Biogeosciences

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. Simulation models are key tools for making predictions, but our current understanding of how soil moisture controls ecosystem functioning is not sufficient to adequately constrain parameterisations.

Canopy-scale flux data from four forest ecosystems with Mediterranean-type climates were used in order to analyse the physiological controls on carbon and water flues through the year. Significant non-stomatal limitations on photosynthesis were detected, along with lesser changes in the conductance-assimilation relationship. New model parameterisations were derived and implemented in two contrasting modelling approaches.

The effectiveness of two models, one a dynamic global vegetation model ("ORCHIDEE"), and the other a forest growth model particularly developed for Mediterranean simulations ("GOTILWA+"), was assessed and modelled canopy responses to seasonal changes in soil moisture were analysed in comparison with in situ flux measurements.

In contrast to commonly held assumptions, we find that changing the ratio of conductance to assimilation under natural, seasonally-developing, soil moisture stress is not sufficient to reproduce forest canopy CO_2 and water fluxes. However, accurate predictions of both CO_2 and water fluxes under all soil moisture levels encountered in the field are obtained if photosynthetic capacity is assumed to vary with soil moisture. This new parameterisation has important consequences for simulated responses of carbon and water fluxes to seasonal soil moisture stress, and should greatly improve our ability to anticipate future impacts of climate changes on the functioning of ecosystems in Mediterranean-type climates.

1 Introduction

The Mediterranean region contains a 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 believed to be the main factor limiting vegetation growth in the Mediterranean region, and secular regional changes in temperatures and precipitation are believed to be already inducing changes in these ecosystems (e.g. Jump et al., 2006; Peuelas and Boada, 2003). 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 low 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). 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 these key 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 status 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 in Mediterranean ecosystems. This problem is exemplified by difficulties in reproducing the effects of seasonal droughts on CO_2 and water fluxes (Krinner et al., 2005; Morales et al., 2005; Reichstein et al., 2007; Jung et al., 2007), and it seems likely that these deficiencies are at least in part due to the temperate bias in model development activities. This paper directly addresses this situation.

Stomata are key organs in determining the ability of plants to thrive in drought-prone regions. A very large number of approaches to modelling stomatal responses to environmental signals has emerged since the seminal work of Jarvis (1976). Perhaps the most widely used approach in modern times is to assume a linear relationship between (leaf- or bulk canopy-level) stomatal conductance, photosynthesis, the leaf surface concentration of CO_2, and the relative humidity or vapour pressure at the leaf surface. This empirical framework is typified by the so-called *Ball-Berry* (BB) and *Ball-Berry-Leuning* (BBL) parameterisations (Ball et al., 1987; Leuning et al., 1995). It has been reported, however, that this empirical model relationship does not hold under conditions of soil moisture stress (Reichstein et al., 2003; Misson et al., 2006). Indeed, stomatal conductance is known to decrease with soil moisture (e.g., Kramer, 1983), where the classical BB-type model does not include this forcing. The effect of water stress on plant photosynthesis and stomatal conductance has been widely studied (e.g., 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), although studies also indicate a direct water stress effect on photosynthesis (e.g. Colello et al., 1998; Medrano et al., 2002; Reichstien et al., 2002; Rambal et al., 2003; Xu and Baldocchi, 2003).

Studies suggest that stomatal conductance responses to short-term water stress can be effectively included in the BB and BBL (BB-type) models by reducing the ratio of conductance to photosynthesis (Tenhunen et al., 1990; Harley and Tenhunen, 1991; Sala and Tenhunen, 1994). Both models include a conductance level under conditions of zero net photosynthesis, and this level has also been reported to change under water stress (Misson et al., 2004). However, there is substantial evidence that photosynthetic capacity is directly affected by soil moisture (e.g. Medrano et al., 1997; Parry et al., 2002). Stomatal conductance and photosynthetic activity tend to be closely correlated (e.g., Cowan, 1977; Wong et al., 1979; Hetherington and Woodward, 2003), leading to the suggestion that it is in fact variations in photosynthetic activity which determines stomatal aperture in order to maintain biochemically optimal rates of CO_2 supply (e.g., 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 concerning responses at different time scales (e.g., Lawlor, 1995; Tezara et al., 1999; Cornic, 2000; Lawlor and Cornic 2002; Flexas and Medrano 2002).

Changes in non-stomatal limitations to photosynthesis under soil moisture stress have been detected (e.g. 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., Evans and von Caemmerer, 1996; Evans and Loreto, 2000; Evans et al., 2004; Terashima et al., 2005, 2006; Warren, 2008). These studies give weight to a number of studies which show 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 dominates under natural water-stressed conditions (e.g. Lawlor, 1995; Tezara et al., 1999; Lawlor and Cornic, 2002; Flexas and Medrano, 2002; Grassi and Magnani, 2005; Breda et al., 2006; Galmes et al., 2007; Keenan et al., 2009).

Such limitations 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 strength of the seasonal droughts encountered annually in such ecosystems. The canopy response to drought is important in governing whole-plant abilities to thrive under given conditions. Thus the model description of drought responses must be accurate in order to get the inter-species competitive potential right, and hence be able to better predict vegetation change, in particular in dynamic global vegetation models like ORCHIDEE.

In this paper, we address the problem of modelling canopy responses to drought 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 observations of CO_2 and water fluxes over four different forest ecosystems growing in Mediterranean climates, we investigate the relationships

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); MH – Measurement Height (m).

Site	Period	Longitude	Latitude	Altitude	Max LAI	SD	SWHC	MH	Species/PFT	Reference
Puéchabon, France	2002–2004	3°35′	43°44′	270	2.9–3.2	4.5	210	13	*Quercus ilex (TeBE)*	Allard et al. (2008)
Roccarespampani, Italy	2003–2004	11°55′	42°23′	223	4.0–5.0	4.5	485	20	*Quercus cerris (TeBS)*	Kowalski et al. (2004)
Collelongo, Italy	1998–1999	13°35′	41°50′	1560	4–5.5	4	287	32	*Fagus sylvatica (TeBS)*	Valentini et al. (1996)
Blodgett, California	2001–2004	−120°37′	38°53′	1315	2.4–4.2	4	583	10.5	*Pinus ponderosa (TeNE)*	Goldstein et al. (2000)

between the observed fluxes and estimated seasonal variations in soil moisture. These data are further analysed to determine the relative roles of stomatal and non-stomatal limitations to photosynthesis.

The understanding derived from this analysis is then used to adjust two contrasting process-based ecosystem models: GOTILWA+ (Growth Of Trees Is Limited by WAter), a detailed biogeochemical forest growth model (Gracia et al., 1999; Keenan et al., 2008; http://www.creaf.uab.es/GOTILWA+) developed in the Mediterranean region and therefore expected to adequately account for regional-specific system behaviour, and ORCHIDEE (ORganizing Carbon and Hydrology In Dynamic EcosystEms), a dynamic global vegetation model (Krinner et al., 2005; http://ORCHIDEE.ipsl.jussieu.fr), which has been found to perform poorest in drought-stressed regions (e.g. Jung et al., 2007). Simulations are performed with both models at each of the four sites in order to test the understanding provided by the data analysis.

2   Materials and methods

2.1   FLUXNET site data and data manipulation

Measurements of forest ecosystem carbon and water fluxes were obtained from the FLUXNET database (http://www.fluxnet.ornl.gov) for three sites in Mediterranean Europe [Puechabon, in France (Allard et al., 2008); Roccarespampani, in Italy (Kowalski et al., 2004); and Collelongo, also in Italy (Valentini et al., 1996)]. The measurement systems in place at these sites were maintained under the CarboEurope-EUROFLUX project. A fourth site at a location with a mediterranean-type climate in California (Blodgett; Goldstein et al., 2000) was also chosen. The instrumentation at this site was maintained under the AMERIFLUX project. Together, the data used from the four sites amount to a total of eleven measurement years (Table 1), and cover a broad range of phenological types: temperate broadleaf deciduous, temperate needleleaf evergreen, and temperate broadleaf evergreen types, with varying levels of summer drought stress between the different sites. These monospecific forest stands include the species *Quercus ilex, Quercus cerris, Fagus sylvatica*, and *Pinus ponderosa*. FLUXNET datasets include

measurements of CO_2 and water fluxes integrated to half-hourly time steps (Baldocchi et al., 2001; Friend et al., 2007). 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). The flux-partitioning algorithm used first estimates the temperature sensitivity from short-term periods, and then applies this short-term temperature sensitivity to extrapolate the ecosystem respiration from night- to daytime. This should reduce seasonal bias in partitioning. Gap-filled data were excluded from the analyses.

2.1.1   Interpreting FLUXNET data

In the following sections we describe how we derive soil water content, bulk canopy conductance, and leaf internal carbon concentrations for the parameterisation of the models and for use in the separation of non-stomatal limitations to photosynthesis during periods of low soil water availability.
Soil moisture. Analysing responses of observed CO_2 and water fluxes to natural changes in soil moisture requires the seasonal evolution of soil water content to be known. Surface soil water measurements are often available, but measurements of soil water content over the total soil column are either limited, or not made at most sites, and can show a very different inter-seasonal variation than that of the surface soil water content. In the absence of direct continuous measurements of total soil water content of the soil column, daily soil moisture content (for the entire soil column up to a site specific soil depth, Table 1) at each site was reconstructed through inverting the evapotranspiration rate (taken to be equivalent to the measured latent heat flux, *LHF*) and applying this flux to a simple water balance model. This model calculates the balance of the input (precipitation) and outputs (evapotranspiration (*LHF*), run-off and below-ground drainage) on a daily basis. The main components of the soil water balance, precipitation and *LHF* were measured, whilst run-off and sub-surface drainage were estimated as follows. Daily run-off, r, was calculated as a function of the rate of precipitation and soil properties as:

$$r = 0.0001\, HG(1 - Por/100)P \tag{1}$$

where *HG* is the site specific hydraulic gradient ($m\, m^{-1}$), *Por* (%)is the water porosity of the upper 25cm of soil (estimated

based on a soil organic carbon basis as in Honeysett and Ratkowsky, 1989), and P (mm) is daily precipitation. Daily sub-surface drainage is set to be a constant proportion (1%) of soil water content (calculated as in Gracia et al., 1999, and Honeysett and Ratkowsky, 1989). Deep soil water content profile measurements during the studied periods were available for Puechabon and Collelongo site. Soil water content measurements at Puechabon correspond to the total 4.5 m soil depth, whilst measurements at Collelongo correspond to the total soil water content of the first 1 m of soil.

Canopy conductance. In order to assess responses of bulk canopy conductance to water to changes in soil water content, we estimate canopy conductance directly from the measured latent heat flux when conditions are suitable. We assume that the bulk canopy stomatal conductance to water vapour (expressed on a ground-area basis) can be estimated from the observed latent heat flux under conditions of a dry canopy surface conditions and negligible evaporation from the soil surface (such conditions are common in a Mediterranean climate; Daikoku et al., 2008). Bulk canopy stomatal conductance to water vapour, G_c, was then estimated from the measured moisture flux, using simplified form of the Penman-Monteith equation assuming that stomatal and atmospheric transfer occur in series, as:

$$1/G_c = 1/G - 1/G_a \qquad (2)$$

where G_a is the aerodynamic conductance from the canopy to the measurement point. G, the total conductance was estimated from the measured latent heat flux as:

$$1/G = (\rho \times Cp/\gamma) \times ([e^*(T_c) - e_{zR}]/(\lambda \times \varepsilon \times LH)) \qquad (3)$$

where $e^*(T_C)$ is the saturation vapour pressure at canopy temperature (T_C), e_{zR} is the ambient vapour pressure at flux measurement reference height z, γ is the psychometric constant, λ is the latent heat of vaporization, ρ is the density of moist air at ambient temperature, C_P is the volumetric heat capacity of moist air at constant pressure, ε is the coefficient for the conversion of latent heat to its water equivalent (giving actual evapotranspiration, Ea). Canopy temperature, T_C was solved from the measured sensible heat flux using the drag law parameterization and the Monin-Obukhov similarity relations for the dependence of the heat flux on the bulk Richardson number (Deardoff, 1967; Hansen et al., 1983). See Friend and Kiang (2005) for more details of the calculations used.

Boundary conductance between the canopy and the point of measurement was calculated as:

$$1/G_a = \qquad (4)$$
$$1/G_e + 1/Gb = k^2 \times u(z)/ln^2[(z-d)/z_0] + B^{-1}/u^*$$

where G_e is the aerodynamic conductance between the measurement height and the canopy surface. z is the height at which the energy balance measurements were made (see Table 1), z_0 is the surface roughness length, assumed proportional to the stand height, h, d is the zero plane displacement (estimated as $d = z - z_0 * exp(U \times k/u^*)$), and k is von Karman's constant. $U(z)$ is the measured wind speed at measurement height z. Gb is the excess leaf boundary layer conductance, B^{-1} is the dimensionless Stanton number (Owen and Thompson, 1963; but see Qualls and Hopson, 1998). u^* is the friction velocity.

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 an empirical stomatal model (BB model) in which stomatal conductance was expressed as a linear function of the leaf photosynthetic rate, relative humidity at the leaf surface, and the leaf surface CO_2 concentration, under conditions of ample water supply (Ball et al., 1987). This model was later modified by Ray Leuning (BBL model) to use the photorespiratory compensation point and vapour pressure deficit in place of relative humidity (Leuning, 1995). This BB-type leaf level model has been applied at the canopy scale through the use of bulk canopy level variables (Leuning et al., 1995):

$$G_c = G_{s0} + (m \times A_n)/((C_a - \Gamma^*) \times (1 + (vpd/D_0))) \qquad (5)$$

where G_{s0} is the value of G_c at the light compensation point (μmol m^{-2} s^{-1}), A_n is the rate of net photosynthesis (μmol m^{-2} s^{-1}), C_a is the atmospheric concentration of CO_2 at the canopy surface (μmol mol^{-1}), Γ^* is the photorespiratory compensation point (μmol mol^{-1}), D_0 (1.5, unitless) is an empirical coefficient that describes the sensitivity of conductance to vpd, and m is an empirical parameter (unitless).

Soil moisture stress has been added to BB-type conductance models through changes in m, and G_{s0}. We looked for possible changes in these parameters using diurnal cycles of net photosynthesis, C_a, vpd, and canopy temperature which were derived from the data under wet and dry conditions. Given G_c, (from Eq. 2) for each cycle, $A_n/((C_a - \Gamma^*) \times (1 + (vpd/D_0)))$ was calculated and regressed against estimated G_c using Eq. (5). The resulting linear regression allowed for the estimation of the m and G_{s0} parameters for each diurnal cycle. 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. Non-stomatal limitations can be identified by simply comparing rates of photosynthesis under similar leaf C_i concentrations, over a soil water gradient. Data relating to a restricted range of leaf C_i concentrations ($220 < C_i < 300$), radiation (>250 W m^{-2}), and

temperature ($<25°C$) was used. Any differences in rates of assimilation under these 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 high temperature effects.

We further analysed the canopy physiological response to soil moisture deficit by estimating the relationship between mesophyll CO_2 concentrations and net photosynthesis. Ci was calculated assuming equilibrium flux of CO_2. Ci, calculated in this way, allows a first-order canopy-level assessment of the contribution of stomatal vs. non-stomatal limitatins to photosynthesis under soil moisture stress. 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, $G_{cCO_2}(=G_c/1.6)$, rates of net photosynthesis derived from the eddy-covariance measurements, and atmospheric CO_2 concentrations using a simple supply and demand function:

$$C_i = C_a - (A_n/G_{cCO_2}) \tag{6}$$

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 mean short-wave radiation of $200\,\mathrm{W\,m^{-2}}$ or greater, and assimilation rates of $2\,\mu\mathrm{mol}\,CO_2\,\mathrm{mground^{-2}\,s^{-1}}$. Screening was also performed to remove data points measured during, or within 2 days following, precipitation events, and extreme temperatures (below $5°$ or above $35°$). Gap filled data was not considered. This reduced the variability in the calculated variables and allowed for a clearer identification of responses due to soil water stress.

Golden days. For model-data comparisons, we focus on days with "good" and stable climatic conditions during the growing period at each site, contrasting both wet and dry periods. Theoretically, for Golden days, the variability in model performance should not be confounded by daily variability in environmental conditions, and the statistical analysis of model performance made easier. Such "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.

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 in the Mediterranean region to simulate tree growth and to explore how it is influenced by water stress, 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. Hourly ecosystem carbon and water fluxes are estimated using 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. Each canopy layer is divided into fractions of sunlit (when direct radiation is present) and shaded 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 for sunlight and shaded leaves 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 concentration of CO_2 within the leaf air spaces. Stomatal conductance is calculated using the BBL model, on a leaf temperature basis. Rates of photosynthesis are dependent on the rate of carboxylation and the proportional rate of electron transport. The canopy average (over space and time) maximum RuBP (ribulose-1,5-bisphosphate) saturated rate of carboxylation, Vc_{max}, and the maximum rate of electron transport, J_{max}, were calculated following Farquhar et al. (1980) and de Pury and Farquhar (1997). Due to model specific differences in light and temperature distribution within the canopy, Vc_{max} and J_{max} need to be calibrated for site specific applications. Here we they were calibrated using the diurnal cycles of observed canopy carbon fluxes for the wet Golden day periods (see below for a description of Golden days) at each site (Vc_{max}: 35, 50, 55, and $40\,\mu\mathrm{mol}$, $\mathrm{m^{-2}}$, $\mathrm{s^{-1}}$, $J_{max} = Vc_{max}/2$ for Puchabon, Blodgett, Collelongo and Roccarespampani respectively). Other photosynthetic parameters were taken from Bernacchi et al. (2001). Other model parameters were set to either site specific (when available) or species specific parameters, as in Gracia et al. (1999).

Each tree cohort is represented by three carbon compartments, leaf, sapwood, and fine roots. Available mobile carbon is allocated to each, and maintenance respiration of each compartment 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 vertically into two layers, an upper organic layer, and a lower mineral layer, with a fixed rate of transfer of soil

organic carbon between them. Soil water processes are described in Sect. 2.1.1.

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 forcings 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, and 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, competition for light, 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.

Plants in ORCHIDEE used in this study are divided into the following functional types, each with different phenological, physiological, and morphological characteristics: temperate needleleaved evergreen, temperate broadleaved evergreen, temperate broadleaved deciduous, and C_3 herbaceous types. 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. For model parameterisations, plant functional types (PFT) (Table 1) parameters were used, taken from Krinner et al. (2005). Prior studies of model optimization against eddy covariance data have shown that the maximum rate of carboxylation in the ORCHIDEE model potentially was underestimated for some PFTs (Santaren et al., 2007). The canopy average maximum rate of carboxylation was increased between 25–40% (to 70, 75, 50, and 40 µmol, m^{-2}, s^{-1} for Puéchabon, Blodgett, Collelongo and Roccarespampani respectively) from the original parameter values (Krinner et al., 2005) to calibrate ORCHIDEE to meet the observed canopy average fluxes during the selected Golden days (see description of Golden days below). Soil water content is treated within two layers, with inputs from precipitation less canopy interception loss, and outputs to sub-surface drainage, runoff, soil evaporation, and transpiration. Further model parameters were taken from Krinner et al. (2005).

2.2.3 Accounting for soil water stress in coupled photosynthesis-conductance models

Two different approaches are frequently used to incorporate the effect of drought stress on the (Farquhar – BB-type) coupled conductance-assimilation model. Tenhunen et al. (1990) originally proposed the application of stomatal limitations under soil moisture stress through applying changes in the slope m of the coupled Farquhar – BB-type model during water stressed periods. This method decreases the empirical scaling coefficient m, with moisture stress, leading to reduced conductance and therefore reduced internal CO_2 available for assimilation. Changing the slope during water stressed periods has since been commonly adopted, and was the methodology for water stress response applied in the GOTILWA+ model. In GOTILWA+, stomata responded to drought stress through the application of a linear scalar of soil moisture, as:

$$G_s = G_{s0} + ((Wfac_{stoma} \times m) \times (A_n - R_d))/ \qquad (7)$$
$$((C_a - \Gamma^*) \times (1 + (vpd/D_0)))$$

where $Wfac_{stoma}$ is a soil moisture-dependent scalar with values between 0 and 1.

The effect of drought stress on the coupled photosynthesis-conductance model (of Farquhar – BB-type) can be implemented through changes in non-stomatal limitations, by reducing photosynthetic potential through the application of a scalar to both the maximum RuBP (ribulose-1,5-bisphosphate) saturated rate of carboxylation, Vc_{max}, and the maximum rate of electron transport, J_{max}, as follows:

$$Vc\max' = Vc\max \times Wfac_{photo},$$
$$J\max' = J\max \times Wfac_{photo} \qquad (8)$$

Where $Wfac_{photo}$ is a soil moisture-dependent scalar with values between 0 and 1. This causes stomatal closure as A_n is reduced in Eqn. (5). The ORCHIDEE model applied a linear scalar in this manner to directly reduce photosynthesis during water stress.

The two approaches were tested in both models, thus avoiding the potential for any model specific biases in results. We used the flux data analysis outlined above to test three hypotheses concerning the responses of canopy net photosynthesis and evapotranspiration to seasonally varying soil moisture supply: 1) directly reducing stomatal conductance by modifying the slope, m, within the BB or BBL model is sufficient to explain observed responses, 2) directly reducing J_{max} and Vc_{max} and hence net photosynthesis within the BB or BBL models is sufficient to explain observed responses, and 3) the simultaneous application of both stomatal and non-stomatal limitations is necessary to capture the timing and extent of the water stress induced decrease in CO_2 and water fluxes at each site.

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. *Wfac* s_{max}, and *Wfac* s_{min} are given in % of maximum soil water holding capacity.

| 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	75	30	0.6
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

To test the different hypothesis, we parameterised the reduction scalars already in use in both GOTILWA+ and ORCHIDEE from the data for both changes in the slope parameter, m, $Wfac_{stoma}$ and non-stomatal related changes in photosynthesis $Wfac_{photo}$. These scalars have the form:

$$Wfac = \begin{cases} 1, & \text{if } S(t) \geq S_{max} \\ \left[\frac{s(t) - s_{min}}{s_{max} - s_{min}} \right]^q, & \text{if } S(t) < S_{max} \end{cases} \quad (9)$$

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, expressed as percentages of maximum soil water holding capacity. These two scalars were parameterised independently for each site and were then applied separately in both GOTILWA+ and ORCHIDEE.

2.2.4 Modelling protocol, hypothesis testing, and model evaluation

Simulations of CO_2 and water fluxes with each model were run separately for the time periods outlined in Table 1 at each of the four sites to evaluate the models and test the outlined hypothesis. For each model and site, 4 runs were made with: 1) with the model's original water stress response parameterisations, 2) the application of the modified stomatal limitations ($Wfac_{stoma}$, Table 2), 3) the application of the modified non-stomatal limitation ($Wfac_{photo}$, Table 2), and 4) the application of both the modified stomatal and non-stomatal limitations together.

To assess the different hypothesis for modeling soil water stress responses using Golden days, we ran simulations with the soil water content at each time step set to the reconstructed soil water content for the corresponding day. This enabled the evaluation of the canopy physiological process descriptions independent of potential inaccuracies in the modelled latent heat fluxes, which would confound any model-data comparison. 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 Thus, in simulations with forced soil water content

the modelled photosynthesis and conductance were calculated as functions of the reconstructed soil water, and any under- or over-estimations of evapotranspiration did not affect the soil water content and thus did not propagate into the next time step. In simulations comparing the two models, GOTILWA+ and ORCHIDEE (presented in Figs. 6, 7), the constraint of a forced soil water content was removed, and a full bi-directional feedback between the soil and the canopy was considered.

Both models were forced with 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 site specific conductance parameters, m and G_{s0} were calculated from the data (m and G_{s0} were the same for both GOTILWA+ and ORCHIDEE) for each site (Table 2). In addition to the above site-level parameters required by the two models, GOTILWA+ used descriptions of stand characteristics (including the structure of the canopy and the DBH class distribution), and also a number of tree physiological parameters (biomass allocations and compartment specific growth and maintenance respiration rates).

GOTILWA+ simulations of CO_2 and water fluxes at each site were initialised by specifying forest structure variables specific to the first year of simulation at each site, with data obtained from the literature. ORCHIDEE simulations were initialised by prescribing the fractional cover of each plant functional type for each site.

Statistics. The hypotheses were evaluated using the correlation coefficient r^2, the Root Mean Squared Error (RMSE), and the statistic Model Efficiency (MEF). The modelling efficiency statistic (MEF) is similar to r^2, which is interpreted as the proportion of variation explained by the fitted line whereas the MEF statistic is the proportion of variation explained by the line Y = f(X1, ..., Xp). This statistic has been extensively used in hydrology models (Byers et al., 1989, Loague and Green, 1991 and Zacharias et al., 1996), but has also been used in biological models. It is related to the RMSE according to: MEF = 1-RMSE2/s^2 where s^2 is the variance of the observations. A value near one (the
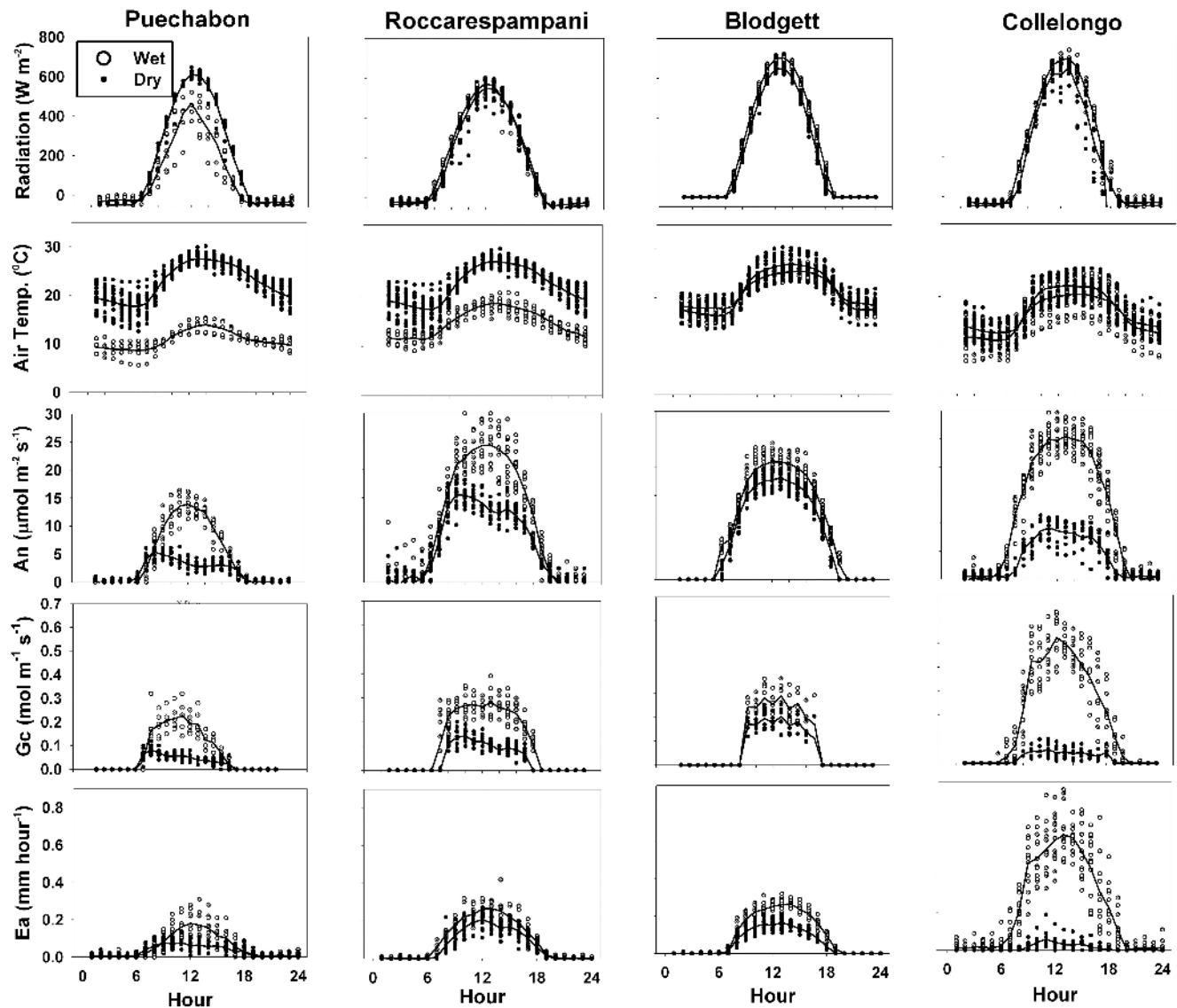
Fig. 1. Hourly meteorological conditions (Radiation, air temperature), flux data (Assimilation $-A_n$, actual evapotranspiration $-E_a$), and estimated Canopy bulk conductance (G_c) at each site day for the well-watered (Wet) and drought (Dry) Golden day periods. Solid lines represent the average diurnal cycle for each period.

upper bound) indicates a close match between observations and model predictions. A value of zero indicates that the model predicts individual observations no better than if it always predicted the average of the observations. Values less than zero indicate that the observation average would be a better predictor than the model results. 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).

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 with reduced photosynthesis and evapotranspiration during peak summer periods (Fig. 1), in contrast to higher fluxes during late spring. This seasonality was particularly noticeable at Puechabon, Collelongo, and Roccarespampani, and less so at the Blodgett site.
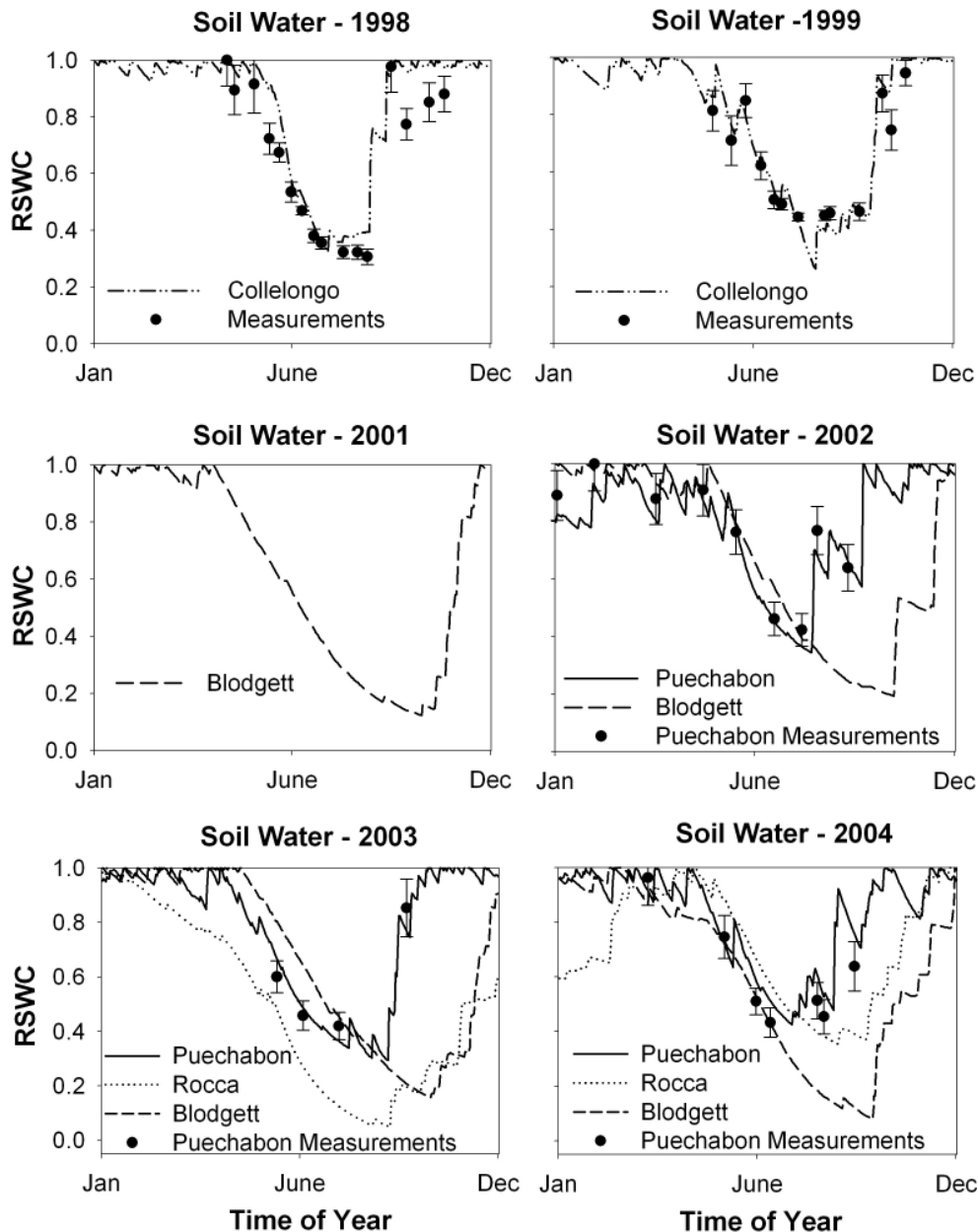
Fig. 2. Reconstructed daily relative soil water content (RSWC – total soil water in the soil column relative to the maximum soil water holding capacity) for the simulated periods at each of the studied sites, separated by year. Data represent soil water measurements at Puechabon (over the total 4.5 m soil profile) and Collelongo (for the top 1 m of soil).

3.2 Data analysis results

Soil Water Content. Figure 2 shows the evolution of estimated relative soil water content (RSWC – total soil water in the soil column divided by the soil water holding capacity) for each simulated site and year, derived by inverting the observed 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 summers 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 soil water content shows little inter-annual variability due to the lack of inter-annual variability in its climate during the studied period. In contrast, at Puechabon annual summer soil water varies over a large range, with levels reaching a prolonged low during 2003 due to the strong drought experienced in that year. This dry summer period is also reflected at the Roccarespampani site, with soil water
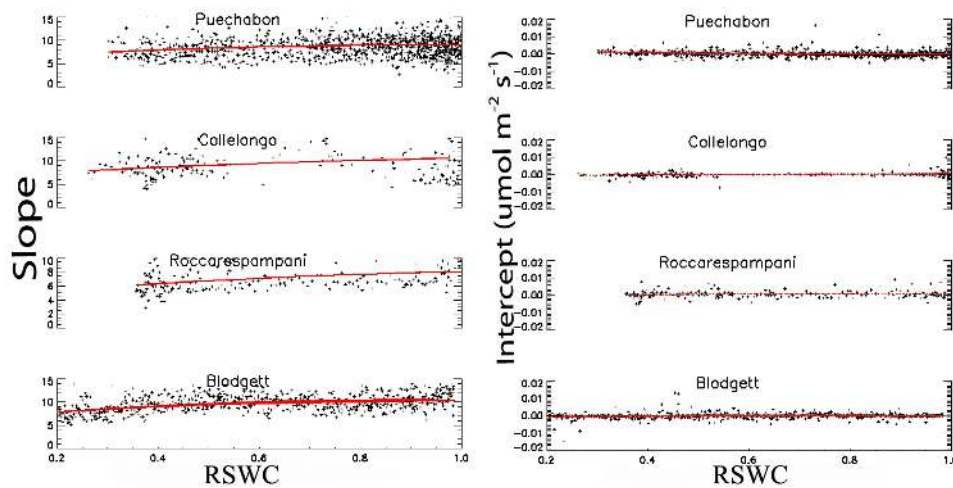
Fig. 3. (Left): Changes in the slope parameter, m, of Eq. 5, (the empirical species specific factor that specifies the baseline ratio between conductance and net photosynthesis) with relative daily soil water content (RSWC – total soil water in the soil column relative to the maximum soil water holding capacity) for each site, calculated using mid-day values. Regression lines represent the functions ($Wfac_{stoma}$) applied in the models; (Right): Intercept parameter (Residual of Eq. 5), at each site, as a function of the RSWC.

levels in 2003 falling below 50% of those in 2004. Soil water measurements are available for Puechabon and Collelongo, and compare well to the reconstructed values (Fig. 1). Both the timing and extent of the soil water drop in summer were accurately captured at each site and year. At Collelongo, the reconstruction slightly overestimated the autumn soil water content in 1998. We are not aware of similar data for the other sites.

Reductions of photosynthesis and conductance due to soil water stress. The estimates of soil water content shown in Fig. 2 are used with the observed flux data to determine whether the m parameter in the BB-type models of canopy conductance, non-stomatal limitations, or both vary significantly with soil moisture. Values for the slope and intercept of the BBL conductance model at high soil water content for each site are given in Table 2. These values were calculated separately for both the BB and BBL canopy conductance model formulations, and were found to be independent of the choice of conductance model.

The fitted empirical parameter in the BB-type model, m, did not change notably during the slow onset of soil water stress at the beginning of each summer, and then declined only slightly at very low soil water levels (<30% relative soil water) (Fig. 3a). The fitted intercept in Eq. 5 did not change with decreases in available soil water at any of the sites (Fig. 3b).

In contrast to the lack of major changes in the BB and BBL model parameters, strong non-stomatal limitations to photosynthesis were found under conditions of soil moisture stress at all sites (Fig. 4). The point at which limitations were first encountered was site dependent and between 50% and 80% RSWC Although inferred soil water in our re-

construction falls quite low in Blodgett, this did not lead to decreases of the extent observed at the other sites in either CO_2 or water fluxes during the summer period (only slight water stress), suggesting either root access to deep ground water not simulated by our reconstruction, or an underestimation of soil water capacity. At the other three sites, fluxes declined with site-dependent intensities. Roccarespampani showed the strongest decline in fluxes, followed by Puechabon and then Collelongo. The fitted $Wfac_{photo}$ functions shown in Eq. 8 are given 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 and flux data. The ability of the alternative hypotheses outlined above to simulate canopy responses to soil moisture stress is tested by incorporating the fitted empirical relationships shown in Figs. 3 and 4 into the framework of the two process-based models. The simulation of the Golden day diurnal courses of CO_2 and water fluxes during periods of high water availability was very accurate for all model combinations (three hypotheses implemented separately in two models) (Fig. 5a₁, a₂, b₁, b₂). As expected, simulated fluxes 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, responses to water stress were highly dependent on the chosen response description.

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

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. However, the different approaches gave marked differences in the root mean squared error (RMSE) and in the model efficiency (MEF). Applying the calculated water stress functions presented in Table 2, to Vc_{max}, and J_{max} led to an 80% reduction in the RMSE for assimilated carbon using the GOTILWA+ model, and 47% in the case of OR-

CHIDEE, when compared to the original model parameterisations. Applying the water stress functions solely to stomatal control produced a marked increase (13% GOTILWA+; 9%, ORCHIDEE, Table 3) in the RMSE, compared to the original model parameterisations, and was the only approach to give a negative average MEF.

The same relative performance of the different hypotheses was observed at all sites, with marked improvements in the accuracy of simulations of the diurnal cycle of both net photosynthesis and evapotranspiration under drought stress
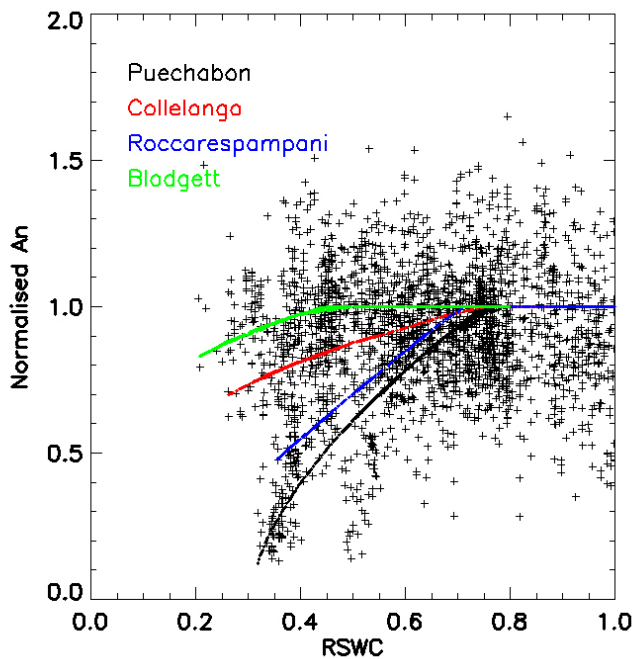
Fig. 4. Non-stomatal limitations to normalised net assimilation, A_n, as a function of relative soil water content (total soil water in the soil column relative to the maximum soil water holding capacity), calculated at each site individually (Using A_n over restricted ranges of leaf C_i concentrations ($220 < C_i < 300$), radiation ($>250\,\mathrm{W\,m^{-2}}$), and temperature ($<25°C$)), (Parameters of the adjusted functions in Table 2). A_n was normalized to the observed average assimilation rate under well watered conditions (>0.8 Relative soil water holding capacity).

when photosynthetic capacity was reduced using Eq. (8). Remarkably, no direct effect of soil moisture on stomatal conductance was necessary to successfully reproduce the response of evapotranspiration to water stress, i.e. both the BBL and BB models were sufficient for this purpose. Conversely, the application of restrictions 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, suggesting that hypothesis two is correct.

3.4 Simulation of diurnal and seasonal fluxes with GOTILWA+ and ORCHIDEE

To evaluate the capacity of the two models to reproduce the Observed diurnal and seasonal fluxes following updating with the best fitting empirical model of soil moisture effects (i.e. non-stomatal limitations only), we repeated the hourly simulations of CO_2 and water fluxes for all years (Table 1) for each site with soil water content calculated from the model simulation itself (Figs. 6, 7).

Simulation of diurnal fluxes.

For well-watered Golden days at Puechabon, both models accurately reproduced the shape of the diurnal time courses of CO_2 and water fluxes, with ORCHIDEE performing slightly better (Fig. 6, Table 4). Under dry conditions at Puechabon, both models responded accurately to drought (Table 4).

CO_2 and water fluxes were accurately modelled by both models in Collelongo (Table 4). Both models were capable of simulating net photosynthesis to a very high degree of accuracy in both wet and dry conditions (Table 4). 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 CO_2 and moisture fluxes (Table 4). The diurnal cycle of CO_2 fluxes at Blodgett was well captured by both models (Table 4, Fig. 6). 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 evapotranspiration rates than those observed.

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

Seasonal cycles and inter-annual variations

Finally, the ORCHIDEE and GOTILWA+ simulations (the same diurnal simulations shown in Fig. 6) 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 forcings, and thus varying levels of drought. The effect of drought on simulated photosynthesis and conductance, which is characterised by a sharp decline in fluxes in otherwise optimal 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 summer reductions in both CO_2 and water fluxes was also well captured in each year. The magnitude of summer reductions in CO_2 and water fluxes
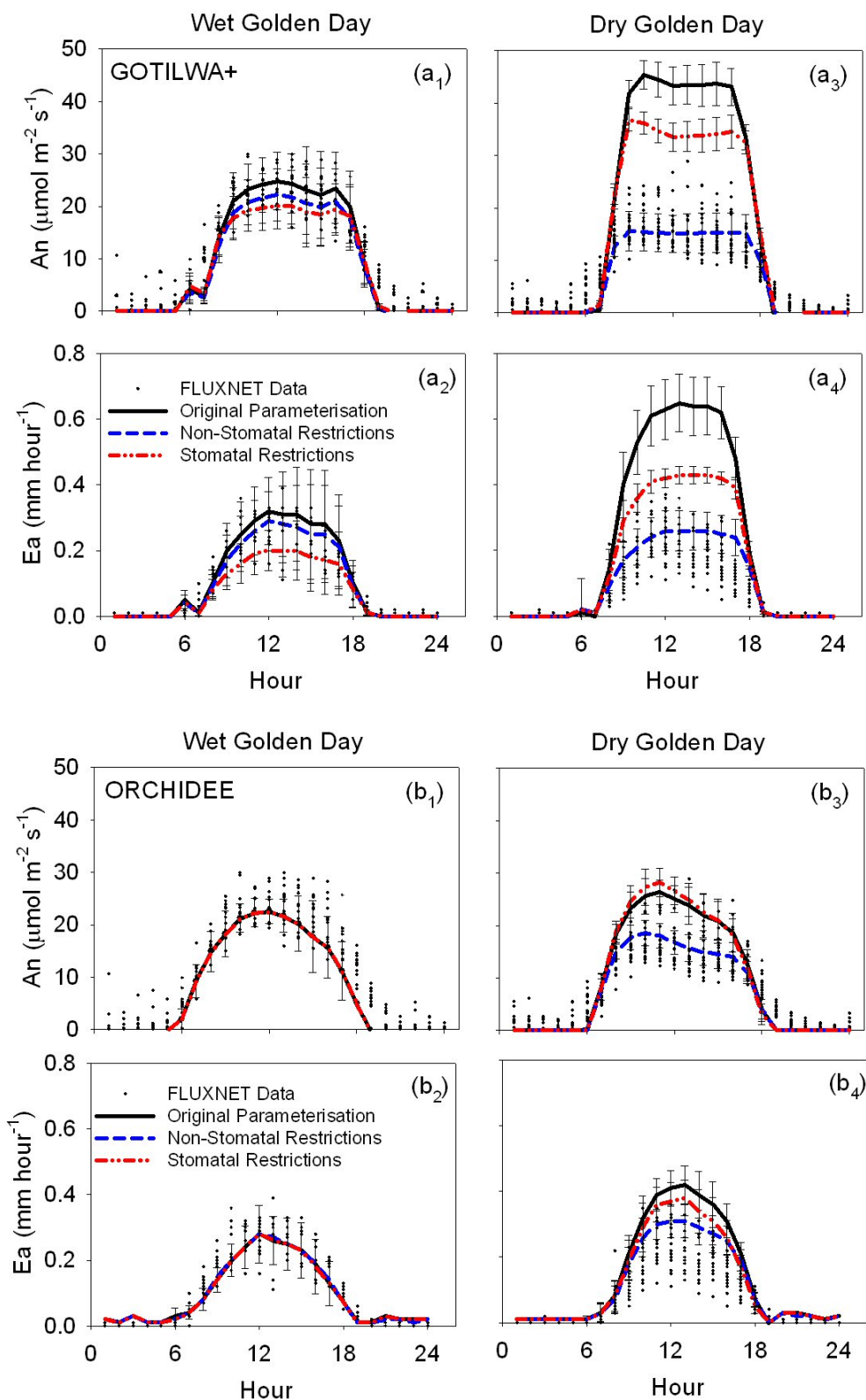
Fig. 5. Golden day diurnal courses for the observed hourly photosynthesis (A_n, in umol m^{-2} s^{-1}) and actual evapotranspiration (E_a, in mm h^{-1}), and average modelled (a: GOTILWA+, b: ORCHIDEE) values for the same Golden days, for the Roccarespampani site, using 3 different modelling approaches, 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. Error bars represent the standard deviation from the mean. Golden day periods for Roccarespampani: 2004, 17 May–1 June (wet), 19 August–8th September (dry)
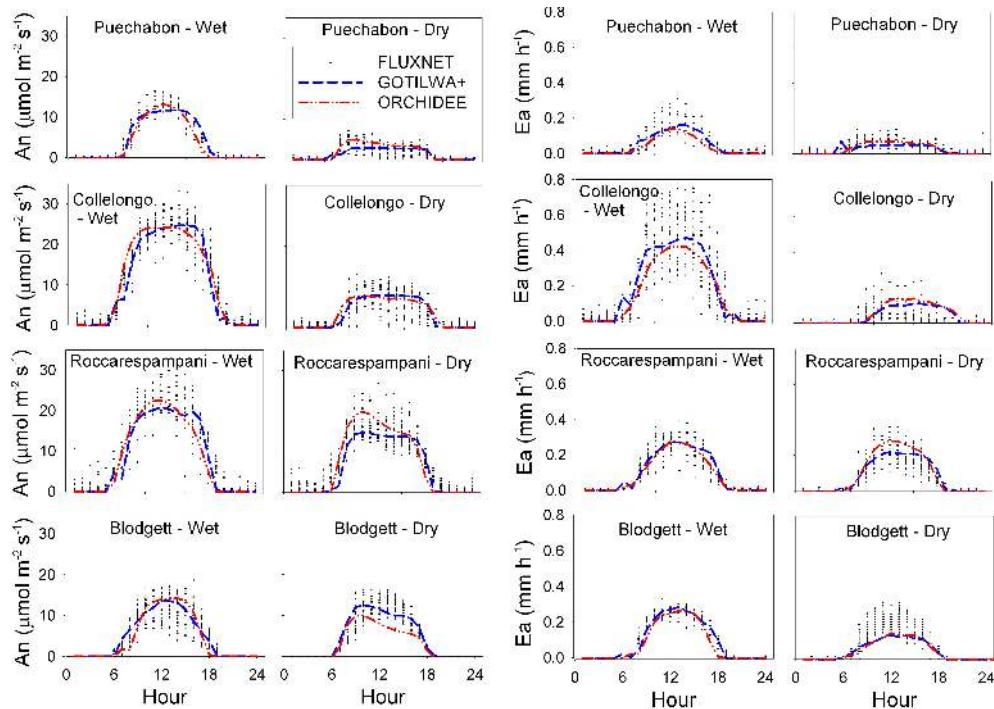
Fig. 6. Diurnal cycles of observed photosynthesis (A_n, in μmol m^{-2} s^{-1}) and actual evapotranspiration (E_a in mm h^{-1}), and average modelled values for the same Golden days for both GOTILWA+ and ORCHIDEE at all sites for both wet and dry Golden day periods (with dynamic soil water). Golden day periods for each site: Puechabon 2002, 22 May to 4 June (wet), 19 August–17 September (dry); Collelongo 1998, 16 June–4 July (wet), 11–29 August (dry); Roccarespampani 2004, 17 May–1 June (wet), 19 August–8 September (dry); Blodgett 2002, 13 April–1st May (wet), 4–17 July (dry).
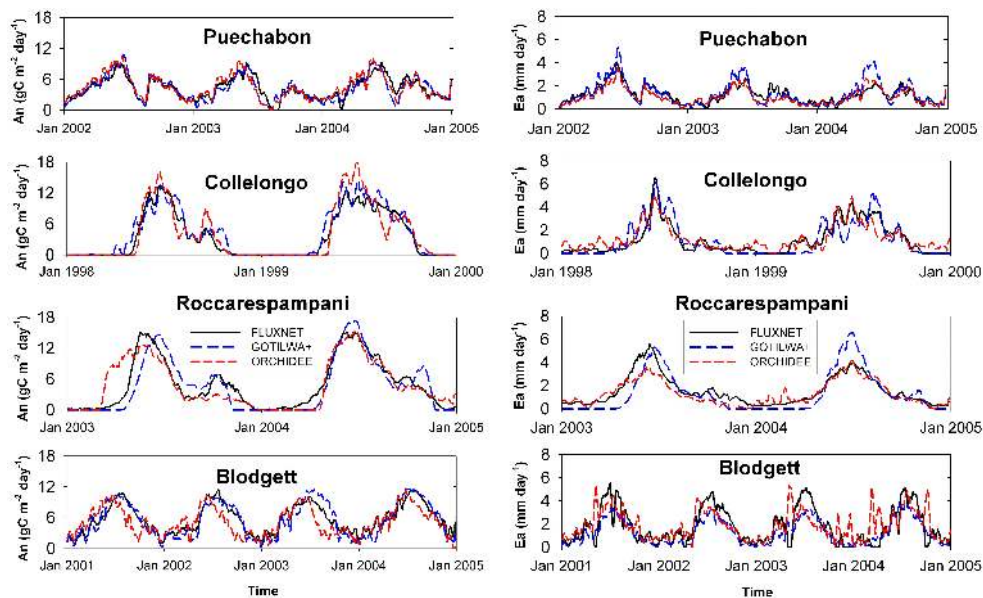

Fig. 7. Measured (black solid line) and modelled (both GOTILWA+ (red long dash) and ORCHIDEE (blue short dash)) seasonal cycles of daily assimilation rates (A_n) and actual evapotranspiration (E_a) at all sites (data shown has been smoothed using a ten-day running mean).

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

encountered was accurately simulated in 2002, but overestimated in 2003 and 2004 when simulating with a full bidirectional feedback between soil water and canopy fluxes. Although with GOTILWA+, evapotranspiration was slightly overestimated in the period of high production before water stress was encountered, GOTILWA+ outperformed ORCHIDEE at Puechabon, giving a better correlation to the EUROFLUX data, a higher model efficiency and a lower standard error (Table 5). GOTILWA+ also performed better at the Blodgett site, where ORCHIDEE accurately captured CO_2 and water flux dynamics during spring, but largely overestimated the effect of drought on assimilation and conductance during summer periods.

Comparisons of simulations with measurements at the two deciduous sites were complicated by an active understorey. Phenology also proved difficult to model, with neither model capable of accurately predicting the timing of budburst or leaf-fall, particularly in 2003. In Roccarespampani, both models produced an equal match to the data, but were prone to higher levels of standard error (Table 5). Roccarespampani had 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 either model, leading to difficulties when simulating the evolution

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

of available soil water at the Roccarespampani site. In Collelongo, ORCHIDEE preformed better than GOTILWA+. GOTILWA+ accurately reproduced the strength and duration of the drought in 1998 and its effect on photosynthesis, but due to inaccuracies in the prediction of budburst and leaffall dates, total photosynthesis over the growing season was overestimated (Table 5, Fig. 7).

Overall, both models accurately capture the observed CO_2 and moisture fluxes at all sites. GOTILWA+ gave 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 with the original models. For GOTILWA+ the new implementation led 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. These statistics suggest signficantly better model performance than that found in recent published model comparisons including water stressed sites (Morales et al., 2005; a study including the original versions of the ORCHIDEE and GOTILWA+ models).

4   Discussion

A number of recent studies have brought into question the ability of process-based models to accurately simulated seasonal changes in CO_2 and water fluxes in Mediterranean-type forest ecosystems (e.g., 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 (e.g. using a BB-type approach), but rather an incomplete description of the mechanisms controlling the seasonal response of the photosynthetic capacity of Mediterranean trees to gradually occurring water stress.

Despite the widespread use of BB-type canopy conductance models, detailed studies that would allow incorporation of the effects of water stress are lacking, and reported results are inconsistent. Several studies reported that the reductions in stomatal conductance with soil water stress is sufficient (e.g. Harley and Tenhunen, 1991; Sala and Tenhunen, 1996), whilst others maintain that it remains constant (e.g. 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, resulting in an almost constant slope parameter, m. This suggests that stomatal conductance changes in parallel with photosynthesis, as originally reported by Wong

et al. (1979). Further, our finding that the residual conductance does not change under soil water stress is contrary to results previously reported at the Blodgett site by Misson et al. (2004).

It is well known that the stomata react to changes in soil water availability (e.g. Kramer, 1983). The water reserves in leaves and stems are very small when compared to the amount of water transpired, and thus these organs 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 reductions in 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 processes have been identified (e.g. Flexas and Medrano, 2002; Galmes et al., 2007), and can be divided into two categories: mesophyll conductance responses and metabolic adjustments. 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 and Medrano, 2002; Flexas et al., 2004). Metabolic adjustments can take many forms, and may include the reduction of enzyme activity necessary for RuBP regeneration (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 responses can 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. None of these processes, however, are taken into account by current large-scale ecosystem models.

The non-stomatal limitations found in this study differ in strength between sites. The two sites with *Quercus* species, Puechabon and Roccarespampani, showed similar responses, likely reflecting similarities in their leaf physiologies and overall anatomy. *Quercus ilex* (present in Puechabon) is an evergreen sclerophyllous species, commonly found in Mediterranean regions, and well adapted to drought stress with tough coarse leaves. *Quercus cerris* (in Roccarespampani), although deciduous, also has a high sclerophyll index (Kutbay and Kilinc, 1994). Highly sclerophyllous leaves have been reported to have relatively 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 hypothetically 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 larger than can be accounted for by stomatal closure.

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 under 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 (e.g. 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, (Gunasekera and Berkowitz, 1992; Kubiske and Abrams, 1993).

The nature of the data analysed here, gathered at the canopy scale under field conditions, leads to large variability in some of the variables necessary to calculate the parameter response functions. The derivation of model parameters using canopy level eddy-covariance data is also subject to a number of uncertainties. For example, we assume all latent heat and CO_2 flux measurements result from the fluxes of water and CO_2 across the canopy surfaces of the dominant species at each site. We recognise that this may not always be true. Other tree species on a site, or an active understorey, could potentially make large contributions to the total measured fluxes. Hence, we tried to minimise this problem by focusing on highly monospecific stands, and excluded sites at which strong contributions from understorey activity had been reported. These measures, however, cannot guarantee that the results are unaffected by the presence of non-dominant species, but we assume that any bias introduced is minimal. Soil evaporation is another potential contributor to the total fluxes. We assume that soil evaporation is minimal in a closed Mediterranean forest with a dry floor. We exclude data related to periods during or soon after rain events to reduce the potential impact of soil evaporation on our calculations.

The usefulness of our analyses depends directly on the accuracy of the flux measurements and calculations for the partitioning of fluxes. Unfortunately, information on observational errors are difficult to obtain for flux measurements (Dore et al., 2003). Error estimates for CO_2 fluxes across different sites range between 30 and 180 g_C m$_2$ yr$_1$. This is of the same order as our model-data differences. Such

errors can be due to instrument calibration, and certain atmospheric processes such as advection and high atmospheric stability. The calculations used in this study also rely on the assumption that the energy balance of the ecosystem measurements is closed, i.e. energy inputs (mainly from downward shorwave and infra-red radiation) equal outputs to latent and sensible heat exchange, with a smaller flux to ground heat. This assumption is frequently not fulfilled by the eddy covariance (EC) method (Wilson et al., 2002). Our understanding of the causes of energy imbalance is limited, but any imbalance could introduce uncertainty in the calculations applied in this study (Wohlfahrt et al., 2009). In particular, latent heat fluxes are often, though not always, underestimated by the order of 10–30% (e.g., Wilson et al., 2002). This would affect the accuracy of the soil water reconstruction and the calculated bulk canopy conductance in this study. This problem is confounded by the potential for seasonal bias in the partitioning method used for partitioning the measured CO_2 fluxes into gross primary productivity and ecosystem respiration. The lack of knowledge of such errors increases the uncertainty related to the derived parameter values obtained in this study, and their seasonal changes. However, we would argue that the qualitative finding that non-stomatal limitations are necessary for the accurate simulation of CO_2 and water fluxes from forest canopies is robust regardless of the uncertainty highlighted above.

Although the main factors of the soil water balance, precipitation and evapotranspiration, are known, the modelled drainage and run-off at each site are subject to various simplifying assumptions (such as homogeneity of soil depth and texture). Uncertainty related to the calculation of reconstructed soil water may affect the slopes of the responses to soil water stress reported in this study, but would not qualitatively affect the general conclusions.

Inaccuracies in the simulation of the seasonal cycle of CO_2 and water fluxes were attributed largely 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 temperature, but were not capable of accurately predicting budburst at either of the two deciduous sites. Leaf-fall date estimation was slightly more accurate. Understorey vegetation potentialy explains difficulties observed for GOTILWA+, as in the current version this is not taken into account. This may explain the underestimation of spring water fluxes at Roccarespampani.

The role of non-stomatal limitations in modelling CO_2 and water fluxes, shown in this study, will be of particular importance for regional scale modelling. Preliminary regional simulations with ORCHIDEE suggest that the new implementation leads, on average, to an 8% reduction in the predicted rate summer net photosynthesis across the Mediterranean Basin. Any regional model applying only stomatal limitations will likely overestimate assimilation by 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. This, coupled with difficulties in accurately modelling phenological events, will be the main challenges for regional modelling efforts in the Mediterranean.

5 Conclusions

We have shown that canopy conductance and photosynthesis co-vary with soil moisture in a consistent manner using observations from four sites with Mediterranean climates. Stomatal conductance was found to vary in parallel with photosynthesis, and with only small changes in the fitted slope of the BB or BBL model formulations. 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 CO_2 and water fluxes during dry and wet periods using either the BB or BBL sub-models. Stomatal regulation of photosynthesis alone is not sufficient to reduce modelled photosynthesis to observed levels during drought periods. Accounting for the empirically-derived non-stomatal soil moisture responses with the derived parameters for each site improved substantially the performance of two ecosystem models, and allowed for the simulation of CO_2 and water fluxes with similar accuracies under both wet and dry 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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