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Improved understanding of drought controls on seasonal variation in Mediterranean forest canopy CO_2 and water fluxes through combined in situ measurements and ecosystem modelling

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Abstract

Water stress is a defining characteristic of Mediterranean ecosystems, and is likely to become more severe in the coming decades. However, our current understanding of how soil moisture controls ecosystem functioning is not sufficient to adequately constrain model parameterisations.

Canopy-scale flux data from four forest ecosystems with Mediterranean-type climates were analysed in order to determine the physiological controls on carbon and water flues through the year. Stomatal and non-stomatal limitations on photosynthesis were separated, and new parameterisations were derived and implemented in two independent modelling approaches.

The effectiveness of the two approaches to ecosystem process-based modelling, one a dynamic global vegetation model (ORCHIDEE), and the other a forest growth model (GOTILWA+), was assessed and modelled canopy responses to seasonal changes in soil moisture were analysed with respect to in situ flux measurements.

In contrast to commonly held assumptions, we find that stomatal control does not dominate photosynthesis under natural seasonally-developing soil moisture stress. However, applying a soil moisture dependency to photosynthetic capacity results in accurate prediction of both carbon and water fluxes under all soil moisture levels encountered in the field. The new parameterisation has important consequences for simulated responses of carbon and water fluxes to seasonal soil moisture stress, and will greatly improve our ability to anticipate future impacts of climate changes on the functioning of Mediterranean ecosystems.

1 Introduction

The Mediterranean region contains a highly distinctive endemic flora and is characterised by warm wet winters and hot dry summers, with ecosystem functioning dominated by the seasonal cycle of water availability (Allen, 2001). Soil water availability is the main factor limiting vegetation growth in the Mediterranean (Boyer, 1982), and changes in regional temperatures and precipitation are placing increasing stresses on these vulnerable ecosystems (e.g. Jump et al., 2006). Climate models predict further increases in temperature in the future, with changes in rainfall patterns (Giorgi et al., 2004; Giorgi, 2006), leading to a decrease in water resources and negative impacts on ecosystem integrity (IPCC 2007, Summary for Policymakers).

However, our ability to predict with confidence the impacts of changing climate on these ecosystems is poor due to a lack of understanding concerning ecophysiological responses to soil moisture stress and consequent effects on primary production and the cycling of carbon and water (Loreto and Centritto, 2008). There is also considerable uncertainty concerning the role of Mediterranean forests as either sinks or sources of CO_2 due to wide variation in published data and their interpretation, particularly with respect to inventory-based estimates (Schimel, 1995). Correctly understanding current, and thus anticipating future land-atmosphere exchanges of water and carbon in the Mediterranean region is essential for predicting water resource availability and the future functioning of ecosystems, which provide services such as the production of raw materials, sequestration of carbon, and numerous recreational benefits (Schröter et al., 2005).

A thorough assessment of the vulnerability and likely future development of Mediterranean ecosystems requires the application of climate-driven, process-based models. Such models must incorporate the relevant ecosystem processes to successfully simulate the sensitivity of ecosystem functioning to soil moisture stress at all time scales of interest. However, existing models tend to have systematic difficulties in simulating processes Mediterranean ecosystems, exemplified by difficulties in reproducing the effects of seasonal droughts on carbon and water fluxes (Krinner et al., 2005; Morales et al., 2005; Reichstein et al., 2007; Jung et al., 2007), and likely due indirectly to the temperate bias in model development priorities. This paper aims to correct this situation.

Stomata are key organs in determining the ability of plants to thrive in drought-prone regions. A common approach to modelling stomatal conductance is to assume a linear relationship with leaf- or canopy-level photosynthesis, the leaf surface concentration of CO_2, and relative humidity or vapour pressure, the so-called "Ball-Berry" (BB) and "Ball-Berry-Leuning" (BBL) parameterisations (Ball et al., 1987; Leuning et al., 1995). Such relationships underpin the coupling of water and carbon cycles in many process-based ecosystem models. Recent studies have suggested, however, that such an empirical relationship does not hold under conditions of soil moisture stress (Reichstein et al., 2003; Misson et al., 2006). The effect of water stress on plant photosynthesis and stomatal conductance has been widely studied (Wilson et al., 2000; Chaves et al., 2002), but there is little consensus as to those processes governing responses over seasonal time-scales (Warren, 2008). The most widely accepted hypothesis for the control on photosynthesis during water-stressed periods is a reduction in the supply of CO_2 to the carboxylation sites through stomatal closure (e.g. Chaves et al., 2002), but some studies also indicate a direct water stress effect on photosynthesis (e.g. Medrano et al., 2002).

Studies suggest that stomatal conductance during short-term water stress can be effectively included in the BB and BBL (BB-type) models by reducing the ratio of conductance to photosynthesis with increasing soil moisture stress (Tenhunen et al., 1990; Harley and Tenhunen, 1991; Sala and Tenhunen, 1994). Both models also take into account a residual, or base conductance level, which has also been reported to change under water stress (Misson et al., 2004). Such functions imply that only stomatal aperture is affected by soil moisture levels, whereas there is substantial evidence that photosynthetic capacity is directly affected by soil moisture (Medrano et al., 1997; Parry et al., 2002). Stomatal conductance and photosynthetic capacity tend to be closely correlated (Cowan, 1977; Wong et al., 1979; Hetherington and Woodward, 2003), leading to the suggestion that it is in fact photosynthetic activity that determines stomatal aperture in order to maintain biochemically optimal rates of CO_2 supply (Cowan, 1977; Wong et al., 1979; Flexas and Medrano, 2002; Medrano et al., 2002; Galmes et al., 2005). This has lead to much discussion concerning the relative roles of stomatal and non-stomatal limitations during drought periods (e.g. Jones, 1985; Ni and Pallardy, 1992; Kubiske and Adams, 1993; Wilson et al., 2000), in particular over responses over different time scales (Lawlor, 1995; Tezara et al. 1999; Cornic 2000; Lawlor and Cornic 2002; Flexas and Medrano 2002).

Changes in non-stomatal limitations have been detected (Wilson et al., 2000; Grassi and Magnani, 2005), which have been hypothesised to relate to either changes in photosynthetic capacity (Medrano et al. 1997; Parry et al., 2002), or the conductivity of the mesophyll cell walls to CO_2 (e.g., Warren, 2008). These studies give weight to a number of studies showing that non-stomatal limitations come into play during seasonal soil water stress (e.g., Colello et al., 1998; Xu and Baldocchi, 2003), with many photosynthetic parameters shown to be closely correlated with stomatal conductance (Medrano et al., 2002). However, conflicting results, often depending on the strength and duration of the water stress, have resulted in great uncertainty as to which limitation is strongest under natural water-stressed conditions (e.g. Lawlor, 1995; Tezara et al., 1999; Lawlor and Cornic, 2002; Flexas and Medrano, 2002; Breda et al., 2006).

Such uncertainty in our knowledge of leaf level responses to seasonal drought, and how to model them, is potentially a large source of error when modelling Mediterranean-type forest ecosystems due to the seasonal drought cycles annually encountered in such ecosystems. In this paper, we address this problem from the pragmatic perspective of determining the most straightforward additional parameterisation that can accurately reproduce observed seasonal cycles of carbon and water fluxes across a range of different forest ecosystem types. Using FLUXNET observations of carbon and water fluxes made over four different Mediterranean-type forest ecosystems, we investigate the relationships between the fluxes and calculated seasonal soil moisture variations. These data are further analysed to determine relative stomatal and non-stomatal limitations to photosynthesis.

The understanding derived from the observations is then incorporated into two independent process-based ecosystem models: GOTILWA+, a biogeochemical forest growth model (Gracia et al., 1999; Keenan et al., 2008; http://www.creaf.uab.es/

GOTILWA+), and ORCHIDEE, a dynamic global vegetation model (Krinner et al., 2005; http://ORCHIDEE.ipsl.jussieu.fr), which each originally used different approaches to modelling drought stress effects. Simulations are performed at each of the four sites in order to test the understanding provided by the data analysis by evaluating modelled responses of photosynthesis and conductance to changes in soil water.

2 Materials and methods

2.1 FLUXNET site data and data manipulation

Measurements of ecosystem carbon and water fluxes were obtained from the FLUXNET database (http://www.fluxnet.ornl.gov) for three sites in Mediterranean Europe (Puechabon, France; Roccarespampani, Italy; Collelongo, Italy.), maintained under the CarboEurope-EUROFLUX project (Allard et al., 2008; Kowalski et al., 2004; Valentini et al., 1996), and one site at a location with a mediterranean-type climate in California (Blodgett, California), maintained under the AMERIFLUX project (Goldstein et al., 2000). Together, these data from the four sites amount to a total of eleven measurement years (Table 1). These sites cover a range of phenological types, including temperate broadleaf deciduous, temperate needleleaf evergreen, and temperate broadleaf evergreen types, with varying levels of summer drought stress. These monospecific forest sites include the species *Quercus ilex, Quercus cerris, Fagus sylvatica*, and *Pinus ponderosa*. FLUXNET datasets include measurements of carbon dioxide and water fluxes at half-hourly time steps (Wofsy et al., 1993). We used the level-4 datasets, in which flux separation techniques for splitting the observed net carbon fluxes into assimilation and respiration have been employed (Reichstein et al., 2005). Gap-filled data were excluded.

2.1.1 Inverting soil moisture and canopy conductance from FLUXNET data

Soil moisture. Interpreting the responses of observed carbon and water fluxes to changes in soil moisture requires the seasonal evolution of soil water content to be known. In the absence of direct measurements in the FLUXNET dataset, daily soil moisture content at each site was reconstructed using a simple water balance model through inverting the evapotranspiration rate inferred from the measured latent heat flux, and determining the balance with inputs from precipitation and outputs to run-off and below-ground drainage. Run-off is calculated as a percentage of precipitation, and depends on the soil hydraulic gradient and porosity of the soil upper layer. Drainage is calculated to be inversely proportional to fractional soil water content (calculated as in Gracia et al., 1999, and Honeysett and Ratkowsky, 1989).

Canopy conductance. In order to assess conductance responses to changes in soil water content we first calculate canopy conductance directly from the measured latent heat flux. The bulk canopy conductance (including the bulk leaf and canopy boundary layers) to water vapour, expressed on a ground-area basis, can be estimated from observed latent heat flux under dry canopy conditions and when it is assumed that soil evaporation is negligible. We inverted the McNaughton and Black equation for canopy latent heat flux (McNaughton and Black, 1973) to estimate bulk canopy conductance, G_c:

$$G_c = LH.\varepsilon.\lambda.\gamma/(\rho.Cp.vpd) \tag{1}$$

where LH is the observed latent heat flux ($\mathrm{W\,m^{-2}}$), ε is the coefficient for the conversion of latent heat to its water equivalent (giving actual evapotranspiration (E_a)), λ is the latent heat of vaporisation of water ($2.27\,\mathrm{MJ\,kg^{-1}}$), γ is the psychrometric constant ($0.66\,\mathrm{kPa\,K^{-1}}$), ρ is the density of air ($\mathrm{kg\,m^{-3}}$), Cp is the heat capacity of air ($1012\,\mathrm{J\,kg^{-1}\,K^{-1}}$), and vpd is the observed vapour pressure deficit (Pa) above the canopy. As all measurements used in the calculation of bulk conductance were made above the canopy, boundary layer effects are implicit in the calculation of bulk conductance.

2.1.2 Deriving relationships between bulk canopy conductance, canopy photosynthesis, and soil moisture stress

Bulk canopy conductance models and soil moisture stress. Ball et al. (1987) proposed a semi-empirical stomatal model (BB model) in which stomatal conductance was expressed by the leaf photosynthetic rate, relative humidity over a leaf surface, and the ambient CO_2 concentration, under conditions of ample water supply (Ball et al., 1987). This model was later developed by Leuning (BBL model) to include the effects of vapour pressure deficit and the photorespiratory compensation point (Leuning, 1995). This BB-type leaf level model can be applied at the canopy scale through the use of bulk canopy level variables (Leuning et al., 1995):

$$G_c = G_{s0} + (m.A_n)/((C_a - \Gamma^*).(1 + (vpd/D_0))) \quad (2)$$

where G_c ($\mathrm{mol\,H_2O\,m^{-2}\,s^{-1}}$) is bulk canopy conductance to moisture, G_{s0} is the value of G_c at the light compensation point ($\mathrm{mol\,m^{-2}\,s^{-1}}$), A_n is the rate of net photosynthesis ($\mathrm{\mu mol\,m^{-2}\,s^{-1}}$), C_a is the atmospheric concentration of CO_2 at the canopy surface ($\mathrm{\mu mol\,mol^{-1}}$), Γ^* is the photorespiratory compensation point ($\mathrm{\mu mol\,mol^{-1}}$), D_0 (unitless) is an empirical coefficient that describes the sensitivity of conductance to *vpd*, and m is an empirical species-specific factor that specifies the baseline ratio between conductance and net photosynthesis (unitless).

Soil moisture stress has been added to BB-type conductance models through changes in m, and $G_{s0.}$ Given G_c, (from Eq. 1) m, and G_{s0} can be calculated for each site (using a bulk parameterisation and one canopy layer) by applying linear regression to Eq. 2, thus obtaining the slope (m) and intercept (G_{s0}) of the linear relation. This was performed for each site using data selected as outlined in Sect. 2.1.3. These values were calculated at different soil water levels to assess possible responses to soil water availability.

Non stomatal conductance-related limitations of photosynthesis due to soil water stress. Evidence for any reductions in photosynthetic capacity under soil moisture stress were assessed by comparing rates of photosynthesis at different soil moisture contents but over a restricted range of leaf C_i concentrations ($220<C_i<300$), radiation ($>250\,\mathrm{W\,m^{-2}}$), and temperature ($<25\,^{\circ}\mathrm{C}$). Any differences in rates of assimilation under otherwise non-limiting conditions could then be attributed to non-stomatal soil water effects, rather than changes in the rate of supply of CO_2 to the intercellular spaces, light limitation, or any temperature effects.

Radiation and temperature are available from FLUXNET measurements. Canopy bulk leaf intercellular CO_2 concentration (C_i) can be calculated using the estimated bulk canopy conductance to carbon, $G_{c_{\mathrm{CO_2}}}$ ($=G_c/1.6$), observed rates of net photosynthesis from the eddy-covariance measurements, and atmospheric CO_2 concentrations using a simple supply and demand function:

$$C_i = C_a - (A_n/G_{c_{\mathrm{CO_2}}}) \tag{3}$$

2.1.3 Data selection

All analysed FLUXNET data were first screened to remove night-time values. Only daytime values were considered by selecting data corresponding to half-hours with radiation of $200\,\mathrm{W\,m^{-2}}$ or greater, and assimilation rates of $2\,\mu\mathrm{mol\,CO_2\,m^{-2}\,s^{-1}}$. Screening was also performed to remove data points measured during, or close to, precipitation events, and extreme temperatures (below 5° or above 35°). Gap filled data was not considered.

2.2 Ecosystem models

2.2.1 GOTILWA+

GOTILWA+ ("Growth Of Trees Is Limited by WAter"), (Gracia et al., 1999; Keenan et al., 2008; www.creaf.uab.es/GOTILWA+) is a process-based forest growth model that has been developed to simulate tree growth and to explore how it is influenced by climate, tree stand structure, management techniques, soil properties, and climate (including CO_2) change. GOTILWA+ simulates carbon and water fluxes within forests in different environments, for different tree species, and under changing environmental conditions, either due to climate or to management regimes.

The model treats monospecific stands which can be even- or uneven-aged. Individual trees are aggregated into 50 DBH (Diameter at Breast Height) classes and calculations are performed for each class. Ecosystem carbon and water fluxes are estimated using hourly meteorological forcing.

GOTILWA+ includes a two-layer canopy photosynthetic model (Wang and Leuning, 1998), coupled to a carbon allocation and growth model and a soil respiration and hydrology model. The photosynthesis sub-model treats the C_3 photosynthetic pathway. Leaves in each layer are split into sun and shade leaves, with intercepted radiation depending on the time of the day, and the area of leaf exposed to the sun based on leaf angle and the canopy's ellipsoidal leaf distribution. Assimilation rates are calculated using the approach of von Caemmerer and Farquhar (1981), with dependencies on intercepted direct and diffuse radiation, species-specific photosynthetic capacities, leaf temperature, and the available leaf C_i concentration. Stomatal conductance is calculated using the BBL model.

Each tree cohort is represented by three carbon compartments, leaf, sapwood, and fine roots. Labile carbon is allocated to each, and maintenance respiration is calculated as a function of temperature. Fine litter fall (i.e. leaves), gross litter fall (i.e. bark, branches) and the mortality of fine roots add to the soil organic carbon content. The soil in GOTILWA+ is divided into two layers, an organic layer and a mineral layer, with a rate of transfer of soil organic carbon between them. Soil water processes are described in Sect. 2.1.1. Flux calculations are performed hourly, whereas slower processes such as growth and other state variables are calculated daily.

2.2.2 ORCHIDEE

ORCHIDEE is a process-based terrestrial biosphere model that simulates terrestrial vegetation and soil energy, water, and carbon fluxes (Krinner et al., 2005). Changes in vegetation structure and distribution in response to environmental parameters are also simulated.

ORCHIDEE consists of three major components: (a) SECHIBA, which calculates the exchanges of energy and water between the atmosphere and the land surface; (b) STOMATE, which simulates photosynthesis, carbon allocation, litter decomposition, soil carbon dynamics, maintenance and growth respiration and (c) the LPJ dynamic vegetation model (Sitch et al., 2003), which simulates long-term changes in the composition and structure of vegetation resulting from sapling establishment, light competition, and tree mortality. Energy, water, and carbon fluxes resulting from photosynthesis and autotrophic and heterotrophic respiration are calculated on a half-hourly basis, whereas plant growth, phenology, and vegetation structure occur on a daily timestep.

Vegetation in ORCHIDEE is classed into plant functional types with different phenological, physiological, and morphological characteristics: temperate needle-leaved evergreen, temperate broadleaved evergreen, temperate broadleaved deciduous, and C_3 herbaceous types are used in this study. In contrast to GOTILWA+, vegetation is represented as an average individual plant, with no accounting for size-distribution.

ORCHIDEE simulates photosynthesis for both C_3 (using the method of Farquhar et al., 1980) and C_4 (using the method of Collatz et al., 1992) photosynthetic pathways, with stomatal conductance calculated using the BB model. Soil water content is treated using two layers, with inputs from precipitation less canopy interception loss, and outputs to drainage, run-off, soil evaporation, and transpiration.

2.2.3 The effect of soil water stress on coupled photosynthesis-conductance models

Two common approaches (the application of stomatal or non-stomatal limitations) are most often used to incorporate the effect of drought stress on the (Farquhar – BB-type) coupled photosynthesis-conductance model. The original GOTILWA+ model applied stomatal limitations, whilst the original ORCHIDEE model applied non-stomatal limitations. We used both models to test three hypotheses: 1) directly reducing stomatal conductance (stomatal limitations) is sufficient to explain variation in carbon and water fluxes during drought stressed periods, 2) directly reducing photosynthesis (non-stomatal limitations) sufficiently constrains carbon and water fluxes during water stressed periods, and 3) the application of both stomatal and non-stomatal limitations is necessary to accurately simulate the observed flux data.

In the original GOTILWA+ model, stomata control the photosynthetic responses to drought stress through the application of a linear scalar of soil moisture, as:

$$G_s = G_{s0} + ((Wfac_{\text{stoma}}.m).(A_n - R_d))/((C_a - \Gamma^*).(1 + (vpd/D_0))) \tag{4}$$

where $Wfac_{\text{stoma}}$ is a soil moisture-dependent scalar with values between 0 and 1. This stomatal limitations function results in a linear reduction in conductance with reductions in soil moisture, thus limiting the CO_2 available for photosynthesis.

The second approach, used by the original ORCHIDEE, incorporates the effect of drought stress on the coupled photosynthesis-conductance model (of Farquhar – BB-type) by the way of non-stomatal limitations, by applying a scalar to photosynthetic potential as follows:

$$Vc\max = Vc\max * Wfac_{\text{photo}} \tag{5}$$

$$J\max = J\max * Wfac_{\text{photo}} \tag{6}$$

Where $Vc\,max$ and $J\,max$ are the maximum rate of RuBP carboxylation, and the maximum rate of electron transport, respectively, and $Wfac_{\text{photo}}$ is a soil moisture-dependent scalar with values between 0 and 1. This non-stomatal limitation function directly reduces photosynthesis under drought stress, thus reducing the demand for carbon and reducing conductance.

The two limitation functions, $Wfac_{\mathrm{stoma}}$ and $Wfac_{\mathrm{photo}}$, in the original models were linear scalars (Eq. 6 without the q factor). We parameterised each, independently for each site, from the stomatal limitations (changes in the slope, m) and non-stomatal limitations calculated in the data analysis, and modified the original functions to allow for the observed non-linear response.

$$Wfac = \begin{cases} 1, & if\, S(t) \geq S_{\max} \\ \left[\frac{s(t)-s_{\min}}{s_{\max}-s_{\min}}\right]^q, & \text{if } S(t) < S_{\max} \end{cases} \tag{7}$$

where q is a measure of the non-linearity of the effects of soil water stress on physiological processes, $s_{\max}$ the soil water content at which reductions are first evident, and $s_{\min}$ is the wilting point.

These modified, $Wfac_{\mathrm{stoma}}$ and $Wfac_{\mathrm{photo}}$, (Eq. 6) functions were then applied independently in both GOTILWA+ and ORCHIDEE, in order to test the different hypotheses.

2.2.4 Modelling protocol, hypothesis testing and model evaluation

Simulations with each model were run separately at each of the four sites to test the effectiveness of the different approaches to modelling drought stress responses. For each model and site, 4 runs were made with: 1) with the model's original water stress response functions, 2) the application of the modified stomatal limitations ($Wfac_{\mathrm{stoma}}$), 3) the application of the modified non-stomatal limitation ($Wfac_{\mathrm{photo}}$), and 4) the application of both the modified stomatal and non-stomatal limitations together.

Both models were run using the same half-hourly meteorological variables (temperature, precipitation, vapour pressure deficit, wind speed, global radiation, and atmospheric CO_2 concentration), which were taken from site observations, and site conditions including soil characteristics and hydrological parameters (Table 1). The conductance parameters, m and G_{s0} were calculated from the data (Table 2). In addition to the above site-level variables required by the two models, GOTILWA+ requires descriptions of stand characteristics (including the structure of the canopy and the DBH class distribution), and also some tree physiological parameters (biomass allocations and compartment specific growth and maintenance respiration rates).

GOTILWA+ simulations were initialised by specifying forest structure parameters specific to the first year of simulation at each site, with data obtained from the literature. ORCHIDEE simulations were initialised by prescribing the cover of each plant functional type for each site.

To enable evaluation of the canopy physiological process descriptions independent of potential inaccuracies in the modelled latent or sensible heat fluxes, which would confound any model-data comparison, the soil water contents in the models were forced to those given by the reconstruction. This decoupling of the simulation of soil and canopy processes was achieved by removing the water volume equivalent of the observed latent heat flux at each time step instead of the simulated evapotranspiration.

Statistics. The models were evaluated using the correlation coefficient r^2, the Root Mean Squared Error (RMSE), and the statistic Model Efficiency (MEF). The last is a complement to the r^2 statistic, and can be interpreted as the proportion of variation explained by a fitted line (Byers et al., 1989; Loague and Green, 1991). The upper bound of MEF is one (perfect match) and the (theoretical) lower bound is negative infinity (Loague and Green, 1991). The MEF statistic is more sensitive than r^2 to systematic deviations and is a useful additional tool in the assessment of goodness of fit (Mayer and Butler, 1993).

Golden Days. In order to evaluate model performance under peak flux conditions, we first consider "Golden Days" at each site, contrasting wet and dry periods. Golden Days are defined as days with no precipitation, midday radiation greater than 400 $\mathrm{W\,m^{-2}}$, frictional velocity of greater than 0.15 $\mathrm{m\,s^{-1}}$, and fully developed canopy leaf area index. Days with gaps in any data were excluded. Theoretically, for such days, the model performance should not be confounded by daily variability in environmental conditions, and the statistical analysis of model performance made easier.

3 Results

3.1 Primary fluxes

All sites showed typical Mediterranean-type climate evolution during the studied years, including an extended summer drought. Strong seasonal patterns were observed of reduced photosynthesis and transpiration during peak summer periods (Fig. 1), in contrast to higher fluxes during late spring. This was particularly noticeable at Puechabon, Collelongo, and Roccarespampani, and less so at the Blodgett site.

3.2 Data analysis results

Soil Water Content. Figure 2 shows the evolution of soil water content for each simulated site and year, derived by inverting latent heat fluxes as described in Sect. 2.1.1. At each site, the soil water content stays high throughout spring, being regularly recharged by precipitation events to compensate for any losses from evapotranspiration. The effect of the dry summer can be seen through strong decreases in the soil water content. Soil water levels generally return to maximum values during autumn, and remain relatively stable through winter. The Blodgett site soil water content shows little inter-annual variability due to the lack of inter-annual variability in its climate during the studied period. In comparison, at Puechabon annual summer soil water varies over a large range, with levels reaching a prolonged low during 2003 due to the notable drought experienced across many regions of Europe in that year. This drought period is also reflected at the Roccarespampani site, with soil water levels in 2003 reaching less than half of those in 2004. These levels correspond well with levels reported in other studies at the Puechabon site (Hoff et al., 2002; Rambal et al., 2003). We are not aware of similar data for the other sites.

Limitations of photosynthesis due to soil water stress. The estimates of soil water content in Fig. 2 are used with the observed flux data to determine whether stomatal limitations, non-stomatal limitations, or both vary significantly with soil moisture. Changes in the calculated slope (m, Eq. 2), and/or intercept (Residual conductance – G_{s0}, Eq. 2) would indicate a stomatal limitation to photosynthesis. Values for the slope and intercept of the BBL conductance model at high soil water content for each site are given in Table 2, and correspond well with reported values (e.g. Ball et al., 1987; Leuning, 1990; Collatz et al., 1991; Schultz and Lebon, 1995). These values were calculated for both the BB and BBL versions of the BB-type conductance model formulation and were found to be independent of the choice of model.

The fitted slope of the relation of stomatal conductance to assimilation in the BBL model, m, did not change notably during the slow onset of soil water stress and declined only slightly at very low soil water levels (<30% soil water holding capacity) (Fig. 2a). The fitted intercept in Eq. 2 did not change with decreases in available soil water in any of the sites (Fig. 2b). A similar lack of response was found at all sites.

Strong non-stomatal limitations were found under conditions of soil moisture stress at all sites except Blodgett. The point at which limitations were first encountered was between 60% and 80% RSWC, though at Blodgett non-stomatal limitations were not detected until 50% RSWC. Although inferred soil water in our reconstruction falls quite low in Blodgett, very little water stress is observed, suggesting either access to ground water, or an underestimation of the maximum soil water content used for the reconstruction. At the other three sites, stress progressed with site-dependent intensities. Roccarespampani showed the strongest non-stomatal limitation, followed by Puechabon and then Collelongo. The fitted $Wfac_{\text{photo}}$ functions from Eq. 5 are shown in Fig. 4, with parameters given in Table 2.

3.3 Modelled diurnal cycle and hypothesis testing

Evaluation of the stomatal vs. non-stomatal limitation hypotheses using process-based models. The effect of the alternative hypotheses is tested by incorporating the observed empirical relationships from Figs. 3 and 4 into the framework of the process-based models. The simulation of the diurnal courses of CO_2 and water fluxes during periods of high water availability was very accurate (Fig. 5a$_1$, a$_2$, b$_1$, b$_2$). Simulations during high water availability were relatively unaffected by the modelling approach chosen, due to the fact that the approaches only differ in their treatment of responses to water stress. Conversely, during periods of drought, responses to water stress were highly dependent on the chosen response description.

The shape of the diurnal cycle during dry periods, shown for the Roccarespampani site (Fig. 5), is relatively insensitive to the chosen soil moisture limitation approach for each process-based model system, demonstrated by a comparable r^2. The different approaches gave marked differences, however, in the root mean squared error (RMSE). Applying the calculated water stress functions presented in Table 2, to photosynthetic potential, led to a reduction of 80% in the RMSE for assimilated carbon using the GOTILWA+ model, and 47% in the case of ORCHIDEE, when compared to the original model parameterisation. Applying the water stress functions solely to stomatal control produced a marked increase in the RMSE (13%, GOTILWA+; 9%, ORCHIDEE, Table 3.).

The same pattern was reproduced at all sites, with marked improvements in the accuracy of simulations of the diurnal cycle of both net photosynthesis and transpiration under drought stress when photosynthetic capacity was reduced using Eq. 5. Remarkably, no direct effect of soil moisture on stomatal conductance was necessary to successfully reproduce the response of transpiration to water stress periods, i.e. both the standard BBL and BB models were sufficient for this purpose. Conversely, the application of the function to only stomatal conductance led to photosynthesis being overestimated under drought stress (by an average of 47% in Puechabon, 55% in Roccarespampani, 34% in Collelongo, and 8% in Blodgett, of monthly net photosynthesis values during water stressed months) (Table 3). Applying a stronger stomatal conductance restriction than that calculated from the data allowed for the effective simulation of stomatal conductance, but the lowered conductance was not sufficient to decrease assimilation rates.

We also tested the effects of applying the calibrated functions to both conductance and assimilation (Eqs. 4 and 5), thus applying stomatal and non-stomatal limitations together. This gave no improvement in the modelled carbon and water fluxes when compared to simulations applying just non-stomatal limitations to photosynthesis.

Comparing GOTILWA+ and ORCHIDEE. To evaluate the capacity of the two models to reproduce the observed fluxes simply by introducing the best fitting empirical model of soil moisture effects (i.e. non-stomatal limitations only), we relaxed the constraint on soil water content by observation (i.e. the models simulate their own water balance based on modelled latent heat fluxes and run-off) and repeated the simulations for each site (Fig. 6).

In well-watered conditions at Puechabon, both models accurately reproduced the shape of the diurnal time courses of CO_2 and water fluxes, with ORCHIDEE performing slightly better. Under dry conditions at Puechabon, both models responded accurately to the effect of drought.

CO_2 and water fluxes were accurately modelled by both models in Collelongo. Both models were capable of simulating net photosynthesis to a very high degree of accuracy in both wet and dry conditions. Water fluxes proved more difficult, with both models encountering the same problems, underestimating actual evapotranspiration during wet periods and overestimating in dry periods.

At Roccarespampani (Fig. 6), both models accurately reproduced carbon assimilation and actual evapotranspiration with an average model r^2 of 0.89 and a Mean Squared Error of 0.025 (Table 4).

Although the seasonal drought at Blodgett does not lead to a drop in assimilation rates and conductance, it does prevent both from reaching their potential seasonal maximum. This was well captured by both models. ORCHIDEE correctly calculated the rate of photosynthesis and conductance in wet conditions, as did GOTILWA+. In dry conditions GOTILWA+ accurately modelled assimilation rates, but both models had difficulties in calculating the quantity of water transpired, giving much lower transpiration rates than those observed.

It is worth noting that, statistically (Table 4), both models simulate the diurnal cycle of assimilated carbon equally well in water stressed conditions as they do in well watered conditions when including the new water stress function.

3.4 Seasonal cycle and inter-annual variations

Finally, ORCHIDEE and GOTILWA+ simulations for each site and the entire time series are compared to the observations in Fig. 7. The eleven site-years cover a wide range of inter-annual and inter-site variability in climatic variables, and thus varying levels of drought, with a particularly strong drought experienced in 2003 at the European sites. The effect of drought on photosynthesis, which is characterised by a sharp decline in assimilation rates in otherwise favourable conditions, is most obvious at Puechabon in all years, at Collelongo in 1998, and at Roccarespampani in 2003.

For Puechabon, both models were capable of accurately predicting photosynthesis in non-water stressed conditions. The timing of the onset of stress was also well captured in each year. The magnitude of stress encountered was accurately simulated in 2002, but overestimated in 2003 and 2004 when simulating with prognostic soil water. This was due to a slight overestimation of evapotranspiration in the period of high production before water stress was encountered, producing a lower soil water content during the water stressed period and a greater reduction in photosynthesis than observed. GOTILWA+ outperformed ORCHIDEE at Puechabon, giving a better correlation to the EUROFLUX data and a lower standard error. GOTILWA+ also performed better at the Blodgett site when simulating with a dynamic soil water content, where ORCHIDEE accurately captured carbon and water flux dynamics during spring, but largely overestimated the effect of drought on assimilation and conductance during summer periods.

Simulations at the two deciduous sites were complicated by an active understorey and problems in the prediction of the timing of phenological events. In Roccarespampani, both models produced an equal match to the data, but were prone to higher levels of standard error. Roccarespampani had significant vegetative growth beneath the canopy, which was not taken into account in GOTILWA+, but was simulated by ORCHIDEE. Relatively high latent heat fluxes were observed outside of the growing season of the deciduous oak, *Quercus cerris*. These were not reproduced by the models, which led to difficulties when simulating the evolution of available soil water at the Roccarespampani site. Phenology also proved difficult to model, with neither model capable of accurately predicting the timing of budburst or leaf-fall, particularly in 2003. In Collelongo, ORCHIDEE preformed better than GOTILWA+, which accurately reproduced the strength and duration of the drought in 1998 and the effect on photosynthesis, but due to inaccuracies in the prediction of budburst and leaf-fall dates, total photosynthesis over the growing season was overestimated.

With the inclusion of the water stress response calculated in Sect. 3.1, both models accurately capture the observed fluxes. GOTILWA+ give an average site r^2 of 0.90 for A_n and 0.82 for E_a, and an average MEF of 0.74 for A_n and 0.41 for E_a, over all sites. ORCHIDEE gave an average site r^2 of 0.84 for A_n and 0.59 for E_a, and an average MEF of 0.61 for A_n and 0.34 for E_a (Table 5). These values represent a marked increase in model accuracy when compared against the original models. For GOTILWA+ the new implementation lead to an average decrease of 22% in the RMSE over all sites for simulated A_n and a decrease of 9% in the RMSE of simulated E_a over all sites when compared against the original model formulation. For ORCHIDEE the RMSE for A_n was relatively unchanged (though the r^2 increased by 15%) and the RMSE for E_a decreased by an average of 21% over all sites. This also represents a big improvement when compared against the last published model comparisons including water stressed sites (Morales et al., 2005) (This study also included ORCHIDEE and

GOTILWA+).

4 Discussion

A number of recent studies have brought into question the ability of process-based models to accurately simulated seasonal changes in carbon and water fluxes in Mediterranean-type ecosystems (Krinner et al., 2005; Morales et al., 2005; Jung et al., 2007). The use of equations in which the photosynthetic response to drought solely depends on stomatal control fails to capture both the timing and extent of the response of the coupled photosynthesis-conductance system to water stress. From our analysis of half-hourly FLUXNET data at four Mediterranean-type sites, this appears not to be due to a fundamental inaccuracy in the description of stomatal conductance using the BB-type approach, but rather an incomplete description of the mechanisms controlling the seasonal response of the photosynthetic capacity of Mediterranean trees to high levels of gradually occurring water stress.

Detailed studies on the effect of water stress on the slope parameter of BB-type conductance models are lacking, and reported results are inconclusive. Several studies assert that the slope decreases as soil water stress increases (Harley and Tenhunen, 1991; Sala and Tenhunen, 1996), whilst others maintain that it remains constant (Sellers et al., 1996; Colello et al., 1998). We found that the relationship between G_s and A_n changed only slightly under soil water stress, giving an almost constant slope parameter. This suggests that stomatal conductance changes in parallel with photosynthesis, as originally reported by Wong et al. (1979). Our finding that the residual conductance does not change under soil water stress is contrary to results previously reported at the Blodgett site (Misson et al., 2004).

It is well known that the stomata react to changes in soil water availability. The water reserves in leaves and stems are very small when compared to the amount of water transpired, and thus could be quickly dehydrated in the absence of fast mechanisms, such as stomatal closure, to limit water loss (Slatyer, 1967). The effect of such stomatal closure is most commonly observed in the mid-day decline in stomatal conductance due to decreasing leaf water potential. This limits photosynthetic activity through reducing C_i. Such short-term responses are essential to conserving the plant hydraulic balance. However, with the slow onset of water stress, as experienced seasonally by all Mediterranean ecosystems, the picture becomes less clear. Other, slow acting processes have been identified, and can be divided into two categories: mesophyll conductance responses and metabolic adjustments (e.g. Loreto and Centritto, 2008). Changes in mesophyll conductance can reduce the concentration of CO_2 in the chloroplast with reference to leaf C_i. Whilst stomatal conductance rapidly changes to maintain the leaf hydraulic status, mesophyll conductance has been related to anatomical features and thus subject to slower responses, with large changes reported during the onset of slowly developing drought (e.g. Flexas et al., 2008). Metabolic adjustments can take many forms, and may include the reduction of enzymes necessary for RuBP regeneration and activity (Maroco et al., 2002), reduced nitrate reductase activity (as an indicator of nitrate utilisation) (Smirnoff and Stewart, 1985), and the reduction of sucrose phosphate synthase (Vassey and Sharkey, 1989). It has been suggested that all of these possibilities play some role in the control of photosynthesis (Loreto and Centritto, 2008), depending on the degree of water stress encountered and the relevant time scales involved.

The non-stomatal limitations in this study vary between sites. The two *Quercus* species, at Puechabon and Roccarespampani, showed similar responses, perhaps reflecting similarities in their leaf structure. *Quercus ilex* is an evergreen sclerophyllous species, commonly found in Mediterranean regions, and well adapted to drought stress with tough well structured leaves. *Quercus cerris*, although deciduous, also has a high sclerophyll index (Kutbay and Kilinc, 1994). Such structures have been reported to have high mesophyll conductance limitations (Loreto et al., 1992; Syvertsen et al., 1995). The *Pinus ponderosa* species studied at Blodgett encountered very little water stress, with only a minimal reduction in photosynthetic activity during periods of low soil water content. This could be explained by access to ground water and mild air temperatures during summer due to high altitude. *Fagus sylvatica*, found at Collelongo, is not a typical Mediterranean species, and is therefore not moisture-stress adapted. The low water stress encountered at this site could also be explained by the possibility of ground water access at this site as suggested by Hickler et al. (2006). The large role of non-stomatal limitations found at each site suggests that the observed reduction in canopy conductance during slowly progressing natural water-stressed periods is, to a large extent, driven by a decrease in demand, and not by a change in the relationship between canopy conductance and photosynthesis. That is to say that there is little evidence that BB-type models do not hold under natural water-stressed conditions.

The work presented here makes several assumptions regarding possible influencing factors which could not be quantified from the available data. It was first necessary to assume that stomatal patchiness does not have a significant effect when making calculations which average over the whole canopy. It has been reported, that, in leaf-level experiments, stomatal patchiness may invalidate leaf C_i calculations, in particular in drought conditions (Buckley et al., 1997; Mott and Buckley, 2000). However, more recent studies have shown that the influence of stomatal patchiness on calculations of leaf C_i is less than once thought (Lawlor and Cornic, 2002). Also, it has been reported that the effect of stomatal patchiness is not as large in the field as it is in laboratory experiments, due to the slow time-scale of the onset of drought (Gunasekera and Berkowitz, 1992; Kubiske and Abrams, 1993). In any case, the nature of the data analysed, gathered at the canopy scale under field conditions, leads to large variability in some of the variables necessary to construct the stomatal and non-stomatal response functions. For example, using observations only from mid-day periods or obtained for the Golden Days studied had minor effects on the calculated parameters of the soil water response functions.

Differences in the modelled soil structure and hydrology can lead to significant differences in evapotranspiration calculations and thus sensitivity of land surface fluxes to drought (Vetter et al., 2008). Furthermore, global model parameterisation, notably the assumed maximum soil water content, contributes significantly to the reported model-data difference (Jung et al., 2007). In this study, the inversion of latent heat flux measurements using a soil water flux model, and utilisation of observed maximum soil water storage capacity, has allowed the photosynthetic component in the models to be isolated, and the sensitivity of photosynthesis to soil water stress carefully examined.

Inaccuracies in the simulation of the seasonal cycle of carbon and water fluxes were attributed to difficulties in modelling phenological events, and the existence of active understory vegetation (which is not taken into account by GOTILWA+). Both models predict phenological events using a running mean of temperature, but were not capable of accurately predicting budburst at either of the two deciduous sites. Leaf-fall estimation was slightly better but was still not consistently accurate. Understory vegetation led to difficulties for GOTILWA+, as in the current version this is not taken into account. This led to the underestimation of spring water fluxes.

The role of non-stomatal limitations in modelling carbon and water fluxes, shown in this study, should apply to all C3 plant functional types, and will be of particular importance for performing regional scale modelling. Preliminary regional simulations with ORCHIDEE suggest that the new implementation leads, on average, to an 8% reduction in the predicted summer photosynthesis across the Mediterranean region. Any regional model applying only stomatal limitations will, therefore, be expected to overestimate assimilation from Mediterranean-type vegetation by an even greater amount. The applicability of the derived water stress parameterisations across different plant functional types is, however, as yet unclear, given the differences observed in the studied species. More research is needed to identify the range of water stress responses and suggest different plant functional types. This, coupled with difficulties in accurately modelling phenological events, which were inaccurately modelled at the two deciduous sites, will be the main challenges for regional modelling efforts in the Mediterranean, particularly for those looking at future vegetation dynamics in the region.

5 Conclusions

We have shown that canopy conductance and photosynthesis co-vary with soil moisture in a consistent manner using observations from four sites. Stomatal conductance was found to vary in parallel with photosynthesis, and with only small changes in the slope or the intercept, of the conductance-assimilation relationship. Changes in photosynthetic capacity not related to stomatal closure under water stressed conditions were found to be very important at each of the sites studied. Incorporating this knowledge into process-based models suggests that accounting for soil-water mediated reductions of photosynthetic capacity alone is sufficient to adequately model carbon and water fluxes during dry and wet periods. Pure stomatal regulation of photosynthesis during seasonal drought episodes is not sufficient to reduce modelled photosynthesis to observed level during drought periods. Accounting for the empirically-derived soil moisture responses of photosynthetic capacity with the derived parameters for each site improved substantially the performance of both models, and allowed for the simulation of carbon and water fluxes with a similar accuracy during wet conditions as under drought conditions. Both models compare well against the FLUXNET data, although GOTILWA+ performed slightly better on average.

This study contributes to improving our ability to model and predict carbon and water fluxes in Mediterranean-type forest ecosystems, and thereby to reducing uncertainty in future European terrestrial carbon and water fluxes. These results are of particular importance for any study of the effects of climatic changes on Mediterranean ecosystem functioning.

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Table 1. Characteristics of the FLUXNET sites chosen. Plant functional types (PFTs) considered are temperate broadleaved evergreen (TeBE), needleleaved evergreen (TeNE) and broadleaved-summergreen (TeBS). Max LAI – Maximum Leaf Area Index (m^2/m^2); SD – Soil Depth (m); SWHC – Soil Water Holding Capacity (kg/m^2).

Site	Period	Longitude	Latitude	Altitude	Max LAI	SD	SWHC	Species/PFT	Reference
Puéchabon, France	2002–2004	3°35′	43°44′	270	2.9–3.2	4.5	172	*Quercus ilex (TeBE)*	Allard et al. (2008)
Roccarespampani, Italy	2003–2004	11°55′	42°23′	223	4.0–5.0	4.5	485	*Quercus cerris (TeBS)*	Kowalski et al. (2004)
Collelongo, Italy	1998–1999	13°35′	41°50′	1560	4–5.5	4	287	*Fagus sylvatica (TeBS)*	Valentini et al. (1996)
Blodgett, California	2001–2004	−120°37′	38°53′	1315	2.4–4.2	4	583	*Pinus ponderosa (TeNE)*	Goldstein et al. (2000)

Table 2. Parameters for the calculation of stomatal conductance, and water stress parameters applied to stomatal conductance (Fig. 3) and photosynthetic potential (Fig. 4) for each site.

Site	Stomata – $Wfac_{stoma}$					Photosynthesis – $Wfac_{photo}$		
	Slope	Intercept ($mol\,m^{-2}\,s^{-1}$)	$Wfac\ s_{max}$	$Wfac\ s_{min}$	q	$Wfac\ s_{max}$	$Wfac\ s_{min}$	q
Puéchabon	9	0.0017	80	10	0.15	65	15	0.5
Roccarespampani	8.5	0.0015	95	10	0.22	70	10	0.85
Collelongo	10.5	0.000025	95	0	0.23	75	5	0.3
Blodgett	10.5	0.00002	85	5	0.18	45	5	0.2

Table 3. Statistics for the comparison of each model (GOTILWA+ and ORCHIDEE) and approach (Stomatal vs. Non-Stomatal restrictions) with FLUXNET data at each site, for assimilation (A_n) and actual evapotranspiration (E_a) during wet and dry period Golden Days, with soil water in both models prescribed (SL – Applying stomatal limitations only, NSL – Applying Non-stomatal restrictions, Original – Original models).

	A_n						E_a					
	SL		NSL		Original		SL		NSL		Original	
	wet	dry	wet	dry	wet	dry	wet	dry	wet	dry	wet	dry
GOTILWA+:												
Puechabon												
Model Efficiency	0.74	−18.6	0.74	−0.41	0.63	−25	0.76	−2.95	0.77	−1.4	0.65	−0.64
R^2	0.84	0.82	0.84	0.82	0.85	0.78	0.81	0.7	0.81	0.65	0.81	0.65
RMSE	2.4	4.76	2.4	1.84	2.7	6.1	0.03	0.07	0.03	0.06	0.02	0.047
Collelongo												
Model Efficiency	0.81	−10.3	0.83	−3.72	0.73	−0.45	0.77	−12.1	0.76	−13.2	0.82	−0.02
R^2	0.91	0.8	0.91	0.81	0.91	0.26	0.85	0.51	0.85	0.5	0.86	0.42
RMSE	4.6	7.5	4.4	5.34	4.9	4.9	0.1	0.16	0.11	0.16	0.1	0.02
Roccarespampani												
Model Efficiency	0.81	−5.21	0.8	0.82	0.76	−3.87	0.73	−8.36	0.59	−0.14	0.42	−5.6
R^2	0.89	0.83	0.88	0.87	0.88	0.83	0.89	0.9	0.89	0.89	0.89	0.9
RMSE	4.0	9.8	4.3	3.24	4.8	8.85	0.05	0.13	0.07	0.06	0.08	0.11
Blodgett												
Model Efficiency	0.62	0.43	0.62	0.36	0.6	0.42	−0.71	0.76	−0.71	0.70	0.54	0.67
R^2	0.83	0.81	0.83	0.82	0.81	0.81	0.71	0.83	0.72	0.83	0.78	0.83
RMSE	3.4	−18.6	3.4	3.4	3.5	3.49	0.08	0.013	0.08	0.015	0.04	0.008
ORCHIDEE:												
Puechabon												
Model Efficiency	0.74	−8.9	0.73	−4.5	0.66	−1.15	0.38	−7.85	0.39	−6.5	0.47	−1.45
R^2	0.74	0.77	0.74	0.78	0.75	0.67	0.66	0.51	0.66	0.5	0.8	0.7
RMSE	2.5	3.98	2.6	3.0	3.0	2.63	0.04	0.09	0.04	0.08	0.04	0.04
Collelongo												
Model Efficiency	0.91	−6.1	0.92	0.7	0.92	−0.57	0.77	−4.8	0.82	−0.4	0.81	−5.07
R^2	0.92	0.82	0.92	0.8	0.92	0.65	0.87	0.53	0.88	0.53	0.87	0.47
RMSE	3.2	5.41	2.9	1.61	2.95	4.34	0.07	0.12	0.08	0.06	0.08	0.22
Roccarespampani												
Model Efficiency	0.87	0.42	0.87	0.88	0.87	0.54	0.81	0.29	0.83	0.62	0.81	−0.11
R^2	0.84	0.79	0.82	0.83	0.83	0.81	0.77	0.78	0.78	0.79	0.77	0.78
RMSE	3.2	4.6	3.2	2.66	3.2	4.1	0.05	0.06	0.04	0.04	0.04	0.06
Blodgett												
Model Efficiency	0.5	0.60	0.5	0.65	0.5	0.59	−19.5	−40.63	−19.66	−41.7	−19.0	−41.4
R^2	0.81	0.77	0.81	0.77	0.81	0.77	0.47	0.61	0.47	0.63	0.47	0.62
RMSE	3.0	2.27	3.0	1.98	2.99	2.3	0.27	0.18	0.27	0.18	0.27	0.18

Table 4. Statistics for the comparison of GOTILWA+ and ORCHIDEE diurnal cycles of assimilation (A_n) and actual evapotranspiration (E_a) with FLUXNET data at each site, for wet and dry period Golden Days, with free simulated soil water content, based on hourly data.

	Wet A_n		Dry A_n	
	GOTILWA+	ORCHIDEE	GOTILWA+	ORCHIDEE
Puechabon				
Model Efficiency	0.83	0.62	0.6	−0.05
R^2	0.87	0.74	0.81	0.76
RMSE	2.1	3.1	1.0	0.5
Collelongo				
Model Efficiency	0.86	0.91	0.70	0.76
R^2	0.91	0.92	0.51	0.82
RMSE	4.0	3.3	2.2	1.9
Roccarespampani				
Model Efficiency	0.81	0.87	0.85	0.86
R^2	0.89	0.84	0.91	0.83
RMSE	4.1	3.2	2.5	2.9
Blodgett				
Model Efficiency	0.64	0.50	0.78	0.64
R^2	0.87	0.81	0.89	0.76
RMSE	3.3	2.9	1.9	2.3
	Wet E_a		Dry E_a	
	GOTILWA+	ORCHIDEE	GOTILWA+	ORCHIDEE
Puechabon				
Model Efficiency	0.68	0.56	−0.27	−0.22
R^2	0.81	0.79	0.65	0.63
RMSE	0.04	0.04	0.03	0.02
Collelongo				
Model Efficiency	0.79	0.78	−0.30	−0.27
R^2	0.86	0.88	0.51	0.52
RMSE	0.10	0.07	0.06	0.05
Roccarespampani				
Model Efficiency	0.64	0.87	0.80	0.81
R^2	0.89	0.90	0.90	0.88
RMSE	0.07	0.04	0.04	0.04
Blodgett				
Model Efficiency	0.63	0.69	−0.68	−1.52
R^2	0.73	0.71	0.89	0.62
RMSE	0.07	0.09	0.24	0.23

Table 5. Assimilation and actual evapotranspiration statistics for the comparison of GOTILWA+ and ORCHIDEE with FLUXNET data at each site, for seasonal daily simulation values. For Collelongo and Roccarespampani, which are deciduous sites, data from outside the growing period was omitted. New and original model formulations are compared.

	GOTILWA+				ORCHIDEE			
	A_n		E_a		A_n		E_a	
	New	Original	New	Original	New	Original	New	Original
Puechabon								
Model Efficiency	0.76	−0.09	0.46	0.42	0.64	0.69	0.18	−0.82
R^2	0.90	0.83	0.92	0.91	0.88	0.68	0.48	0.39
RMSE	1.23	1.96	0.61	0.36	1.32	1.36	0.63	0.92
Collelongo								
Model Efficiency	0.82	0.69	0.5	0.45	0.77	0.74	0.6	0.55
R^2	0.93	0.93	0.79	0.79	0.91	0.90	0.68	0.7
RMSE	1.68	1.78	0.93	0.92	1.88	1.91	0.74	0.83
Roccarespampani								
Model Efficiency	0.68	0.31	0.16	−0.11	0.67	0.58	0.64	−0.46
R^2	0.88	0.85	0.87	0.86	0.84	0.85	0.82	0.66
RMSE	2.36	3.11	1.08	1.23	2.34	2.44	0.64	1.32
Blodgett								
Model Efficiency	0.69	0.006	0.53	0.36	0.37	−0.1	0.18	0.23
R^2	0.89	0.79	0.71	0.70	0.71	0.47	0.49	0.50
RMSE	1.47	1.74	0.65	0.62	1.95	2.21	0.93	1.03

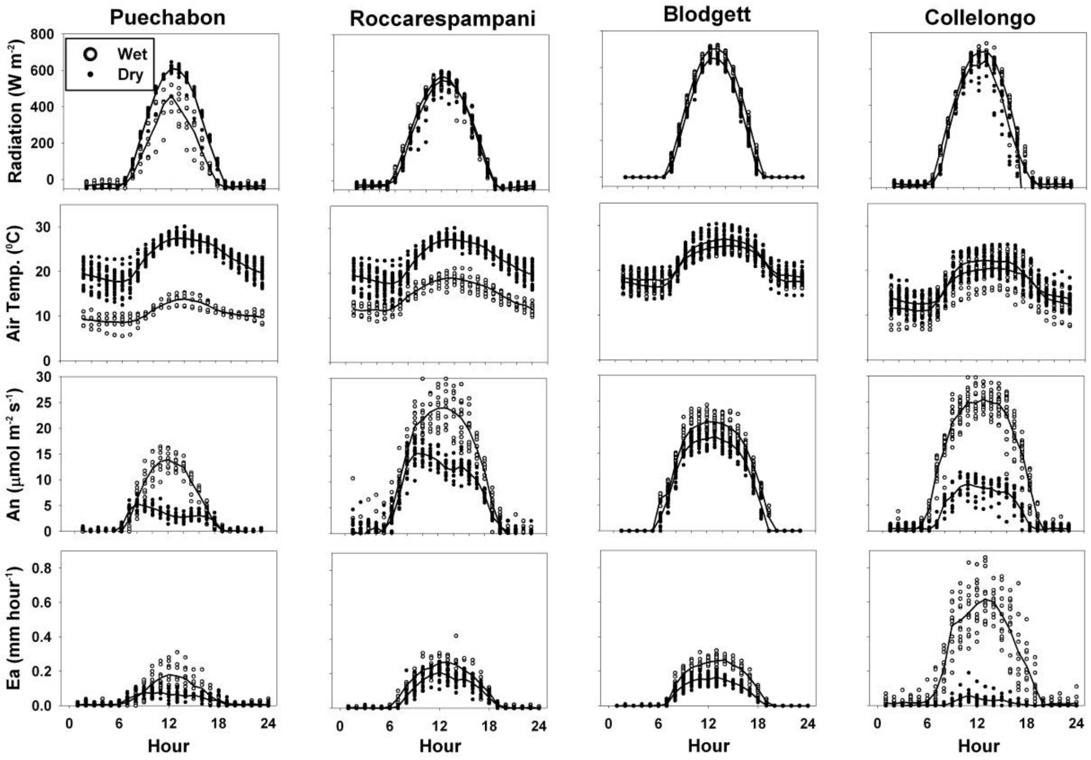

Fig. 1. Hourly meteorological conditions (Radiation, air temperature) and flux data (Assimilation (A_n), actual evapotranspiration (E_a)) at each site day for the well-watered (Wet) and drought (Dry) Golden Day periods. Solid lines represent the average diurnal cycle for each period.

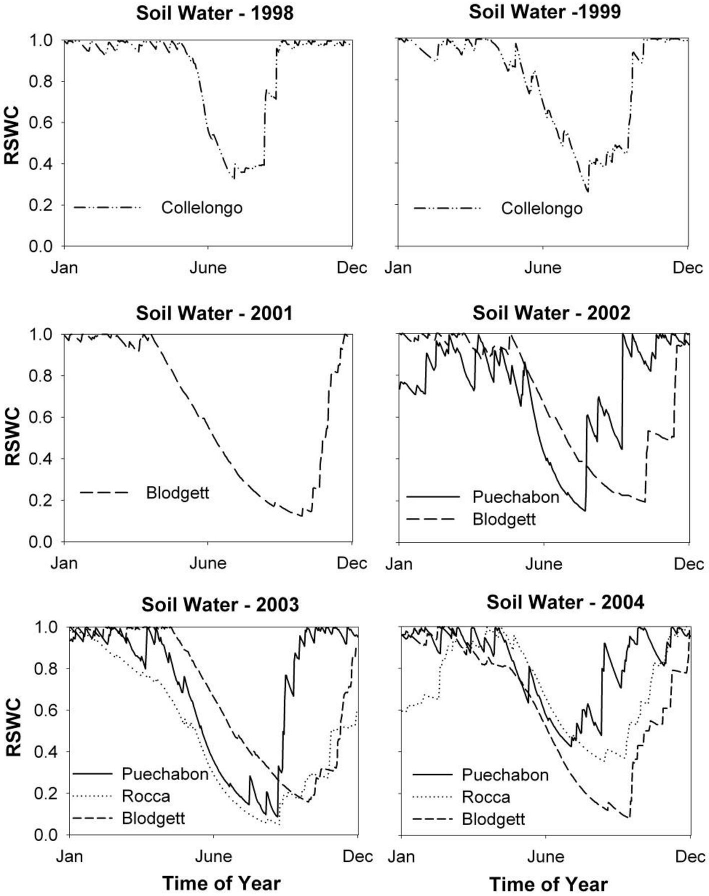

Fig. 2. Reconstructed daily relative soil water content (RSWC) for the simulated periods at each of the studied sites, separated by year.

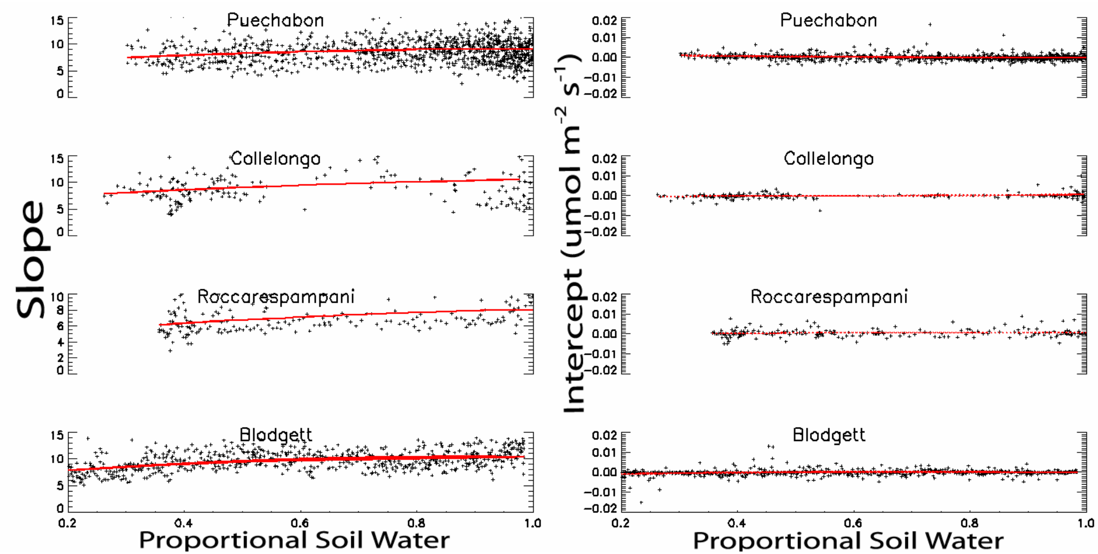

Fig. 3. (Left): Changes in the slope parameter, *m*, of Eq. 2, (the empirical species specific factor that specifies the baseline ratio between conductance and net photosynthesis) with relative available water for each site. Regression lines represent the functions ($Wfac_{\text{stoma}}$) applied in the models; (Right): Intercept parameter (Residual of Eq. 2), at each site, as a function of soil water content (proportional to maximum soil water content).

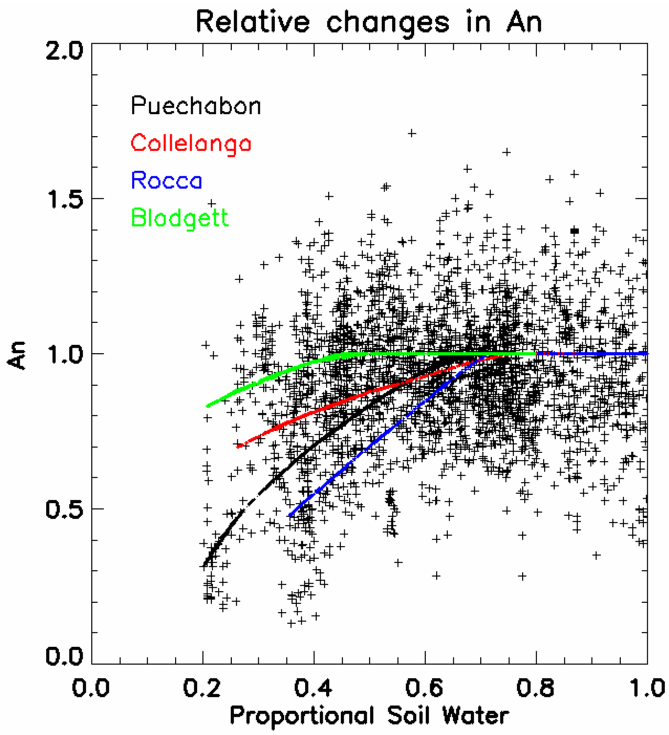

Fig. 4. Non-stomatal limitations to normalised net assimilation, A_n as a function of relative soil water content, calculated at each site individually (Using A_n over restricted ranges of leaf C_i concentrations ($220<C_i<300$), radiation (>250 W m^{-2}), and temperature (<25 °C)), (Parameters of the adjusted functions in Table 2).

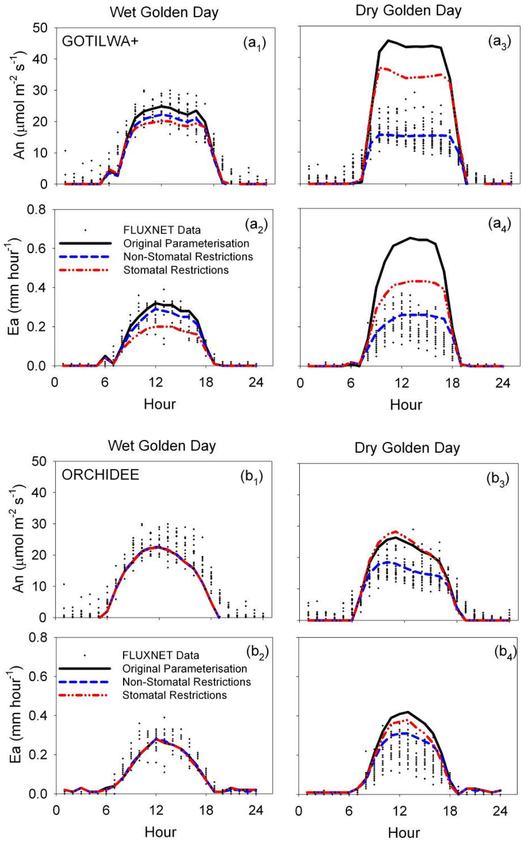

Fig. 5. 20 dry Golden Day diurnal courses for the observed hourly photosynthesis (A_n, in umol m^{-2} s^{-1}) and actual evapotranspiration (E_a, in mm h^{-1}), and average modelled (a: GOTILWA+, b: ORCHIDEE) values for the same Golden Days, for the Roccarespampani site, using 3 different modelling approaches, with the soil water content prescribed in each: 1) Applying the factors to stomatal conductance only. 2) Applying the factors to Photosynthetic potential only, and 3) Applying the original parameterisations. Wet and dry Golden Day periods are compared.

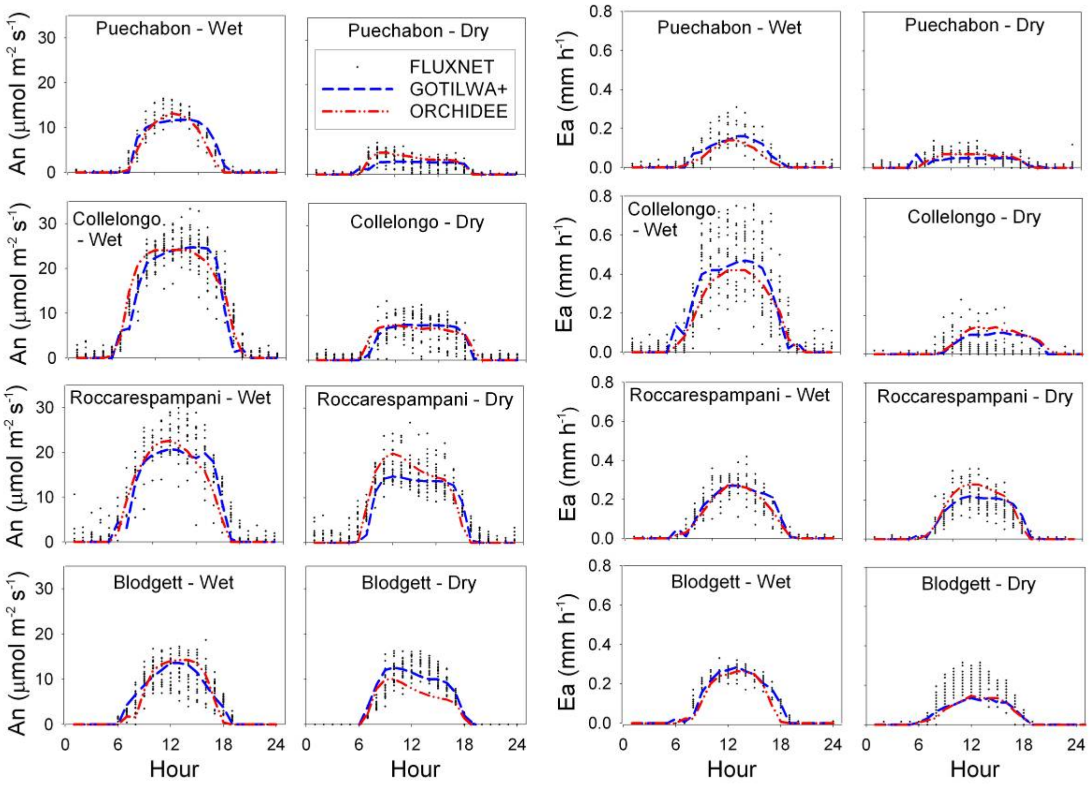

Fig. 6. Diurnal cycles of observed photosynthesis (A_n, in μmol m^{-2} s^{-1}) and actual evapotranspiration (E_a in mm h^{-1}))), and average modelled values for the same Golden Days for both GOTILWA+ and ORCHIDEE at all sites for both wet and dry Golden Day periods (with dynamic soil water).

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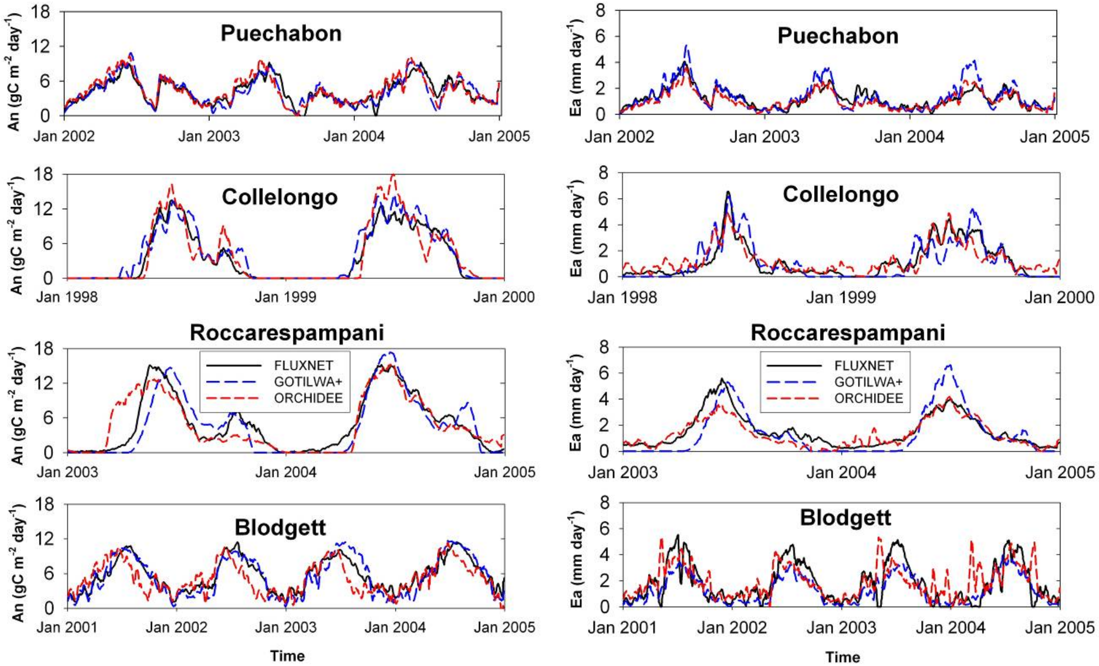

Fig. 7. Measured (black solid line) and modelled (both GOTILWA+ (red long dash) and ORCHIDEE (blue short dash)) seasonal cycles of daily assimilation rates (A_n) and actual evapotranspiration (E_a) at all sites (data shown has been smoothed using a ten-day running mean).