosystem respiration in forests is often less than the summed component respiration estimates. It was shown by different authors (Aubinet et al., 2000; Goulden et al., 1996; Gu et al., 2005; Papale et al., 2006), that independently of the problems related to data acquisition, eddy flux measurements can underestimate the net ecosystem exchange during periods with low turbulence and air mixing. This underestimation acts as a selective systematic error: it only occurs during the night when CO<sub>2</sub> is produced by the ecosystem. As a consequence, the ecosystem respiration is underestimated and the carbon sequestration overestimated (Moncrieff et al., 1996). This result is in agreement with similar to the observations of Goulden et al. (1996) and Lavigne et al. (1997) where eddy covariance flux estimates averaged 20% to 40% less than scaled chamber estimates. Furthermore, the approach generally known as "u\* correction" is used as criterion to discriminate low and well mixed period. As the u\* correction is affected by several drawbacks and must be applied with care (Papale et al., 2006), a statistical approach was used to evaluate this additional source of uncertainty that resulted to be substantial using different u\* thresholds. Is possible to get either an overestimation that an underestimation, it's depends on the selected threshold.

In winter there was a good agreement ( $R^2 = 0.97$ ) between Reco estimated by chamber method and Reco estimated by partitioning of the Net Ecosystem Exchange measured by eddy covariance but not during the growing season. The strong reduction of Reco<sub>eddy</sub> occurred in summer was slightly present in the up-scaled measurements of R<sub>s</sub> and R<sub>stem</sub> and was absent in R<sub>l</sub>. The up-scale of leaf respiration rates was made with LAI of the year 2012 but using parameters estimated on data of the year 2010 when summer drought did not occurred. Data not shown of photosynthesis uptake, measured in the same days of the leaf dark respiration measurements during the growing season 2010, may also confirm this assumption. The typical midday depression in assimilation was not observed in this year and if on the one hand is demonstrated the high degree of tolerance of oak species to drought (Epron & Dreyer, 1993; Valentini et al., 1995), on the other, is widely observed that photosynthetic CO<sub>2</sub> fixation is suppressed under drought stress by enhanced diffusive resistance (closure of stomata and decline of mesophyll conductance) and by drought-induced impairment of metabolic processes (Flexas et al., 2004, 2006; Reddy et al., 2004). Furthermore, concerning the summer peaks, both partial refixation of the CO<sub>2</sub> and the reduction of non- respiratory CO<sub>2</sub> release were not considered in this study although is widely reported a reduction in non-photorespiratory R<sub>l</sub> in the light (Galmés et al., 2006; Haupt-Herting & Fock, 2002; Haupt-Herting, 2001) that could cause a 15%

overestimation of  $R_l$  in the illuminated leaves (Luyssaert et al., 2009). The available studies suggest that water stress is likely to inhibit rates of  $R_l$  in the light, in leaves where  $R_l$  in the dark is inhibited. In most studies carried out using well-watered plants, rates of  $R_l$  in the light are lower than  $R_l$  in the dark (Atkin et al., 1998; Brooks & Farquhar, 1985; Parnik & Keenberg, 1995; Villar et al., 1995; Wang, et al., 2001; Zaragoza-Castells et al., 2007) even when re-fixation of respiratory  $CO_2$  is taken into account (Parnik & Keenberg, 1995). Atkin et al. (2008) suggest that accounting for acclimation is important because e.g. it may decrease predicted rates of  $R_l$  by up to 20% in high-temperature biomes.

Through model validation techniques was possible to quantify the uncertainty. The results showed that method of estimation used, sample size, and biotic and abiotic factors influencing the respiration rates, can lead to both underestimation and overestimation higher than 50%.

The main contribution of errors was showed by stem  $CO_2$  efflux because of the bad model performance during the growing period.  $R_{stem}$  can be reasonably well predicted from  $T_{stem}$  during the dormant season but during the growing season  $T_{stem}$  is only one of numerous factors that can contribute to variation in  $R_{stem}$  and other physiological factors should be considered. In order to develop robust predictions of  $R_{stem}$  for the entire year, many factors in addition to temperature need to be taken into account. Therefore, the sources of uncertainty identified either through validation techniques that through the bibliography, suggest how the comparison between the estimation of ecosystem respiration from up-scaled chamber measurements and ecosystem respiration estimated with the eddy covariance method, is feasible only if the errors are minimized, by measuring a sample of adequate size and representative of the spatial variability of the population, by using prediction models suitable for Mediterranean environments and trying to apply standardized methods as much as possible.

## 5. Conclusions

The ecosystem respiration and its main components shown a strong seasonal variability. Summer aridity played a crucial role on the observed reduction of respiration that was evident both in soil and stem CO<sub>2</sub> efflux rates. Soil respiration and stem respiration increased from winter to spring, decreased in summer and suddenly increased in autumn after rainfall events. In this coppice oak forest, soil respiration was solely controlled by soil temperature above a threshold of 18% volumetric water content in the top 5 cm, and below that threshold by soil moisture.

The limitation in soil water availability can lead the reduction of stem growth rate and consequently in stem CO<sub>2</sub> efflux.  $R_{\text{stem}}$  was well controlled by stem temperature during the dormant season but not during the growing period, probably because numerous factors in addition to temperature that can influence  $R_{\text{stem}}$  during the growing season, are not present during the dormant season. Diameter at breast height has been found to be correlated with  $R_{\text{stem}}$ . It suggests that for a robust prediction of  $R_{\text{stem}}$  for the entire year, in addition to  $T_{\text{stem}}$  should be taken into account also the DBH.

The sudden die back of the crown of several coppice shoots at the end of August and the resulting increase in stem CO<sub>2</sub> efflux from these plants, highlights the need of better investigations at local scale about the drought induced trees die-off since this phenomena is likely to increase (Allen et al., 2010).

Based on up-scaled chamber measurements, Reco showed a significant temporal variation over the year.  $R_s$  and  $R_{\text{stem}}$  followed the same trend of  $\text{Reco}_{\text{eddy}}$  with a reduction during summer months consequently to summer drought. On the contrary,  $R_l$  peaked in August and decreased in autumn and, was responsible for the decoupling of the two Reco estimates. The total annual  $\text{Reco}_{\text{eddy}}$  chosen as reference was 9.11 t C ha<sup>-1</sup> y<sup>-1</sup> while, the total annual contribution of  $R_s$ ,  $R_{\text{stem}}$  and  $R_l$  was 6.79, 1.77 and 4.74 t C ha<sup>-1</sup> y<sup>-1</sup>, respectively. Thus, the relative contribution of each component was 51% for the soil, 13% for the stem and 36% for leaves, confirming that whole ecosystem respiration is dominated by soil respiration (Bolstad et al., 2004; Law et al., 1999; Valentini et al., 2000).  $\text{Reco}_{\text{cuv}}$  was 32% larger than ecosystem respiration estimated by eddy covariance. It was shown by different authors (e.g. Papale et al., 2006) that eddy flux measurements can underestimate the net ecosystem exchange during periods with low turbulence and air mixing. Furthermore, is widely pointed out the lack of agreement between scaled-up

chamber measurements and estimates of Reco by eddy covariance (Lavigne et al., 1997; Law et al., 1999).

Through model validation techniques was possible to quantify the uncertainty. The results showed that method of estimation used, sample size, and biotic and abiotic factors influencing the respiration rates, can lead to both underestimation and overestimation higher than 50%. The main contribution of errors was showed by stem CO<sub>2</sub> efflux because of the bad model performance during the growing period. For leaf respiration was not possible to evaluate the uncertainty but several studies report that R<sub>l</sub> substantially decrease in leaves experiencing increasing levels of drought. Biotic and abiotic factors are involved in this process and the solely temperature is not sufficient to predict R<sub>l</sub> even more if the prediction is made with parameters estimated using data of different years whit different environmental and physiological conditions. In order to develop robust predictions of R<sub>stem</sub> and R<sub>l</sub>, for the entire year, many factors in addition to temperature need to be taken into account. Therefore, the sources of uncertainty identified either through validation techniques that through the literature, suggest how the comparison between the estimation of ecosystem respiration from up-scaled chamber measurements and ecosystem respiration estimated with the eddy covariance method, is feasible only if the errors are minimized. For a better agreement of the estimates with the two methods, samples of adequate size and representative of the spatial variability of the population, prediction models suitable for Mediterranean environments and, standardized methods as much as possible, are needful.



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