HOW DROUGHT SEVERITY CONSTRAIN GPP AND ITS PARTITIONING AMONG CARBON POOLS IN A *QUERCUS ILEX* COPPICE?

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ABSTRACT

The partitioning of photosynthates toward biomass compartments has a crucial role in the carbon sink function of forests. Few studies have examined how carbon is allocated toward plant compartments in drought prone forests. We analyzed the fate of *GPP* in relation to yearly water deficit in an old evergreen Mediterranean *Quercus ilex* coppice severely affected by water limitations. , Carbon fluxes between the ecosystem and the atmosphere were measured with an eddy-covariance flux tower running continuously since 2001. Discrete measurements of litterfall, stem growth and f_{APAR} allowed us to derive annual productions of leaves, wood, flowers and acorns and an isometric relationship between stem and belowground biomass has been used to estimate perennial belowground growth. By combining eddy-covariance fluxes with annual productions (*NPP*), we managed to close a C budget and derive values of autotrophic, heterotrophic respirations and carbon use efficiency (*CUE*, the ratio between *NPP* and *GPP*). Average values of yearly *NEP*, *GPP* and R_{eco} were 282, 1259 and 977 g C m^{-2}. The corresponding *ANPP* components were 142.5, 26.4 and 69.6 g C m^{-2} for leaves, reproductive effort (flowers and fruits) and stems. *NEP*, *GPP* and R_{eco} were affected by annual water deficit. Partitioning to the different plant compartments was also impacted by drought, with a hierarchy of responses going from the most affected, the stem growth, to the least affected, the leaf production. The average *CUE* was 0.40, which is well in the range for Mediterranean-type forest ecosystems. *CUE* tended to decrease more slightly in response to drought than *GPP* and *NPP*, probably due to drought-acclimation of autotrophic respiration. Overall, our results provide a baseline for modeling the inter-annual variations of carbon fluxes and allocation in this widespread Mediterranean ecosystem and highlight the value of maintaining continuous experimental measurements over the long term.

1. INTRODUCTION

Forest ecosystems exert a strong influence on the global C cycle (Bonan, 2008) as forests may contribute up to 60% of the total land carbon uptake (Beer et al., 2010). Estimations and simulations of carbon uptake by forest ecosystems have been greatly improved in recent decades, but unfortunately how this assimilated C is transferred from the atmosphere to the terrestrial biomass remains poorly known. Luo et al. (2011) highlighted a lack of mechanistic understanding on this question and suggested "to develop generalizable models of C allocation to biomass growth of plant parts, respiration, nonstructural C reserve, reproduction and defense" as a challenging issue. A recent synthesis has demonstrated that the partitioning of gross photosynthetic production (*GPP*) among above- and below-ground production and respiration can vary greatly across biomes according to climate and fertility (Litton and Giardina, 2008). However, a more detailed understanding of how environmental factors affect the distribution of C among the different tree parts at the ecosystem scale remains a crucial step to improve the accuracy of local and global vegetation models (Fatichi et al., 2013; Leuzinger and Quinn Thomas, 2011).

Understanding C allocation patterns appears particularly important in drought prone areas, such as those with a Mediterranean-type climate, which are particularly vulnerable to the ongoing climate change (Giorgi, 2006). According to global and regional climate models, Mediterranean-type ecosystems (MTEs) will suffer longer and more intense droughts as a result of 1) increasing temperature and decreasing rainfall (Hoerling et al., 2011), 2) a change in large-scale circulation conditions (Kjellström et al., 2013), and 3) the persistence of heat wave anomalies (Jaeger and Seneviratne, 2011). In MTEs, drought is already the prevailing constraint on the net ecosystem productivity (*NEP*) (Allard et al., 2008; Grünzweig et al., 2003). This sink strength is likely modified by the differential sensitivity to water limitation of leaf photosynthesis and whole-tree respiration, and of the C allocation to short- and long-lived pools. The representation of C use in models currently lacks consensus and is achieved by a plethora of concurrent approaches (Franklin et al., 2012). This modeling deficiency seems to be due to the difficulty in interpreting this information in generic schemes that are valid under a wide range of conditions, and particularly water limitation.

So far, studies addressing the question of C-use in MTEs have relied on the coupling of field data of standing biomass and growth compartments with simulation models. Pioneering works started in the 70s onwards (López et al., 2001b). Oechel and Lawrence (1981) applied the process-based model MEDECS to eight woody Mediterranean species growing in California chaparral and Chilean matorral. The model scaled up leaf level respiration and assimilation together with stem respiration to yield yearly C budgets using a radiation transfer scheme. The hierarchy of C allocation to leaves, stems, and roots followed species-specific rules and a phenological calendar. From this modeling exercise, the authors deduced changes in C use that deeply modified the respiratory costs in response to changes in air temperature. Yet, the effect of drought on C use remains more difficult to understand and simulate.

Forests and woodlands dominated by the evergreen oak *Quercus ilex* L. occupy large areas in the surrounding of the Mediterranean Sea (Quézel and Médail, 2003) and are emblematic of the MTEs. Due to its resprouting nature, *Q. ilex* can persist in the same place for hundreds of years and populations display minimal changes in stool number per area. Very large survival rates and fast recovery of its foliage after complete dieback (Lloret et al., 2004) reflect its high ability to damp climate extremes (Misson et al., 2011). In contrast, co-occurring obligate seeders are subjected to all the vicissitudes of regeneration, and are particularly affected by drought mortality at the seedling stages and by wildfires (Ackerly, 2004; Zavala, 1999). The growing interest in resprouting ability as a major plant functional trait is reflected in a number of recent contributions aimed at understanding the biogeography and developing functional models of resprouting species (Clarke et al., 2010; Vesk and Westoby, 2004; Vilagrosa et al., 2014). Resprouters have the particularity to store considerable amounts of C belowground at the cost of high maintenance respiration (Iwasa and Kubo, 1997). Characterizing the ecosystem C use for such species is important for managing and predicting the response of Mediterranean forests to the on-going climate changes.

The functioning of *Quercus ilex* stands in Southern France was simulated by Hoff et al. (2002) and Hoff and Rambal (2003) using the Forest-BGC model. C-use rules in this simple model are implemented so as to follow an optimal trajectory: trees use C first into leaves and fine roots for maximizing productivity while minimizing water limitation; finally stems appear as an end-product built with the remaining C. Other modeling exercises with *Q. ilex* ecosystems also retained water-related constraints for their C-use rules. Gracia et al. (1999) developed a dynamic growth model where the partitioning of growth between leaves and perennial wood compartments is performed so as to fulfill the assumptions of the pipe model theory (Shinozaki et al., 1964; see also Mäkelä, 1986 for substantial accounts; Valentine, 1985), i.e. so as to maintain the sap area/foliage area ratio constant. Gracia et al. (1999) also constrain growth to fine roots to follow the functional balance hypothesis

(Brouwer, 1962). Both abovementioned modeling exercises yielded credible results when validated against yearly variations of radial growth. Fortunately, the increasing availability of long term field measurements of productivity and eddy covariance fluxes can now help to refine these previous modeling hypotheses.

In this study, our main objectives were: 1) to evaluate the fraction of *GPP* partitioned to above- and below-ground parts in a *Quercus ilex* forest by comparing different ecosystems across a range of climate, management, and drought resistance of dominant species, and 2) to assess how year-to-year variation in drought severity impacts the partitioning of *GPP* between production and respiration, and among above- and below-ground C pools. For these purposes, we used long-term data of eddy covariance fluxes and primary productivity of aboveground components (leaves, flowers, fruits and stems), plus punctual data of root biomass taken from literature and our own excavation of four *Q. ilex* trees.

2. MATERIAL AND METHODS

2.1. Site description

The study site is located 35km north-west of Montpellier (southern France), on a flat plateau in the Puéchabon State Forest (3°35'45"E, 43°44'29"N, 270m a.s.l.). This forest has been managed as a coppice for centuries and the last clear cut was performed in 1942. Vegetation is largely dominated by a dense overstorey of the evergreen oak *Quercus ilex*. The top canopy height is about 5.5m. In 2010, stem density was 4900 stems$\cdot$ha^{-1}. Stems with diameter at breast height (*DBH*) < 4cm represented 6 % of total stems, whereas those with *DBH* > 10cm represented 20.6 %. Understorey species *Buxus sempervirens*, *Phyllirea latifolia*, *Pistacia terebinthus* and *Juniperus oxycedrus*, compose a sparse shrubby layer with a percent cover lower than 25% and a height less than 2 m.

The area has a Mediterranean-type climate. Rainfall mainly occurs during autumn and winter, with about 80% taking place between September and April. The mean annual precipitation is 916 mm, with a range of 556-1549 mm recorded over the 1984-2011 period. Mean annual temperature over the same period was 13.0°C, with a minimum in January (5.5°C) and a maximum in July (22.9°C). The rocky soil is formed on Jurassic limestone; on average, the volumetric fractional content of stones and rocks is about 0.75 for the top 0-50 cm and 0.90 below. The stone-free fine fraction of the soil is a homogeneous silty clay loam (USDA texture triangle) within the top 0-50cm layer (38.8% clay, 35.2% silt and 26% sand). The fine fraction fills up the space between stones and rocks and provides a source of water throughout the long dry summers for the deep-rooted *Q. ilex* (Rambal, 2011). The highly permeable soil prevents any surface runoff to occur even for high intensity rain events.

2.2. Water limitation: Soil water balance model and drought index

Soil water storage integrated over the rooting depth, that is c.a. 4.5 m (Rambal, 2011), has been measured during the vegetative periods of 1984-1986 and since July 1998 onwards, at approximately monthly intervals, using a neutron moisture gauge (see Hoff et al., 2002). Discrete measurements were interpolated at a daily time step with a soil water balance model proposed in Rambal (1993) and further used in Grote et al. (2009). The drainage curve relating deep drainage to soil water storage depends on the stone content over the whole-soil profile (Rambal, 1990). The model was driven by daily values of incoming solar radiation, minimal and maximal temperature and rain amount. Soil water storage and soil water potential were related by a Campbell-type retention curve (Campbell, 1985) whose parameters are strongly dependent on soil texture (see details in Rambal et al., 2003). Comparison of measured against simulated values of soil water storage (in mm), and predawn leaf water potential (in MPa), displayed very good agreement. Leaf water potential values came from discrete measurements performed on the study site (see Limousin et al., 2012 for a substantial account). For soil water storage, reduced major axis (RMA) regressions yielded $SWS_{sim} = \alpha_{\mathrm{rma}}\, SWC_{obs} + \beta_{\mathrm{rma}}$ with α_{rma} ± standard-error (SE) = 0.94±0.03, β_{rma} ± SE = 6.0±4.4, $R^2 = 0.93$, F = 1137, $p<0.0001$ and n = 91; for the predawn potential, $\psi_{pdsim} = \alpha_{\mathrm{rma}}\, \psi_{pdobs} + \beta_{\mathrm{rma}}$ with α_{rma} ± SE = 0.93±0.05, β_{RMA} ± SE = -0.09±0.09, $R^2 = 0.840$, F = 273.3, $p<0.0001$ and n = 54. The continuous daily course of relative water content, *RWC*, was derived from SWS_{sim} divided by the soil water storage at field capacity that we chose to fix at 205 mm. This value corresponds to that observed after 2 days of free drainage in a cool wet period after a substantial rain event. For characterizing the whole-year water limitation, we calculated the water stress integral (*WSI*) as the yearly sum of ψ_{pdsim}. For days with $RWC \geq 1$ ψ_{pdsim} is fixed to -0.03 MPa. The *WSI* are expressed in MPa day.

2.3. Drought frequency analysis

The return periods for drought events were calculated, using a monthly 239-year precipitation historical dataset (1762-2011) for Montpellier downtown. This dataset was scaled to our experimental site using overlapping precipitation data from 1984 to 2011. As shown by Rambal and Debussche (1995) and López-Moreno et al. (2009), the coefficient of variation for precipitation is regionally conserved and was used to fit theoretical lognormal distribution functions for extreme precipitation events at our site. Return periods were calculated as $1/p$, where p is the probability of occurrence (Rambal and Debussche, 1995).

2.4. Carbon fluxes and ancillary data

Daily climate data, further used as model inputs for a water budget model, came from a weather station located 200 m away from the flux tower.

Eddy covariance fluxes of CO_2, sensible heat, latent heat and momentum were measured continuously since 2001 at the top of a 12 m high tower that is approximately 6 m above the canopy. Our eddy covariance facility included a three-dimensional sonic anemometer (Solent R3, Gill Instruments, Lymington, England) and a closed path infrared gas analyser (IRGA, model LI 6262, Li-Cor Inc., Lincoln, Nebraska, USA), both sampling at a rate of 21Hz. Flux data were processed with protocols defined within the Carbo-Europe network (www.carboeurope.org, Aubinet et al., 2000). Processing schemes of Fluxnet have been used for filling data gaps and partitioning *NEP* into *GPP* and ecosystem respiration R_{eco} (Papale, 2006; Reichstein et al., 2005). The half-hourly fluxes were summed at a yearly time steps for further analysis. Photosynthetically active radiation PAR_{top} was recorded at the top of the flux tower. The fraction of PAR absorbed by the canopy (f_{APAR}) was derived from 14 *PAR* sensors randomly set up in understorey locations and measuring PAR_{below}:

$$f_{APAR} = 1 - PAR_{below}/PAR_{top} \; (1)$$

2.5. Leaf production and other growth components

$ANPP_{stem}$ was estimated from yearly measurements of stem *DBH* and the allometric relationship between stem biomass and stem *DBH*. $ANPP_{leaf}$ and $ANPP_{reprod}$ were derived from monthly litter falls measured on 26 x 0.141 m^2 litter traps. $ANPP_{reprod}$ comprised flowers and acorns. $ANPP_{leaf}$ was derived by estimating yearly changes of leaf mass at peak leaf area index plus the amount of leaves lost as litter. Leaf production in year *t* occurred from May to June and $M_{leaflitter}$ was calculated as the sum of monthly values of leaf litter fallen from August *t-1* to July *t*. $M_{leaflitter}$ was corrected for mass loss at abscission using the results of Cherbuy et al. (2001):

$$ANPP_{leaf} = M_{leaf}(t) - M_{leaf}(t-1) + M_{leaflitter} = \Delta M_{leaf} + M_{leaflitter} \; (2)$$

Peak *LAI* = *PAI* – *SAI* was estimated from continuous measurements of half-hourly f_{APAR} between 11 AM and 1 PM from DOY 205 to 225. We first derived the plant area index *PAI* by using a Beer's Law with an extinction parameter equal to k/sinβ. The parameter k was set to 0.72 as in Rambal et al. (2003) and β is the solar elevation angle. The Stem Area Index *SAI* was estimated by image processing of hemispheric photography. It was assumed constant for the whole period and equal to 0.5 (Poncelet unpublished data). *LAI* was converted to leaf mass with a canopy-averaged leaf mass per area of 215 g m^{-2} (see Rambal et al., 1996). The below-canopy *PAR* sensor network was set up in 2001 so the leaf production for 2001 was not available. Even though *Q. ilex* is a strong emitter of terpenoids (Staudt et al., 2002), biogenic volatile compound emissions are relatively minor C sources and they were neglected here. So, the aboveground net productivity was computed as:

$$ANPP = ANPP_{leaf} + ANPP_{stem} + ANPP_{reprod} \; (3)$$

In 2005 we observed a massive outburst of *Lymantria dispar*. Grazing from caterpillars drastically impacted the leaves so we decided to exclude data from this year in our calculations. Data for the belowground perennial components were obtained by excavating four stumps at our site, and from literature values published by Canadell and Roda (1991) and Djema (1995) for *Q. ilex* coppices growing in northeast Spain under similar climate conditions. We compiled 19 biomass values for root crown, roots greater than 5 cm, and roots ranging from 1 to 5 cm diameter. The whole perennial belowground compartment is the sum of root crown and large roots. We obtained an isometric relationship between stem and belowground biomass, with a slope equal to 1.068 ± 0.1235 ($s_{x.y}$ = 62.2, n=19, p<0.001) (Fig. A1). All these data came from excavations in very stony soils and only concerned the top 0-1 m layer. A significant part of the root system was not extracted because we have observed that tap roots are able to uptake soil water at depths ranging between four and five meters (Rambal, 2011). We thus applied a conservative correction factor of 10% to account for the missing root part. Our belowground to aboveground ratio could be considered constant whatever the stool size, so we propose an isometric partition of C between these two perennial compartments. We postulate that the error we made in estimating $BNPP_{coarse}$ is equivalent to the one we made in evaluating the change in stem biomass:

$$ANPP_{stem} = \alpha BNPP_{coarse} \; (4),$$

with *BNPP* representing belowground net primary productivity. Fine root production was taken from literature values. López et al. (2001a) extensively monitored fine root productivity in a *Q. ilex* coppice. They found annual fine root production over the 0-60 cm soil layer to be quasi identical to leaf production (average fine root to leaf production ratio over two years was 1.04). We correct this value for the whole profile using a ratio of 1.25, based on the distribution of fine roots over the soil profile proposed by Jackson et al. (1997) for sclerophyllous shrubs and trees, and the increase in fine root turnover rate with depth (López et al., 2001b):

$$BNPP = BNPP_{coarse} + BNPP_{fine} \; (5)$$

Biomasses were converted to C using tissue-specific C contents whenever available; else 0.48 was used as a default.

2.6. Carbon budget estimate

The different components were related to each other according to three identities considered here as yearly sums:

$$NPP = ANPP + BNPP = GPP - R_a \; (6)$$

$$NEP = NPP - R_h = GPP - R_{eco} \; (7)$$

$$R_{eco} = R_a + R_h (8)$$

R_a is the autotrophic respiration, including both growth and maintenance components, with R_{aa} and R_{ab} standing for the above-and below-ground parts, respectively. R_h is the heterotrophic respiration. Uncertainty estimation of fluxes were around 20 g C m^{-2} y^{-1}, 30 g C m^{-2} y^{-1} and 40 g C m^{-2} y^{-1} for NEE, GPP and R_{eco}, respectively (Misson et al., 2010; see also Stauch et al., 2008).

$$GPP = ANPP + R_{aa} + TBCF \ (9)$$

Total belowground carbon allocation ($TBCF$) was defined as that carbon allocated belowground by plants to coarse and fine roots production, root respiration, and root exudates and mycorrhizae. $TBCF$ is either respired by microbes or roots (measured as soil-surface CO_2 efflux) or stored in soil as organic matter in the litter layer or in living and dead roots. Growth respiration was calculated using the yield of growth processes Y (Thornley, 1970). This yield is the amount of biomass increment per unit of C substrate used in growth processes. It was expressed in g C of new biomass (g C of substrate used in the growth processes)$^{-1}$. For *Q. ilex* in Puéchabon, the Y parameter has been estimated to 0.8 g C appearing in new biomass per g of C substrate utilized (Rambal et al., 2004). In equations 6, 7 and 9, we neglect nonstructural C storage above or belowground. In the carbon budget we wrote an equation in which C balance is zero independently of the water limitation, and consequently the storage of nonstructural C pool remains constant (see Ryan, 2011; Sala et al., 2010; Stauch et al., 2008 for the role of nonstructural carbohydrates in coping with drought).

3. RESULTS

3.1. Environmental conditions and exceptional years

Over the study period (2001-2011), annual rain amounts ranged from 638.2 mm in 2007 to 1310 mm in 2003. The average value over this period (976.8 mm) was slightly greater than the longer term mean (1984-2011, 916 mm). *WSI* ranged from -112.6 MPa day in the wettest year (2004) to -358.6 MPa day in the driest year (2006). There was no relationship between the annual rainfall amount and the annual *WSI* that the vegetation underwent. Lower *WSI* occurred in years when the dry period began early in the spring season. In the driest year 2006 the rain deficit began in February, and from February to June the rainfall amount reached only 109.8 mm. We calculated a probability of 0.015 for the 2006 drought, corresponding to a return period of 67 years. Other years with dry spring seasons in the historical series were: 1779, 1780, 1817, 1929, 1945 and 1995, but all these years displayed less severe droughts than 2006. So, over the 2001-2011 period, we observed a very large range of water limitation from well-watered conditions to severe drought. There was no significant covariation between mean annual temperature and *WSI*.

3.2. C fluxes and production

The mean gross C input, *GPP*, was 1259 g C m^{-2} yr^{-1} and its coefficient of variation (CV) or between year variation was 13.3%. For *NEP* the mean value was 281.7 g C m^{-2} yr^{-1} with a larger CV of 33.5%; and for R_{eco} it was 977.2 g C m^{-2} yr^{-1}, with a CV = 8.9%.

The average LAI was 2.25 ± 0.2, which corresponds to a supported leaf mass of 231.7 g C m^{-2} (n = 10) with a coefficient of variation CV = 9% (Fig. A2.). Our calculation of the leaf production yields an average value of 142.5 g C m^{-2} yr^{-1}(n = 9) with a large CV of 28.5%. The leaf production ranged from 202.8 ± 77.1 g C m^{-2} yr^{-1} in 2006, the year after the *Lymantria dispar* outburst and heavy grazing, to 69.6 ± 58.2 g C m^{-2} yr^{-1} the following year in 2007. The reproductive effort, $ANPP_{reprod}$, evaluated in pooling flowers and acorns, displayed the greater between-year variation, with a 42.5% CV, and a mean value of 26.4 g C m^{-2}. The components of $ANPP_{reprod}$ were, on average, 11.0 g C m^{-2} yr^{-1} for flowers (CV = 48.5%) and 15.4 g C m^{-2} yr^{-1} for acorns which displayed the largest variation (CV = 87.8%). Summing leaves plus flowers and acorns we obtained an average 169.6 g C m^{-2} yr^{-1}, which accounted only for 16.9% of the yearly *GPP*.

3.3. Relationships between production components and water limitation

Significant linear declines of *GPP*, *NEP* and R_{eco} with increasing drought severity were observed across years (Table 1; Fig. 1). Respectively 72% and 80% of the variance in *GPP* and *NEP* was explained by the *WSI*. The slopes of the *WSI*-*GPP* and -*NEP* lines were 1.91 ± 0.43 and 1.15 ± 0.20, respectively, which means that we project a decline of *GPP* of 191 g C m^{-2} yr^{-1} and of *NEP* of 115 g C m^{-2} yr^{-1} for an increase in drought severity of 100 MPa day expressed in terms of *WSI*. The sensitivity to drought of R_{eco} was lower than for the two other components of the whole-ecosystem C budget, with a lower slope of 0.77 ± 0.32 associated with a lower explained variance, 42%.

Among the aboveground tree compartments, the most affected by drought was the stem (Fig. 2), with $dANPP_{stem}/dWSI$ = 0.42 ± 0.10 (Table 1; Fig. 2). According to the linear equation fitted between $ANPP_{stem}$ and *WSI*, the predicted allocation of C to the stem ranged from 120.9 g C m^{-2} for a hypothetic wet year that underwent a *WSI* of -100 MPa day (*WSI* in 2004 equaled -112.6 MPa day), to zero in a severely dry year with a *WSI* of -390 MPa day. Reproduction was also affected by water stress, with $dANPP_{reprod}/dWSI$ = 0.10 ± 0.04 (Fig. 3). In contrast, no significant relationship was found between *WSI* and $ANPP_{leaf}$. $ANPP_{leaf}$ was, however, significantly related to the *WSI* of the previous year, with a slope of 0.41 ± 0.15 and an explained variance of 52% (Fig. 4).

3.4. Relationship between CUE and water limitation

By combining the latter results with equations 6 to 9, a model of C use changes with drought severity can be proposed. Fig. 5 depicts the changes of *GPP* and *NPP*, and of the above and belowground compartments with *WSI*. *CUE*, the ratio of net primary production to gross primary production is also presented. For *WSI* declining from -100 MPa day in a wet year to -400 MPa day in a particularly dry year, *NPP* and *CUE* decline from 621.4 to 339.4 g C m^{-2} yr^{-1} and from 0.419 to 0.373 respectively.

Fig. 6 depicts the declines of R_{eco}, *NEP* and *NPP* with *WSI* and the corresponding changes of the ratios of autotrophic respiration to *GPP* (R_a/GPP) and heterotrophic respiration to whole-ecosystem respiration (R_h/R_{eco}). The R_a/GPP ratio increased from 0.581 to 0.627 for a change of *WSI* from -100 to -400 MPa day. For the same decline in *WSI*, the ratio of R_h/R_{eco} increased from 0.192 to 0.321, with R_h slightly increasing from 205.1 to 268.1 g C m^{-2} yr^{-1}.

4. DISCUSSION

4.1. Carbon use efficiency in a Mediterranean coppice – management and drought-adaptation constraints on carbon allocation rules

Carbon use efficiency (*CUE*), the ratio of net primary production (*NPP*) to gross primary production (*GPP*), describes the capacity of forests to assimilate C from the atmosphere into terrestrial biomass. *CUE* of forests has been assumed, by some authors, to be a constant value of 0.47 ± 0.04 (Gifford, 2003; Waring et al., 1998), which supposes that tree respiration is a constant fraction of *GPP*. Contrary to this assumption of constancy, substantial variations in *CUE* have been reported in forest ecosystems. Medlyn and Dewar (1999) demonstrated that *CUE* likely ranges between 0.31 and 0.59, and a more recent synthesis by DeLucia et al. (2007) showed that the slope of the relationship between *NPP* and *GPP* (*CUE*) was 0.53, ranging from 0.23 to 0.83 among forest types. *CUE* decreased with increasing age, and a substantial portion of the variation among forest types was caused by the ratio of leaf mass-to-total mass. For a ratio of leaf mass-to-total mass of 0.03 corresponding to our *Q. ilex* forest, DeLucia et al. (2007) predicted a *CUE* of 0.38, similar to the mean of 0.40 obtained here, and the same value that Oechel and Lawrence (1981) obtained for Californian and Chilean shrub and tree species. With the process-based simulation model Gotilwa applied to a *Q. ilex* coppice in northeastern Spain, Gracia et al. (1999) predicted a *CUE* of 0.41. In contrast, Luyssaert et al. (2007) derived a surprisingly high value of 0.54 from a global database for their so-called “Mediterranean warm evergreen” biome (table 2).

The low ecosystem *CUE* observed at our site (around 0.40) could be due to the ancient management of the ecosystem as a coppice. The large belowground biomass and respiratory maintenance costs associated to this management system may alter C-use rules and constrain *CUE* compared to more productive tall forests (Salomón et al., 2013). Furthermore, relatively high R_{aa} (see below), could be associated to the role of above-ground organs in storing nitrogen and nonstructural carbohydrates. One-year old leaves act as reservoirs contributing to spring shoot growth (Cherbuy et al., 2001) while stumps and stems contain large amount of parenchyma helping the tree to resprout after perturbations. Accurately quantifying the relative importance of respiratory sources is an important step towards understanding the whole C budget. Under the steady-state assumption of Eq. 9 (Raich and Nadelhoffer 1989)(Raich and Nadelhoffer, 1989), our values of *GPP*, *ANPP* and R_{aa} resulted in *TBCF* = 670 g C m^{-2} yr^{-1}. R_{aa} was 460 g C m^{-2} yr^{-1}, a value estimated from leaf respiration and stem CO_2 efflux measurements made at our site and upscaled to the stand (Rodríguez-

Calcerrada et al., 2011; Rodriguez-Calcerrada et al., 2014). Applying the same *TBCF* approach to the Misson et al. (2010) data of soil respiration for the wet 2004 year yielded a *TBCF* of 630 g C m^{-2} yr^{-1}. With our estimate of *BNPP* = 270 g C m^{-2} yr^{-1}, the R_{ab} ranged between 360 and 400 g C m^{-2} yr^{-1}. Finally, we could deduct an R_h ranging between 210 and 230 g C m^{-2} yr^{-1} by summing the three respiration components to reach the whole-ecosystem respiration R_{eco}. For comparison, the meta-analysis of Litton and Giardina (2008) report a *TBCF* of 705 g C m^{-2} yr^{-1} and a *BNPP* of 334 g C m^{-2} yr^{-1}, and Rodeghiero and Cescatti (2006) measured, in a more mesic *Quercus ilex* coppice in which the soil respiration is very high (1079 g C m^{-2} yr^{-1}), a *TBCF* of 564 g C m^{-2} yr^{-1} with the two belowground respiration components R_{ab} and R_h being equal.

4.2. Sensitivity of carbon use and partitioning to between-year variation in water limitation.

To characterize year to year variations in drought severity we used a long-term cumulated water stress index, the *WSI*. This concept likely originated in (Schulze et al., 1980a; Schulze et al., 1980b) who related changes in normalized maximal assimilation rates and daily carbon gain with the sum of water stress obtained by cumulating daily pre-dawn water potentials from the day of the last rainfall to the day under consideration. Later, Wullschleger and Hanson (2006) did the same with transpiration rates from trees growing in a throughfall displacement experiment. This cumulated water-stress, called water-stress integral or *WSI* by Myers (1988), has been applied to predict growth processes occurring at longer time scales such as canopy development, litter fall dynamic and tree radial growth (Benson et al., 1992; Raison et al., 1992a; Raison et al., 1992b). In our study we demonstrated that *WSI* was significantly related to the current year reproductive effort, secondary growth and all ecosystem C fluxes (see also Arneth et al., 1998), and useful in explaining how the previous year drought limitation affected the leaf production in the subsequent year.

GPP, R_{eco} and *NEP* were largely impacted by water limitation. The decline of *GPP* with drought has been observed in our site at different time and space scales. At a seasonal time scale, Limousin et al. (2010) intensively discussed how leaf photosynthetic limitations were related to predawn water potential. At a daily time scale, *GPP* estimated from eddy correlation fluxes was related to predawn water potential (Rambal et al., 2003). The *ANPP* components have also been shown to be impacted by drought severity, with a hierarchy of responses going from the more affected, the stem, to the less affected, the leaves (Table 1). The larger sensitivity of stem growth validates the hypothesis of the Forest-BGC model (Hoff et al., 2002) in which trees allocate C first to leaves and fine roots, for maximizing productivity while minimizing water stress, and then to stems, which appears as an end-product built with remaining C. The reproductive effort also declined significantly with increasing drought, although it represented a smaller C use. Acorn production, the larger component of reproduction, has been shown to be influenced by water availability during the fruiting process, in particular during the initial (spring) and advanced (summer) stages of the maturation cycle (Pérez-Ramos et al., 2010).

The leaf production was not related to the current-year *WSI* but to the previous year *WSI*. Limousin et al. (2012) observed that in *Q. ilex* the leaf litterfall was also positively correlated with the previous year *WSI* so that more leaves were shed and replaced following wet years than following dry years. This phenomenon might be explained by the cost-benefit hypothesis (Chabot and Hicks, 1982; Kikuzawa, 1991): if the leaf carbon assimilation is reduced by water limitation during a dry year, the leaf life span should increase for the leaf lifetime carbon gain to pay back the leaf construction cost, and thus fewer new leaves need to be produced to maintain the *LAI*. This results in an alternation of years with high leaf production /shedding following wet years and years of opposite characteristics, as commonly observed in evergreen species and in particular in *Q. ilex* (Montserrat-Marti et al., 2009; Ogaya and Penuelas, 2006; Rapp, 1969). Such a mechanism may also contribute to maintain the water transport capacity of *Q. ilex* under long lasting drought as proposed by Martin-StPaul et al. (2013). Current-year drought causes GPP and less so NPP to decline, so that CUE declines slightly. In a wet year following a drier one, CUE could decline because $\mathrm{ANPP}_{\mathrm{stem}}$ would be ruled by current climate and would be high as corresponds to a wet year, while leaves would be produced in fewer amounts due to one-year-lag effect of drought on leaf production and CUE could decline. Further researches could be necessary to quantify such carry-over effect on CUE. Perhaps the strategy of *Q. ilex* to buffer the hydraulic system from climatic extremes has a penalty on CUE.

Based on the responses to drought of the different compartments and on the assumptions stated above (see Materials & Methods) we calculated the yearly *CUE* response to drought (Fig. 5). *CUE* slightly decreased with drought from 0.419 at *WSI* = -100 MPa day to 0.373 at *WSI* = -400 MPa day. Interestingly, *CUE* declined at a slower rate than *GPP* and *NPP* in response to water deficit (Fig. 5). Maseyk et al. (2008) reported a constant CUE of 0.4 in a *Pinus halepensis* forest growing in a semi-arid Mediterranean-type climate and proposed that acclimation of maintenance respiration to dry conditions could help maintaining *CUE* and productivity relatively high under such water limited climate. Recent studies at our site showed that respiration rates declined exponentially in both leaves and stems as tree water availability decreased through summer months (Rodríguez-Calcerrada et al., 2011; Rodriguez-Calcerrada et al., 2014). Based on the relationships between leaf/shoot predawn water potential and leaf/stem respiration we calculated that stem and foliage CO_2 efflux declined by 4.7% and 7.1%, respectively, for an increase of drought severity of *WSI* = 100 MPa day. Altogether, acclimation of leaf, stem and root respiration to plant water deficit buffers *NPP* sensitivity to drought and contributes to maintain *CUE* relatively constant across years of widely different rainfall and vegetation stress. The ultimate reasons for such reduction in respiration rates are still unclear, but it appears that reduced demand of respiratory products from growth and maintenance processes may cause a down-regulation of mitochondrial activity (Atkin and Macherel, 2009).

Besides reductions in autotrophic respiration, changes in R_h contribute to complicate our understanding of the impact of drought on the whole ecosystem C sink strength. In trees, acclimation refers to strictly physiological processes; while in soils changes in R_h refer to ecosystem-level phenomenon potentially driven by multiple mechanisms including substrate depletion, changing microbial community composition, and physiological changes. Substantial questions remain about its response to soil water status, the interactions with substrate quality, and the role of the top soil drying-rewetting cycles (Wei et al., 2010). The course of soil water content at time scales shorter than the season is not necessarily correlated to the *WSI*. In Mediterranean-type ecosystems, R_h is likely more influenced by an unpredictable supply of substrate to the rhizosphere than by changes in the microbial community or its efficiency (Curiel Yuste et al., 2014). Finally we suggest as Hopkins et al. (2013) did that substrate availability *sensu lato*, including *GPP* and storage of nonstructural C pool (neglected here), may be the ultimate driver of the two respiration fluxes.

5. CONCLUSIONS

Comparative measures of ecosystem fluxes and production components across 11 years of contrasting water limitations in a *Q. ilex* stand help to better understand how Mediterranean-type forest ecosystems will respond to the ongoing climate change and to better project future C sequestration capacity.

We observed a clear effect of water availability in limiting all the ecosystem fluxes *GPP*, R_{eco} and *NEP*, and that the drought-induced decline in R_{eco} dampens the decline of the ecosystem C sequestration under drought conditions. In parallel, all the growth components were found to be affected by water limitation, with a partition of *GPP* into tissues that tends to minimize the negative impacts of drought on growth. An important result is that all the changes followed the same trajectory as water stress varied over a large range of conditions, from a wet year to a dry year occurring only once every 67 years. We did not observe any tipping point or discontinuity in the C partitioning pattern. On average, only 40% of the carbon assimilated as gross photosynthesis was used to construct new tissues, with the remaining 60% being respired back to the atmosphere as autotrophic respiration. This low ecosystem *CUE* could be inherited from the ancient management of the ecosystem as a coppice and its large amount of standing belowground biomass.

There are several ecological issues that question the values of the estimated C fluxes and their changes with increasing drought severity. It appeared in our case that autotrophic respiration by trees and heterotrophic respiration by soil microorganisms are primarily responsible for mediating the larger part of the carbon exchanges between the biosphere and atmosphere. Climate changes and projected increasing dryness have the potential to influence the activity of trees regulating exchanges among the carbon pools. Functional 'down-regulation' or acclimation of plant respiration could reduce the respiratory autotrophic loss of ecosystems, but unlike plant components, the existence of this phenomenon in heterotrophic respiration remains more controversial (Harmon et al., 2011; Wieder et al., 2013). Current models can simulate *GPP* relationships with autotrophic fluxes in a warmer environment (Piao et al., 2010; Wythers et al., 2013), yet the parameterization of models able to capture the apparent respiratory acclimation of both R_a and R_h to water limitation of ecosystems is an emerging challenge for the modeling and flux research communities. We suggest that both communities should adopt a bottom-up approach to advance our understanding at tissue, tree and ecosystem scales to increasingly larger time and space scales.

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TABLES

Table 1. Parameters of the linear ordinary least-square regression lines between the water stress integral *WSI* in MPa day and components of the ecosystem yearly C budget and aboveground components of the productivity. α_{OLS} is the slope of the Y *vs.* X relationship. *GPP*, R_{eco} and *NEP* are gross primary productivity, ecosystem respiration and net ecosystem productivity respectively, in g C m^{-2} yr^{-1}. The components of the aboveground productivity for leaves, reproductive effort and stem $ANPP_{leaf}$, $ANPP_{reprod}$ and $ANPP_{stem}$ are also expressed in g C m^{-2} yr^{-1}

Y versus X	α_{OLS}± SE	β_{OLS}± SE	r^2	F	p	n
GPP versus WSI	1.91 ± 0.43	1675 ± 97.5	0.72	20.1	0.0021***	10
R_{eco} versus WSI	0.77±0.32	1144±72.5	0.42	5.8	0.042*	10
NEP versus WSI	1.15 ± 0.20	531.3 ± 46.2	0.80	32.2	0.0005***	10
$ANPP_{leaf}$(t)°versus WSI(t-1)	0.41 ± 0.15	233.0 ± 34.6	0.52	7.5	0.03*	9
$ANPP_{leaf}$(t)°versus WSI(t)	-0.12 ± 0.19	116.1 ± 43.6	0.05	0.41	0.54ns	9
$ANPP_{reprod}$ versus WSI	0.10 ± 0.04	49.1 ±8.8	0.48	7.2	0.027*	10
$ANPP_{stem}$ versus WSI	0.42 ± 0.10	162.9 ± 22.5	0.69	17.9	0.0029***	10

Table 2. Literature values of carbon use efficiencies (CUE) for a broad range of forests

Ref.	Vegetation	*CUE*
This work	*Quercus ilex* coppice	0.40 (0.37-0.42)
Oechel & Lawrence 1981	MTE spp.	0.38
Waring et al. 1998	Broad range of forests (BRFs)	0.47±0.04
Medlyn & Dewar 1999	BRFs	0.31-0.59
Gracia et al. 1999	*Quercus ilex* coppice	0.41
De Lucia et al. 2007	BRFs	0.53(0.23-0.83)
Luyssaert et al. 2007	Mediterranean warm evergreen	0.54
Litton & Giardina 2008	BRFs	0.43
Luyssaert et al. 2009	Temp. & boreal forests	0.51±0.02
Piao et al. 2010	BRFs (MAT = 13°C)	0.475
Vica et al. 2012	BRFs with low-nutrient availability	0.42±0.02

FIGURES

Fig. 1. Ordinary least-square regression lines between the water stress integral WSI and gross primary productivity *GPP* (light grey circle) and net ecosystem productivity NEP (dark grey circle). *WSI* is expressed in MPa day and both *GPP* and *NEP* in g C m^{-2} yr^{-1}. 2005 data not used in the analysis were also plotted (empty square for GPP and empty triangle for NEP).

Fig. 2. Ordinary least-square regression lines between the water stress integral *WSI* and the net productivity of stems (dark grey circle and standard-deviation). *WSI* is expressed in MPa day and $ANPP_{stem}$ in g C m^{-2} yr^{-1}. 2005 data not used in the analysis were also plotted (empty triangle).

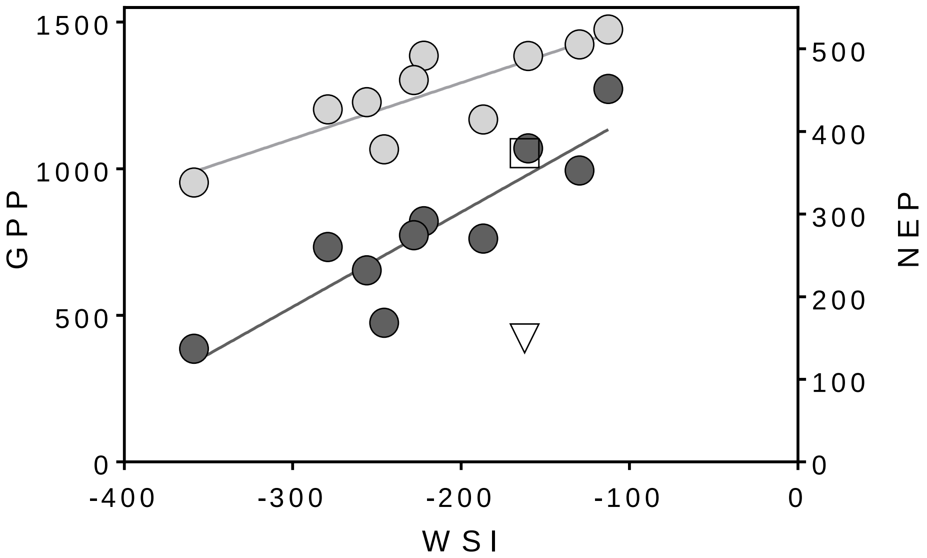
Fig. 3. Ordinary least-square regression lines between the water stress integral *WSI* and the net productivity of the reproductive effort (flowers and fruits; dark grey circle and standard-deviation). *WSI* is expressed in MPa day and $ANPP_{reprod}$ in g C m^{-2} yr^{-1}. 2005 data not used in the analysis were also plotted (empty triangle).

Fig. 4. Ordinary least-square regression lines between the water stress integral *WSI* of the previous year and the aboveground net productivity of leaves of the current year (dark grey circle and standard-deviation). *WSI* is expressed in MPa day and $ANPP_{leaf}$ in g C m^{-2} yr^{-1}. 2005 data not used in the analysis were also plotted (empty triangle).

Fig. 5. Change in the partition of gross primary productivity (*GPP*) with increasing drought intensity (*WSI*). The red line displays the decline of *GPP* with decreasing *WSI*. The net primary productivity (*NPP*) components are: perennial aboveground + belowground parts (dark grey), reproductive effort (flowers and fruits; medium grey), leaves and fine roots (light grey). The dashed red curve is for the carbon-use efficiency *CUE*.

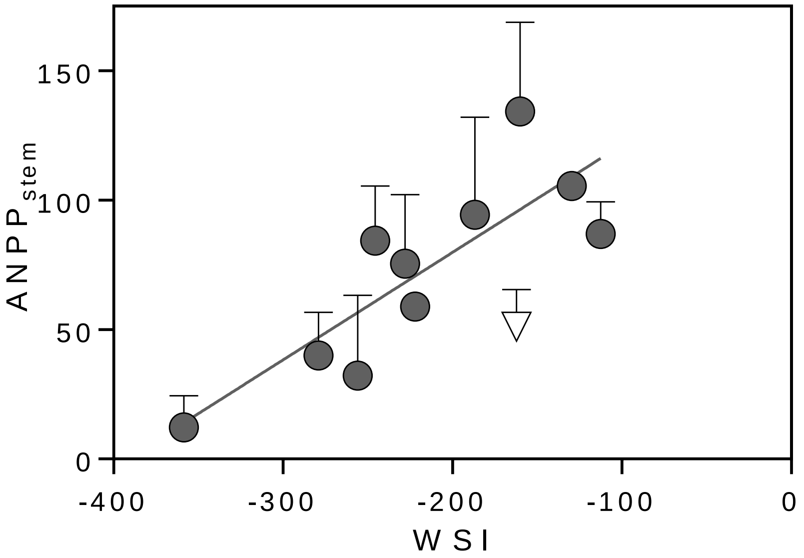
Fig. 6. Change in the ecosystem respiration, R_{eco} (grey curve), net ecosystem productivity, NEP (dark line) and net primary productivity, *NPP* (light grey area) with increasing drought intensity (*WSI*). The dashed red curve is for the R_a/GPP ratio and the brown curve for the R_h/R_{eco} ratio.

807 **Fig. 1.**


GPP
1500
1000
500
0
NEP
500
400
300
200
100
0
-400
-300
-200
-100
0
WSI

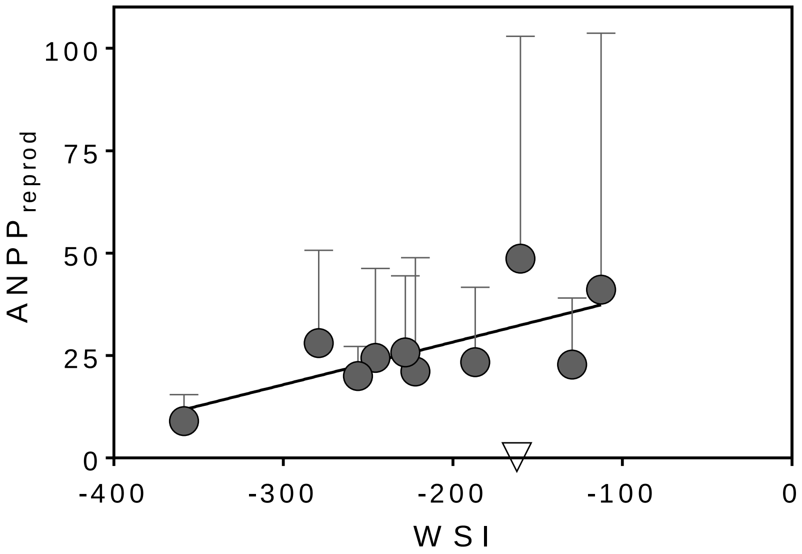
808

809 **Fig. 2.**



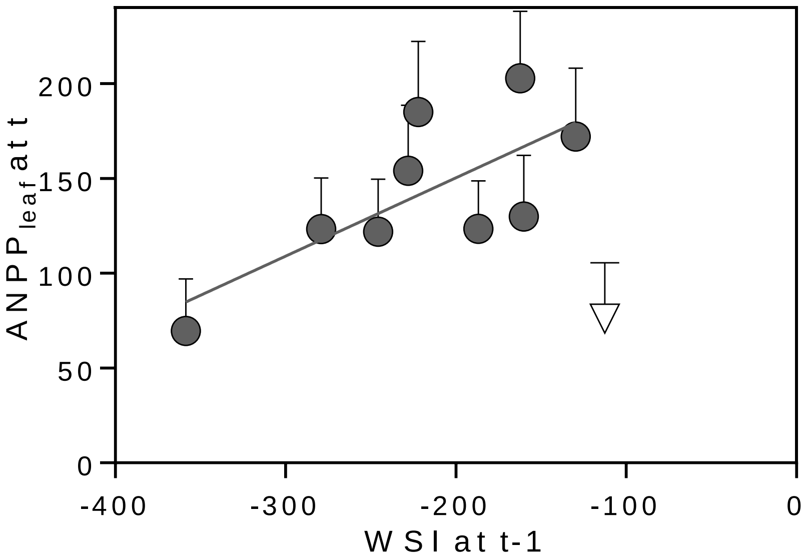
810

811 **Fig. 3.**



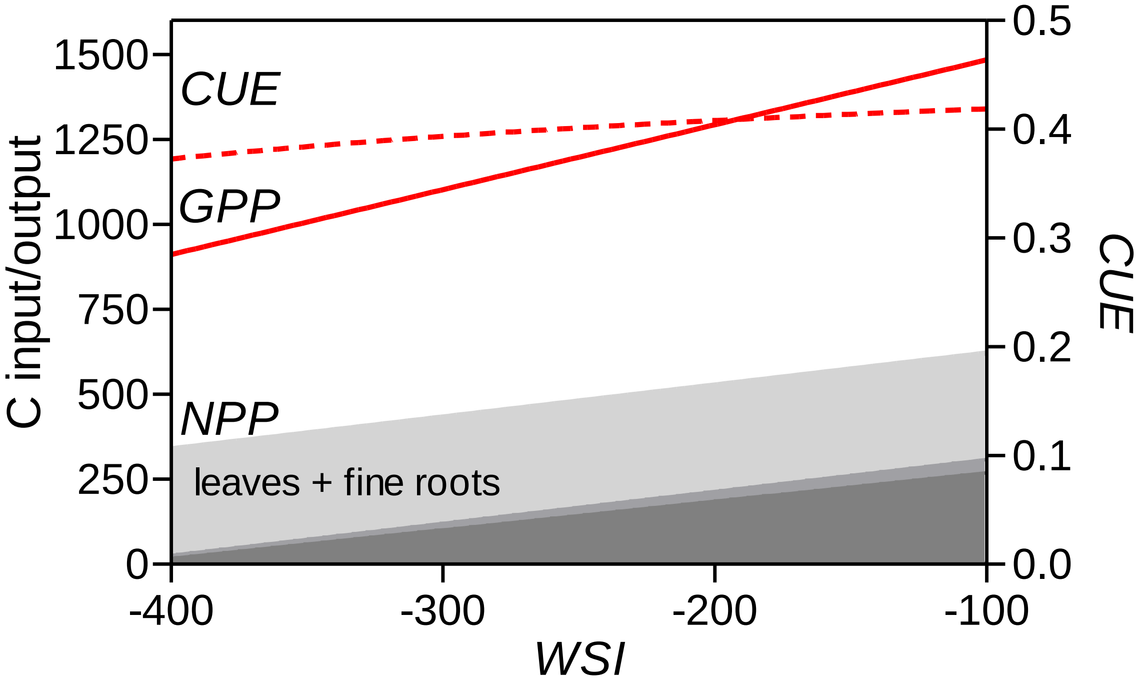
812

813 **Fig. 4.**



814

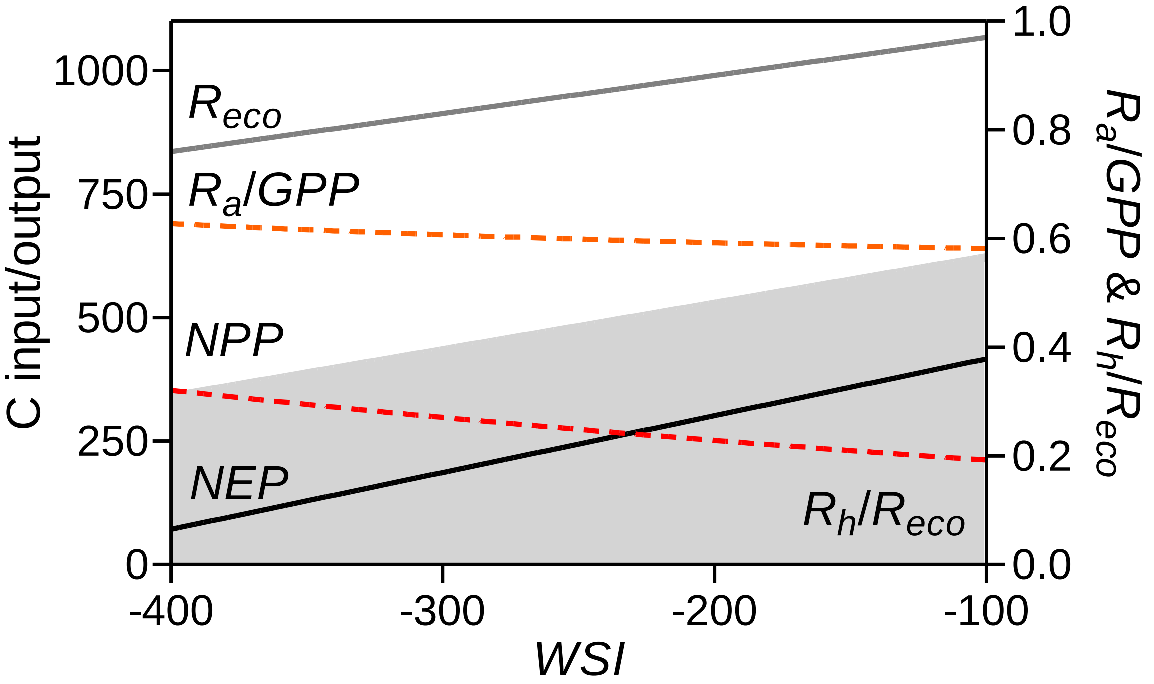
815 **Fig. 5.**



CUE
GPP
NPP
leaves + fine roots
C input/output
1500
1250
1000
750
500
250
0
0.5
0.4
0.3
0.2
0.1
0.0
CUE
-400
-300
-200
-100
WSI

816

Fig. 6.



1000
750
500
250
0
C input/output
R_{eco}
R_a/GPP
NPP
NEP
R_h/R_{eco}
1.0
0.8
0.6
0.4
0.2
0.0
R_a/GPP & R_h/R_{eco}
-400
-300
-200
-100
WSI

APPENDICES

Fig. A1. Relationship between aboveground perennial biomass and the corresponding belowground biomass. The belowground biomass is the sum of biomass values for root crown, roots greater than 5 cm, roots ranging from 1 to 5cm diameter.

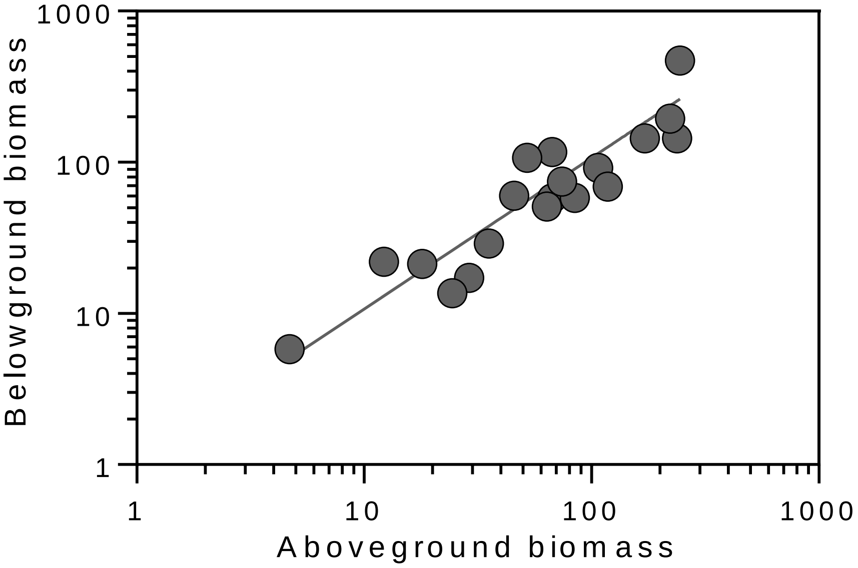


Fig. A2. Time course of the peak LAI derived from continuous measurements of half-hourly f_{APAR} between 11 AM and 1 PM from DOY 205 to 225. The Stem Area Index *SAI* was estimated by image processing of hemispheric photography and assumed constant for the whole period and equal to 0.5. The relationship between leaf area index and water stress integral (WSI) is statistically non-significant.