

## Inverse modeling of seasonal drought effects on canopy CO<sub>2</sub>/H<sub>2</sub>O exchange in three Mediterranean ecosystems

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[1] We present a two-criteria inverse modeling approach to analyze the effects of seasonal drought on ecosystem gas exchange at three Mediterranean sites. The three sites include two nearly monospecific *Quercus ilex* L. forests, one on karstic limestone (Puéchabon), the other on fluvial sand with access to groundwater (Castelporziano), and a typical multispecies shrubland on limestone (Arca di Noè). A canopy gas exchange model Process Pixel Net Ecosystem Exchange (PROXEL<sub>NEE</sub>), which contains the Farquhar photosynthesis model coupled to stomatal conductance via the Ball-Berry model, was inverted in order to estimate the seasonal time course of canopy parameters from hourly values of ecosystem gross carbon uptake and transpiration. It was shown that an inverse estimation of leaf-level parameters was impossible when optimizing against ecosystem H<sub>2</sub>O or CO<sub>2</sub> fluxes alone (unidentifiable parameters). In contrast, a criterion that constrained the optimization against both H<sub>2</sub>O and CO<sub>2</sub> fluxes yielded stable estimates of leaf-level parameters. Two separate model inversions were implemented to test two alternative hypotheses about the response to drought: a reduction in active leaf area as a result of patchy stomatal closure or a change in photosynthetic capacities. In contrast to a previously tested hypothesis of classical (uniform) stomatal control, both hypotheses were equally able to describe the seasonality of carbon uptake and transpiration on all three sites, with a decline during the drought and recovery after autumn rainfall. Large reductions of up to 80%, in either active leaf area or photosynthetic capacities, were necessary to describe the observed carbon and water fluxes at the end of the drought period. With a threshold-type relationship, soil water content was an excellent predictor of these changes. With the drought-dependent parameter changes included, the canopy model explains 80–90% of the variance of hourly gross CO<sub>2</sub> uptake (root mean squared error (RMSE): 1.1–2.6 μmol m<sup>-2</sup> s<sup>-1</sup>) and 70–80% of the variance of hourly transpiration (RMSE: 0.02–0.03 mm h<sup>-1</sup>) at all sites. In addition to drought effects, changes in leaf photosynthetic activity not related to water availability, i.e., high spring activity, were detected through the inverse modeling approach. Moreover, our study exemplifies a kind of multiconstraint inverse modeling that can be profitably used for calibrating ecosystem models that are meant for global applications with ecosystem flux data. **INDEX TERMS:** 1615 Global Change: Biogeochemical processes (4805); 1812 Hydrology: Drought; 3210 Mathematical Geophysics: Modeling; **KEYWORDS:** carbon balance, drought, inverse modeling, data assimilation, photosynthesis, water use efficiency

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### 1. Introduction

[2] Drought is considered an important ecological factor in semiarid ecosystems [Di Castri, 1981; Verhoef *et al.*, 1996; Gucci *et al.*, 1997]. In Mediterranean ecosystems, drought is predicted to become more pronounced through global change [Gregory and Mitchell, 1995] and strong effects on ecosystem functions are expected [Rambal and Debussche, 1995; Botner *et al.*, 1995; Rambal, 2001].

[3] Eddy covariance measurements of ecosystem gas exchange together with meteorological and pedological

observations (e.g., global radiation, air and soil temperature, vapor pressure deficit, soil water, soil texture and organic carbon content), although limited to estimating net exchange, permit ecosystem-level monitoring of activities sensitive to drought and thus to environmental change. Simultaneously, we would like to understand the response of component processes to environmental shifts. This is usually difficult for technical reasons (e.g., root respiration is hard to measure without disturbance: Cheng *et al.* [1993]), a high spatial heterogeneity [Joffre *et al.*, 1996], or due to the lack of manpower or resources to carry out many required observations.

[4] Under such circumstances, where parameters and processes cannot be observed directly, the inverse modeling method has successfully been applied, particularly in soil hydrology, remote sensing, and paleoresearch [Boonstra and Bhutta, 1996; Kabat *et al.*, 1997; Asner *et al.*, 1998; Guiot *et al.*, 1999]. This method often aims at resolving fine-scale properties from coarse-scale data through the use of a mechanistically based fine-scale model. In principle, this is accomplished by identifying values for fine-scale parameters which let the model satisfactorily describe the coarse-scale data. Of course, if a model contains many uncertain parameters, there might exist several parameter sets which give similar descriptions of the data (i.e., nonuniqueness of model solution, non-identifiability of model parameters Mous [1993]). Additional problems emerge when the model is simplified [Rastetter *et al.*, 1992] and/or when model process formulations are uncertain. Then only effective (or apparent) parameters can be estimated, which are not equal in value to the “real” fine-scale parameters. But even if the correspondence is not 100%, research needs can be focused, hypotheses about fine-scale properties can be formulated, and subsequently, these can be directly tested. Although Luo and Reynolds [1999] have recommended the inverse modeling approach to resolve questions related to ecosystem biogeochemical cycles and carbon sequestration, experience in applying the inverse modeling approach to ecosystem flux data is sparse.

[5] Previously, in the work of Reichstein *et al.* [2002b], a very simple inverse approach demonstrated that it is extremely unlikely that only classical (uniform) stomatal conductance influences the response of canopy gas exchange to summer drought. Instead, four other possible mechanisms were visualized (see Reichstein *et al.* [2002b] for a thorough discussion): drought effects (1) on physiological leaf photosynthetic capacities ( $J_{\max}$ ;  $V_{c,\max}$ ) and (2) on partial leaf area deactivation via patchy stomatal closure, (3) on mesophyll resistance for  $\text{CO}_2$ , and (4) on photoinhibition. While assumption (3) has been rendered unlikely by Roupsard *et al.* [1996], assumption (4) did not conform to the fact that model errors were largest in the morning (and not in the afternoon). Thus the assumptions (1) and (2) are tested with a more detailed two-criteria inverse modeling approach, at three Mediterranean sites. It is shown that the inverse modeling approach can be utilized to interpret simultaneous ecosystem flux data in response to drought as observed by eddy covariance and sapflow methods, if and only if both,  $\text{CO}_2$  and  $\text{H}_2\text{O}$  fluxes, are used to constrain model parameters. Then drought effects as well as other seasonal patterns like

enhanced leaf photosynthetic activity can be detected via this approach.

## 2. Materials and Methods

### 2.1. Site Description

[6] An overview over the site characteristics is given in Table 1. The three sites include two closed-canopy Mediterranean evergreen forests dominated by holm oak (*Quercus ilex* L.) and one multispecies shrubland (macchia) dominated by *Juniperus phoenicea* L. Although climatically quite similar, the three sites differ substantially with respect to water availability due to pedological conditions. Owing to the very low maximum soil water availability, the Puéchabon and Arca di Noè sites are much more xeric than the Castelporziano site, where roots have access to groundwater [Valentini *et al.*, 1992]. See the works of Merzouki [1986], Joffre *et al.* [1996], Manes *et al.* [1997], and Benincasa *et al.* [1999] for a more extensive description of the sites.

[7] All three sites exhibited typical Mediterranean climate conditions during the respective study years (Figure 1), including an extended summer drought. At the Castelporziano site, the drought lasted from the beginning of June until October. However, as this site is influenced by groundwater availability, only the upper soil layer dried out severely, while the other layers retained relatively high water contents (Figure 1k).

### 2.2. Data Collection and Treatment

[8] Net ecosystem  $\text{CO}_2$  exchange was measured continuously by eddy covariance [Baldocchi *et al.*, 1996]. The instruments were a 3-D sonic anemometer (Solent, Gill Instruments Ltd., Lymington, United Kingdom), which measures wind speed and direction and air temperature, and a closed-path infrared gas analyser sampling at 10 Hz (IRGA; LI6262, Li-Cor Inc., Lincoln, United States). The eddy covariance system and data processing were as described by Aubinet *et al.* [2000] [see Table 1 for further information]. The half-hourly data sets of  $\text{CO}_2$  exchange ( $F_c$ ) and meteorological conditions were aggregated to hourly data by averaging two observations per hour. In a preparatory step, nighttime  $\text{CO}_2$  fluxes at air temperatures between  $10^\circ\text{C}$  and  $15^\circ\text{C}$  and with apparently well-watered conditions (near field capacity) were plotted against friction velocity ( $u^*$ ). At all sites, these fluxes increased with  $u^*$  at low  $u^*$  and saturated at higher friction velocities. On the basis of a fitted function  $F_c(u^*) = F_{c,\max}(1 - e^{-ku^*})$  [ $F_c$ , observed  $\text{CO}_2$  flux;  $u^*$ , friction velocity;  $F_{c,\max}$ , saturated  $F_c$  (when  $u^*$  not limiting);  $k$ , exponential parameter], at least 95% of the maximal nighttime  $\text{CO}_2$  flux was reached at friction velocities above  $0.2 \text{ m s}^{-1}$  ( $k$  in the function always  $>15 \text{ s m}^{-1}$ ). Consequently, all eddy covariance data with  $u^* < 0.2 \text{ m s}^{-1}$  were excluded from the analysis since it is likely that under these conditions, storage and advection can alter gas fluxes through the boundary layer. Similarly, negative night fluxes (i.e., with night C uptake) were excluded. The transpiration component of the evapotranspiration was observed using sapflow techniques that indirectly measure the velocity of water transport through the wood of the stem or branch, as described in Table 1.

[9] Soil water content (SWC) was measured biweekly at Castelporziano by time domain reflectometry (TDR) and

**Table 1.** Site Characteristics and Data Collection at Puéchabon, Castelporziano, and Arca di Noè<sup>a</sup>

Characteristics	Puéchabon	Castelporziano	Arca di Noè
Location and terrain	France, flat plateau (43.75°N, 3.6°W, 250 m above sea level (asl))	Italy, flat basin (41.7°N, 12.3°E, 7 m asl)	Sardinia, flat plateau, (40.4°N, 8.9°E, 100 m asl)
Annual mean temperature, °C	13.4	15.5	16.8
Annual precipitation, mm	812	740	643
Canopy species cover, %	<i>Quercus ilex</i> L. (>90%); <i>Quercus pubescens</i> L.; <i>Buxus sempervirens</i> L.	<i>Quercus ilex</i> L. (>90%); <i>Quercus suber</i> L. (<10%)	<i>Juniperus phoenicea</i> L. (53%); <i>Pistacia lentiscus</i> L. (22%); <i>Phyllirea angustifolia</i> L. (6%)
Leaf area index, m <sup>2</sup> m <sup>-2</sup>	2.9 <sup>b</sup>	3.5 <sup>b</sup>	1.6 <sup>c</sup>
Stand height, m	6	10	2
Soil texture	clay loam, >70 vol % coarse fraction (>2 mm)	sand, <5 Vol-% coarse fraction	clay loam, ca. 60 vol % coarse fraction
Soil parent material	Jurassic limestone	aeolic sands	limestone
Management history	coppice, last cut shortly after 1945	unmanaged for centuries	natural reserve
Data collection			
Flux measurements	eddy covariance system at 13 m, sapflow with Granier-type sensor at 12 trees <sup>d</sup>	eddy covariance system at 15 m, sapflow with Granier-type sensors at three trees <sup>d</sup>	eddy covariance at 3 m, sapflow with 40 stem heat balance-type sensors on branches of the three most dominant species <sup>e</sup>
Soil conditions	neutron probe at six locations and from 0- to 450-cm depth	TDR at five locations in depths 0–20, 30–50, and 70–90 cm, soil temperature at 10 cm, three locations	TDR at three locations in 0–20 cm, soil temperature at 10 cm, three locations
Meteorological variables	above the canopy: air temperature, global and net radiation, and H <sub>2</sub> O pressure, wind speed, all at 13 m	above the canopy: air temperature, global and net radiation, and H <sub>2</sub> O pressure at 16.5 m, wind speed at 12.5 m	above the canopy: air temperature, global and net radiation and H <sub>2</sub> O pressure all at 3 m
Observation year	1998	1997	1999

<sup>a</sup>Temperature and precipitation for the three sites are average values from 1984 to 1994, 1987 to 1998, and 1955 to 1995, respectively.

<sup>b</sup>LICOR LAI-2000 measurements.

<sup>c</sup>Destructive sampling of major species [cf. *Pecchiari et al.*, 2000].

<sup>d</sup>cf. *Granier* [1987].

<sup>e</sup>cf. *Baker and van Bavel* [1987].

monthly at Puéchabon with a neutron moisture gauge (cf. Table 1). The soil moisture data in between have been interpolated with a mechanistic soil water and heat balance model (see validation results in the work of *Reichstein et al.* [2002a]). Continuously measured soil water content (0–20 cm) was available at Arca di Noè. SWC can either be expressed as volumetric water content (m<sup>3</sup> water per m<sup>3</sup> total soil volume; symbol  $\theta$ ) or as relative soil water content (RSWC) as a fraction of field capacity, i.e.,  $RSWC = \theta/\theta_{at \text{ field capacity}}$  (field capacity operationally defined as SWC at a matric potential of 330 hPa). At Castelporziano and Puéchabon, RSWC was computed for the 0–20, 20–100, and 100 cm to rooting depth centimeter layers. The second layer RSWC (20–100 cm) was most indicative of drought stress of the vegetation (most closely related to canopy conductance, see *Reichstein et al.* [2002b]) at those sites and therefore is shown in the graphs concerning vegetation response to drought. At Arca di Noè, where the soil is very shallow and no information about deeper-soil properties was available, the RSWC in the 0–20 cm layer was used in all graphs.

### 2.3. Estimation of Hourly Gross Carbon Uptake

[10] The estimation of hourly gross carbon uptake ( $F_{cGPP}$ ) from net ecosystem exchange (NEE) requires an estimate of ecosystem respiration ( $R_{eco}$ ) since  $F_{cGPP} = -NEE + R_{eco}$ . Ecosystem respiration was estimated as  $y$  intercept from the empirical relationship between global radiation and NEE and subsequently related to soil temperature and soil water content via a regression model as described in detail by *Reichstein et al.* [2002a]. When applied to hourly values of soil temperature and water content, the fitted regression

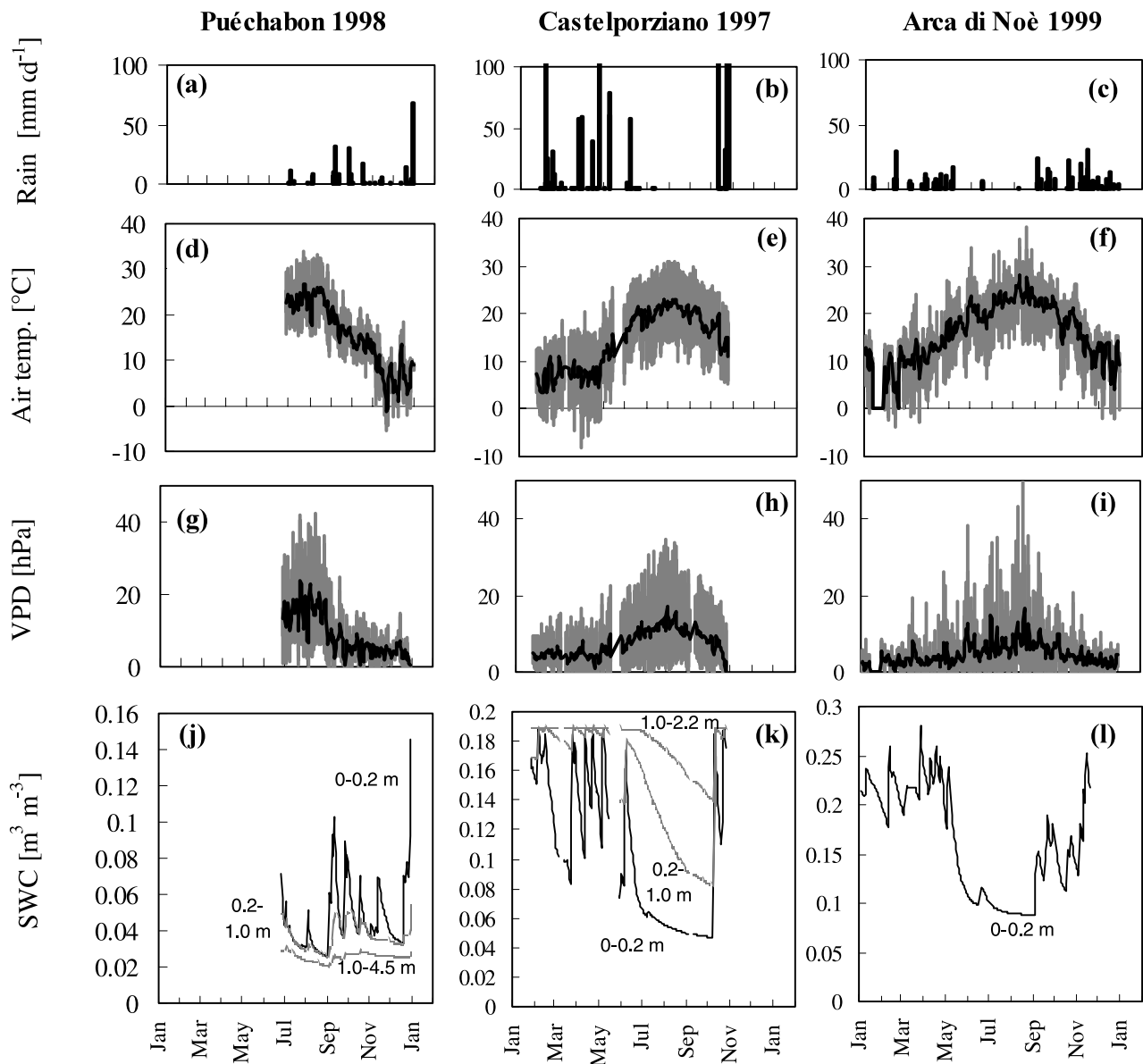
model then delivered hourly estimates for ecosystem respiration. These were used for the calculation of hourly gross carbon uptake ( $F_{cGPP}$ ) from NEE according to  $F_{cGPP} = -NEE + R_{eco}$ .

### 2.4. Mechanistic Model Basic Description

[11] We modeled ecosystem H<sub>2</sub>O and CO<sub>2</sub> fluxes using the Process Pixel Net Ecosystem Exchange model (PROXEL<sub>NEE</sub>), a model of the short-term dynamics (hourly to <10 years) of whole ecosystem CO<sub>2</sub> and H<sub>2</sub>O exchange. The model combines a 1-D canopy model [*Caldwell et al.*, 1986; *Tenhunen et al.*, 1994], a 1-D soil physical model of water and heat fluxes [*Moldrup et al.*, 1989, 1991], and a new model of root water uptake, as described in detail by *Reichstein* [2001]. Briefly, the general assumption of the canopy submodel is that the plant canopy can be represented by several horizontally homogeneous layers, for which microclimate (air and leaf temperature, incident radiation, relative humidity, wind speed) and subsequently leaf stomatal conductance and leaf gas exchange can be computed separately for Sun and shade leaves. At the leaf level, photosynthesis is treated using the basic formulation described by *Farquhar and von Caemmerer* [1982], as modified by *Harley and Tenhunen* [1991]. Stomatal conductance ( $g_s$ ) is linked to assimilation and environmental controls via the Ball-Berry equation [*Ball et al.*, 1987; *Harley and Tenhunen*, 1991]:

$$g_s = g_{s,min} + m \frac{(P_{net} + 0.5R_d)RH}{c_s} \quad (1)$$

[12] Here  $g_{s,min}$  is the minimal leaf conductance,  $m$  is the Ball-Berry coefficient,  $P_{net}$  is the net photosynthesis,  $R_d$  is



**Figure 1.** Meteorological conditions and soil water content at the three study sites. (a–c) Daily precipitation above the canopy; (d–f) daily mean (black line) and range (shaded bars) of air temperatures above the canopy; (g–i) daily mean (black line) and range (shaded bars) of vapor pressure deficit above the canopy; (j–l) modeled soil water content according to indicated layers. At Arca di Noè, soil water content is from continuous time domain reflectometry measurements.

the dark respiration, and  $RH$  and  $c_s$  are the relative humidity and the  $CO_2$  concentration at the leaf surface, respectively. See the work of *Falge* [1996] and *Reichstein* [2001] for details. The canopy model is conceptually similar to the CANOAK model [*Baldocchi*, 1997; *Law et al.*, 2000], except that within-canopy turbulence is not addressed. The soil submodel simulates unsaturated water flow according to Richards equation parameterized with *Van Genuchten* [1980] soil hydraulic parameters.

[13] The canopy model was parameterized for the sites as previously for a Spanish *Quercus ilex* L. forest [*Sala and Tenhunen*, 1996]. This parameterization included an exponential extinction of carboxylation and RuBP regeneration

capacities and dark respiration ( $V_{c_{max}}$ ,  $J_{max}$ ,  $R_d$ ) from the top to the bottom of the canopy as a function of cumulative leaf area index (LAI) [cf. *Rambal*, 2001].  $V_{c_{max}}$  declined from  $41.0 \mu\text{mol m}^{-2} \text{s}^{-1}$  at the top of the canopy to  $18.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  in the lowest (=tenth) layer. Accordingly,  $J_{max}$  varied from  $141.0$  to  $63.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ . For nonstressed conditions the Ball-Berry coefficient was set to default  $m = 15$ . For more details see the work of *Reichstein* [2001]. Leaf area index was set to the observed values at the sites (cf. Table 1). Owing to the new hypotheses under consideration, which is that drought affects ecosystem exchange via changes in leaf photosynthetic capacities or via induction of stomatal patchiness, details related to

modifications in the model formulation are now added and a description of the inverse modeling approach is given.

## 2.5. Model Reformulation

[14] To examine the hypothesis that stomatal patchiness may play an important role in controlling canopy gas exchange during drought, stomatal patchiness must be included in the leaf-level model. Stomatal patchiness is generally defined as a statistically nonnormal spatial distribution of stomatal apertures on the leaf [Beyschlag and Eckstein, 1998]. In the current model formulation, a bimodal distribution of stomatal aperture was assumed, i.e., stomata are either closed ( $g_s = 0$ ) or open at a uniform value. This implies that only part of the leaf area exhibits gas exchange (active patches or leaf area). In principle, the active and inactive patches have different energy balances because latent heat fluxes are different, resulting in higher temperatures at patches with closed stomata. Consequently, conductive heat fluxes between the patches are to be expected. However, these effects have been neglected in this model version, resulting in the same simplified approach as in a former theoretical leaf-level analysis [Buckley *et al.*, 1999; p. 136, “bimodal distribution”), where the calculated fluxes through the open stomata are multiplied by the proportion of active leaf area. In the current study, the proportion of active leaf area was allowed to change as a model parameter over the course of the summer. For this study, no diurnal or within-canopy variation of the proportion of active leaf area was implemented into the model.

## 2.6. Inverse Parameter Estimation

[15] According to the two assumptions that either reduction in photosynthetic capacities (= “capacity approach”) or in active leaf area (= “patchiness approach”) occurs in response to drought, two alternative parameter estimation procedures were developed. In the first procedure, the leaf-level Ball-Berry coefficient ( $m$ ) and the standardized (25°C) photosynthetic and respiratory capacities [ $V_{c_{\max}}$  (25°C),  $J_{\max}$  (25°C),  $R_d$  (25°C)] were estimated for consecutive 5-day intervals. In the second approach the Ball-Berry coefficient ( $m$ ) and the proportion of active leaf area were estimated for the same periods.

[16] The parameters were optimized by inverting the canopy model simultaneously against both observed gross CO<sub>2</sub> uptake and transpiration rates. Thus a multicriteria optimization [sensu Janssen and Heuberger, 1995] had to be performed. The problem which arises in the multicriteria problem is that one criteria (e.g., residual sum of squares for transpiration) might rise when the other decreases (e.g., residual sum of squares for CO<sub>2</sub> flux). This problem was circumvented by building a combined criterion, namely the following objective (misfit) function:

$$\text{misfit}(\theta) = \left[ \sum_{i=1}^n \left( \frac{\text{OBS}_{i,\text{H}_2\text{O}} - \text{SIM}(\theta)_{i,\text{H}_2\text{O}}}{\overline{\text{OBS}}_{\text{H}_2\text{O}}} \right)^2 + \sum_{i=1}^n \left( \frac{\text{OBS}_{i,\text{CO}_2} - \text{SIM}(\theta)_{i,\text{CO}_2}}{\overline{\text{OBS}}_{\text{CO}_2}} \right)^2 \right]. \quad (2)$$

[17] This allows the minimization of the sum of the squares of all “normalized” residuals for carbon and water fluxes. In equation (2), the superscripts indicate if carbon

dioxide or water fluxes are considered;  $\text{OBS}_i$  and  $\text{SIM}_i$  are the  $i$ th observed and  $i$ th simulated flux, respectively, where  $\text{SIM}_i$  is a function of the parameter vector  $\theta$ ;  $\overline{\text{OBS}}$  denotes the arithmetic mean of the observed fluxes. (For clarification the parameter vector  $\theta$  in the capacity approach consists of the two parameters “relative photosynthetic capacities” and “ $m$ ”). Normalized residuals are necessary as errors in CO<sub>2</sub> and H<sub>2</sub>O fluxes are not directly comparable (different units and quantities). Through equation (2), errors normalized with respect to the mean observed value of 20%, for instance, get the same weight for carbon and water fluxes. The minimization of the objective function was accomplished by the Levenberg-Marquardt algorithm as implemented in the data analysis package PV-WAVE 6.21. In the capacity approach, the assumption was added that  $V_{c_{\max}}$  (25°C),  $J_{\max}$  (25°C), and  $R_d$  (25°C) may only vary proportionally (meaning a constant ratio between them). A new parameter (termed “relative capacity”) was introduced as a multiplier of the original photosynthetic capacities (i.e., a relative capacity of 1.0 means “original parameter,” cf. section 2.4, while 0.5 means “ $V_{c_{\max}}$  (25°C),  $J_{\max}$  (25°C), and  $R_d$  (25°C) are all reduced to 50%”). This constraint, which reduces the number of free parameters from three to one, is based on the frequent observation that the temperature-corrected photosynthetic capacities and respiration are highly intercorrelated among and within species [cf. Wullschleger, 1993; Leuning, 1997; Reich *et al.*, 1998] and even within single trees [Fleck, 2001]. For consistency in both approaches, a “relative”  $m$  parameter was introduced as a multiplier of the original  $m$  of 15. The procedure resulted in either 5-day estimates of the relative capacities and relative  $m$  (capacity approach) or alternatively in 5-day estimates of the proportion of “active leaf area” and relative  $m$  (patchiness approach). The parameter estimates were then related to the dynamics of soil water content at all three sites (see above).

[18] The credibility of the optimization results and the identifiability of the parameters were tested for the capacity approach, with an emphasis on whether differences in parameters between drought and nondrought periods could be identified. This was accomplished by an exhaustive sampling from the 2-D parameter space (relative  $m \times$  relative capacities), ranging from 0.1 to 2.0. For each parameter combination the model was run and the mean absolute errors (MAE) of the model for CO<sub>2</sub> and for H<sub>2</sub>O fluxes were calculated. For both, carbon and water fluxes, a relative mean absolute error was defined as

$$\text{MAE}_{\text{rel}}(\theta)_i = \frac{\text{MAE}(\theta)_i}{\min\{\text{MAE}(\theta)_i \quad \forall i\}}, \quad (3)$$

where  $\theta_i$  is the  $i$ th parameter combination and the denominator denotes the minimum of the MAEs of all parameter combinations. For clarity, an  $\text{MAE}(\theta)_i$  of 1.3, for example, means that for parameter combination  $i$  the mean absolute error is 30% higher than for the “best” parameter combination. The geometric means of the relative mean absolute errors of CO<sub>2</sub> and H<sub>2</sub>O fluxes were computed to get a combined average relative mean absolute error for each parameter combination. The geometric mean should be applied when ratios are averaged [cf. Sachs, 1996]. The model run for each parameter combination was

then ranked according to their relative mean absolute error. Results are shown here for the Puéchabon site.

### 2.7. Statistical Analysis

[19] Standard errors of the inversely modeled parameter estimates were estimated by the following bootstrapping algorithm: The original data sets (split into 5-day periods) consisting of hourly gross carbon uptake, transpiration, and meteorological drivers were randomly resampled (with replacement) 250 times, where each “resample” was made up to the same number of data points as the original data set. The model parameters were estimated by minimizing the objective function equation (2) for each resample, resulting in 250 parameter estimates per original data set. The standard deviation of these 250 estimates is a good measure of the random error associated with the individual regression parameters [Efron and Tibshirani, 1993].

[20] The model performance was evaluated against the data by different validation statistics according to Janssen and Heuberger [1995]. There, modeling efficiency (MEF) is defined as

$$MEF = 1 - \frac{\sum_{i=1}^N (OBS_i - SIM_i)^2}{\sum_{i=1}^N (OBS_i - \overline{OBS})^2}, \quad (4)$$

where  $OBS_i$  and  $SIM_i$  are the corresponding observed and simulated values. In contrast to the  $r^2$  value, the modeling efficiency not only measures the association (or correlation) between modeled and observed data but also their coincidence, and it is sensitive to systematic deviations between model and observation [cf. Smith *et al.*, 1996]. Additional evaluation statistics used in this study are the mean absolute error,

$$MAE = \frac{1}{n} \sum_{i=1}^n \text{abs}(RES_i),$$

the median of the absolute errors,

$$MEDAE = \text{median}\{\text{abs}(RES_i)\}_{i=1,\dots,n},$$

the arithmetic mean over all errors (MErr), and the root mean squared error,

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n RES_i^2}.$$

$RES_i$  denotes the residual at the  $i$ th observation, i.e.,  $OBS_i - SIM_i$ . Finally, linear regression parameters (slope  $a$ , intercept  $b$ ) of observed versus modeled data were estimated by least squares regression to detect systematic (linear) deviations between model and observation [cf. Janssen and Heuberger, 1995].

## 3. Results

### 3.1. CO<sub>2</sub> and H<sub>2</sub>O Fluxes Via Eddy Covariance

[21] Monthly average diurnal courses of gross ecosystem CO<sub>2</sub> uptake and H<sub>2</sub>O loss are shown in Figure 2. Clear,

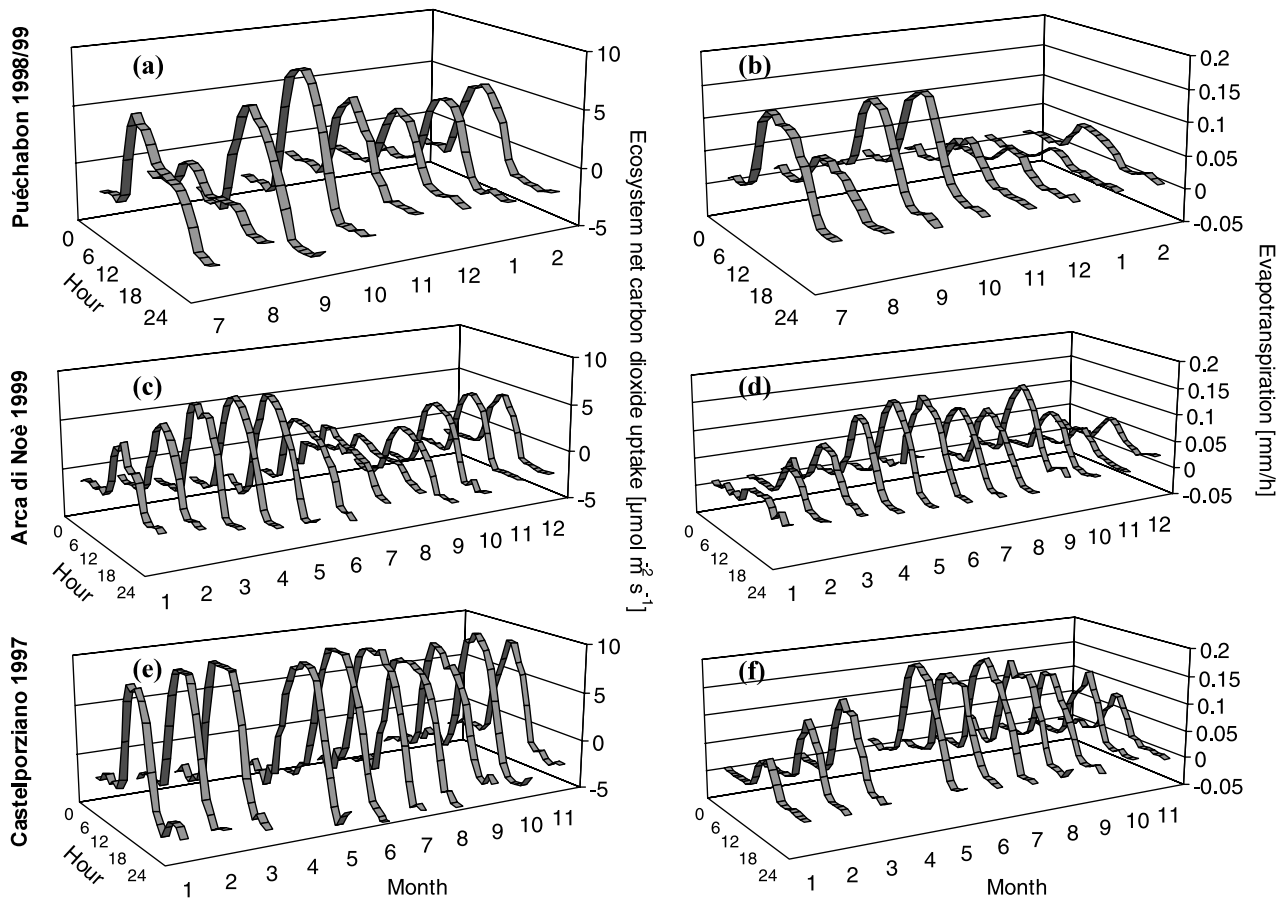
increasing drought effects with a large reduction of CO<sub>2</sub> and H<sub>2</sub>O fluxes and a typical midday depression of CO<sub>2</sub> uptake can be seen from July to August at Puéchabon and from June to August at Arca di Noè. At Castelporziano, fluxes are generally higher and drought effects are much less pronounced (August–September), although summer precipitation was absent as on the other two sites (compare Figure 1).

### 3.2. Bottom-Up Analysis and Model Inversion

[22] The solutions found for the parameters (relative capacities and  $m$ ) were well constrained and distinctly different between drought and nondrought conditions only when both water and carbon fluxes were used for the parameter estimation, as depicted in Figures 3 and 4 for the Puéchabon site. Under nonstress conditions, for carbon fluxes the minimum MAE is  $1.66 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure 3a) and at maximum, 10% higher MAE can be reached with all relative  $m$  values from 0.6 to 1.6, if the capacities vary correspondingly from 1.4 to 1.0. For water fluxes the minimum MAE is  $0.029 \text{ mm h}^{-1}$  and relative  $m$  values are constrained between 1.2 and 1.6, while relative capacities may vary between 0.7 and 1.4 if the MAE for water is allowed to be within 10% of the minimum MAE of all model runs (Figure 3b). However, if the criterion that the MAE must not be more than 10% higher than the minimum MAE should be fulfilled for both carbon and water fluxes, the relative  $m$  and capacities are better constrained: the relative  $m$  must be around 1.4 and the relative capacities around 1.1 (i.e., parameters must lie within the intersection of the respective parameter spaces in Figures 3a and 3b (white areas)). Under drought conditions this characteristic becomes even clearer (Figures 3c and 3d), where the capacities are not constrained by the water fluxes but strongly by the carbon fluxes. Precisely, water fluxes under drought are correctly described even with relative capacity at 1.0, if only  $m$  drops to 20% of its original value (Figure 3d). However, then the MAE for carbon flux would be more than twice as high than the minimum MAE of  $0.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Thus relative  $m$  and capacities are constrained to values of around 0.4 and 0.25, respectively, if both water and carbon fluxes are considered. Thus they differ distinctly from the parameters derived in the nonstressed period.

[23] In Figure 4 the model runs are ranked by ascending relative MAE (averaged for carbon and water fluxes, cf. equations (2)–(3)) and the parameters (relative capacity, relative Ball-Berry coefficient) are plotted against the model rank. It is evident that parameters of “good” model runs fall into a narrow range (i.e., they can be estimated from the flux data) and that they clearly change between drought and nondrought conditions: Even if we allow a large error of more than 30% of the minimum absolute error (i.e., a relative MAE of 1.3), then still relative  $m$  and capacities are constrained to values above 0.9 under nonstressed conditions (Figures 4a and 4c), and in contrast to below 0.6 and 0.4, respectively, under drought conditions (Figures 4b and 4d). These results show that a criterion that simultaneously evaluates CO<sub>2</sub> and H<sub>2</sub>O fluxes is necessary and such a criterion (equation (2)) has been utilized in the subsequent results.

[24] When the physiological canopy model is inverted in the analysis of the eddy covariance flux and sapflow data,



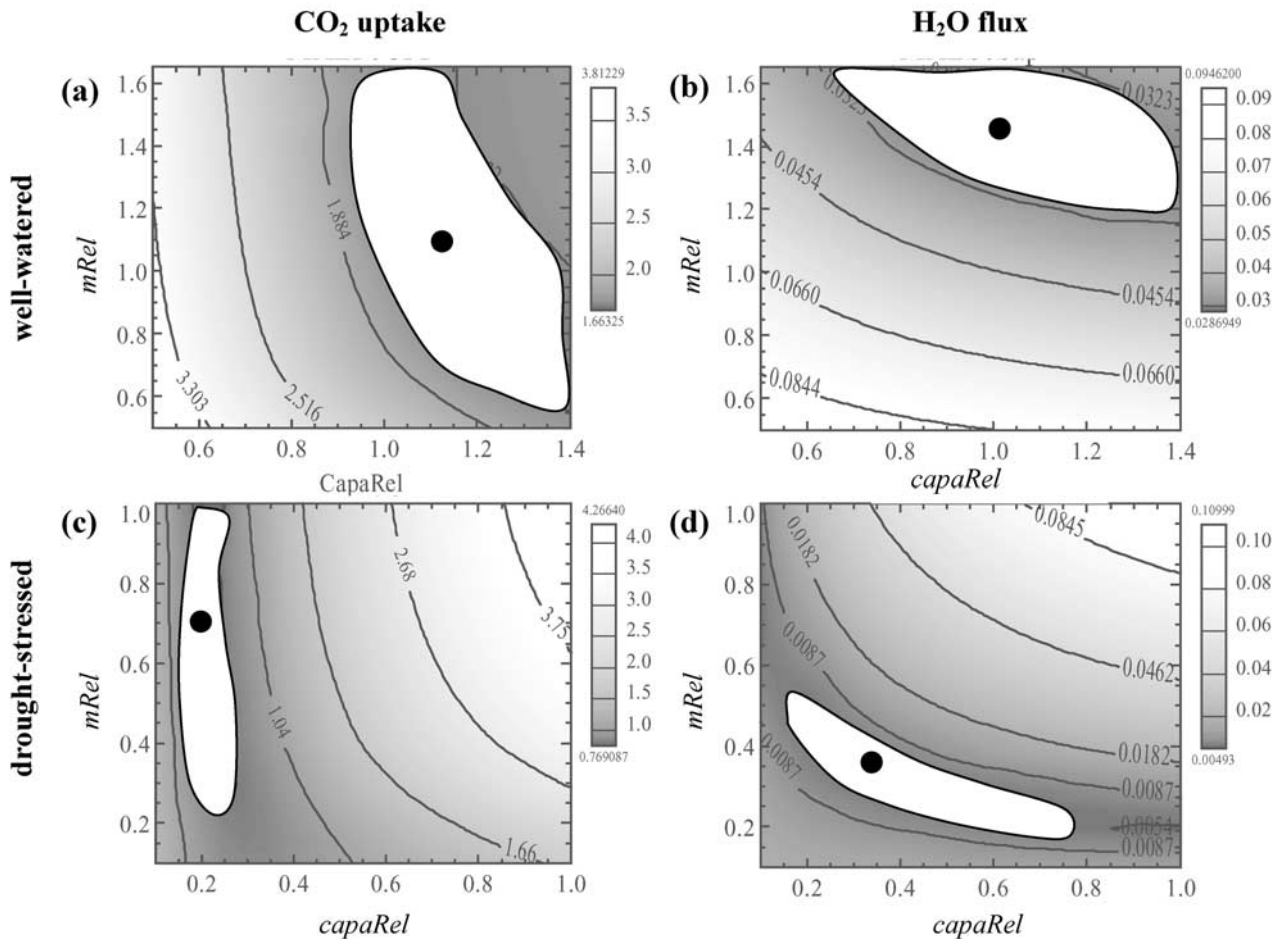
**Figure 2.** Monthly average diurnal courses of (a, c, e) ecosystem net CO<sub>2</sub> uptake and (b, d, f) evapotranspiration for the three sites (top) Puéchabon, (middle) Arca di Noè, and (bottom) Castelporziano as observed by eddy covariance.

the drought effects on CO<sub>2</sub> and H<sub>2</sub>O fluxes (compare Figure 2) translate into a pronounced seasonality in model parameters (Figure 5). In both, the capacity approach (Figures 5a–5c) and the patchiness approach (Figures 5d–5f), the respective parameters (relative capacity or active leaf area) were estimated from the flux data for each 5-day interval with satisfactory precision (standard errors most often below 10%). At all sites the modeled parameters (capacity or active leaf area) decline during the drought period and recover after the autumn rainfalls. The most severe decline is found at the Puéchabon and Arca di Noè sites (Figures 5a and 5c–5f), where capacities and the active leaf area decrease to below 20% of the original values. For those sites, a reduction in the same parameter values is also determined for the winter months (November–December for Puéchabon; January–February for Arca di Noè). Apart from the apparent drought effect on either photosynthetic capacities or active leaf area, it is noteworthy that particularly high values >1 are found in early spring (February–April) for the Arca di Noè and Castelporziano sites.

[25] Both the estimated photosynthetic capacities and the active leaf area are clearly significantly related to the relative soil water content under dry soil conditions and at all sites (correlation coefficients 0.76–0.96; Figures 6a–6f). Above a certain threshold water content, which is ca. 20–25% of field capacity at the Castelporziano and the Arca di

Noè sites, but more than 40% at the Puéchabon site, the parameters are virtually unrelated to soil moisture. Especially at the Castelporziano and the Arca di Noè sites, a large variation in photosynthetic capacities occurs at high soil moisture, with particularly high values in early spring (Figure 6, solid symbols). In contrast to the capacity/active leaf area parameters, the fitted Ball-Berry coefficient ( $m$ ) is predicted to vary less strongly through time, shows no consistent trend through the drought, and often is less precisely determined from the flux data (larger standard errors, not shown).

[26] With both assumptions (changing photosynthetic capacities or active leaf area), the diurnal courses of modeled water and CO<sub>2</sub> fluxes match the observed fluxes well (Figure 7). This contrasts strongly with the model, in which only the Ball-Berry coefficient  $m$  is affected by drought (gross primary productivity under drought conditions was severely overestimated; Figure 7d, dashed line; cf. Reichstein *et al.* [2002b]). Also, the water use efficiency of gross carbon uptake under drought is much better described with the new assumptions (Figure 7f). Nevertheless, Figures 7a and 7d still reveals some model error under drought conditions, where morning CO<sub>2</sub> and H<sub>2</sub>O fluxes are slightly underestimated by the model while afternoon fluxes are overestimated. For water fluxes under drought conditions, the differences between the sapflow and the eddy



**Figure 3.** Mean average model errors for CO<sub>2</sub> uptake ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and H<sub>2</sub>O fluxes ( $\text{mm h}^{-1}$ ) dependent on the parameters relative Ball-Berry coefficient (mRel, y axis) and relative capacities (capaRel, x axis) for the Puéchabon site. (a, c) Errors in ecosystem CO<sub>2</sub> uptake. (b, d) Errors in H<sub>2</sub>O fluxes. Figures 3a and 3b are under well-watered conditions (25–30 September 1998) and Figures 3c and 3d are under drought stress (11–16 August 1998). The white areas denote that part of the parameter space where the mean absolute error (MAE) was less than 10% higher than the minimum MAE. The black dots indicate the location of the absolute minimum of the MAE.

covariance method are relatively high since the observed sapflow water transport lags behind the water use observed via eddy covariance.

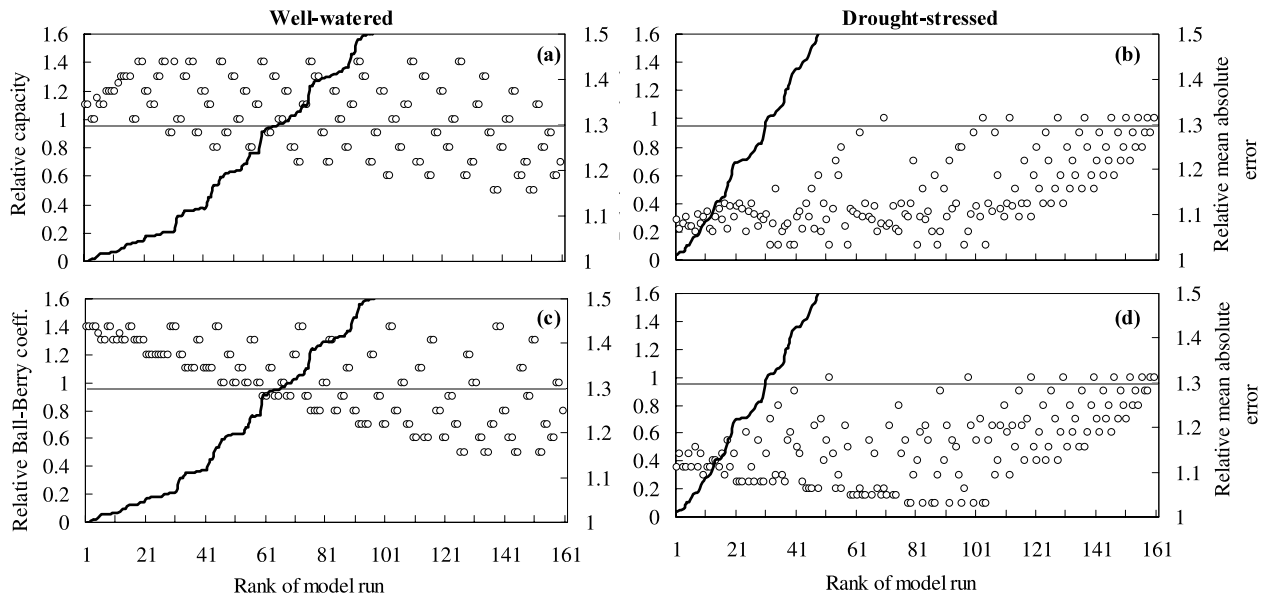
[27] In contrast to the model with the “classical stomatal control” hypothesis (only the Ball-Berry coefficient is variable), the seasonal course of the water use efficiency of gross carbon uptake ( $\text{WUE}_{\text{GPP}}$ ) is adequately described by the model with the active leaf area/capacity hypothesis (Figure 8, compare Reichstein *et al.* [2002b] for the same figure but with the approach only varying the Ball-Berry coefficient). At all sites a decline in  $\text{WUE}_{\text{GPP}}$  through the drought is followed by a recovery after the autumn rain falls.

[28] The overall model performance on an hourly basis for CO<sub>2</sub> and H<sub>2</sub>O fluxes is presented in Figure 9 and Table 2. Generally, fluxes of gross carbon uptake are well described by the model, with modeling efficiencies from 0.79 to 0.91 and mean absolute errors below 25% of the average flux when nighttime observations are included (Figure 9, Table 2). The regression of observed versus

modeled gross carbon uptake is near the 1:1 line (slopes between 0.98 and 1.04; Table 2). Through most of the range, the deviations of the modeled flux from the observed carbon flux are of the same magnitude as in the night, where modeled gross carbon uptake (correctly) is zero. This is shown for the Puéchabon site where statistical distributions of the residuals of CO<sub>2</sub> flux are very similar during nighttime and daytime (Figure 10).

[29] The deviation between modeled and observed water fluxes is greater than with CO<sub>2</sub> fluxes, resulting in lower modeling efficiencies and relatively higher mean absolute errors (Figure 9, Table 2). Still, for the Puéchabon site, a very good agreement between modeled and observed sapflow is achieved (MEF of 0.82 or 0.76, and MAE of 0.017 or 0.022, if all fluxes or only daytime fluxes are considered, respectively; Table 2). At the Castelporziano site, the error terms are somewhat higher, but still high modeling efficiencies above 0.6 are obtained. In contrast, despite the relatively low model errors at the Arca di Noè site, the lowest modeling efficiencies and  $r^2$  values are obtained because the





**Figure 4.** Distribution of model parameters (relative capacities and Ball-Berry coefficient, open circles) in relation to model performance (ranked model run, “1” on x axis is the best model run, “160” is the worst model run in terms of the relative mean absolute error; see text for its calculation) for the Puéchabon site, (a, c) under well-watered conditions, 25–30 September 1998, and (b, d) under drought stress, 11–16 August 1998). The solid line is the relative mean absolute error as a function of ranked model run. Horizontal lines indicate where the relative mean absolute error is 30% higher than for the best model run.

water fluxes are less variable than at the other sites. On all sites, the coincidence between modeled and observed water flux is better with sapflow than with the eddy covariance method.

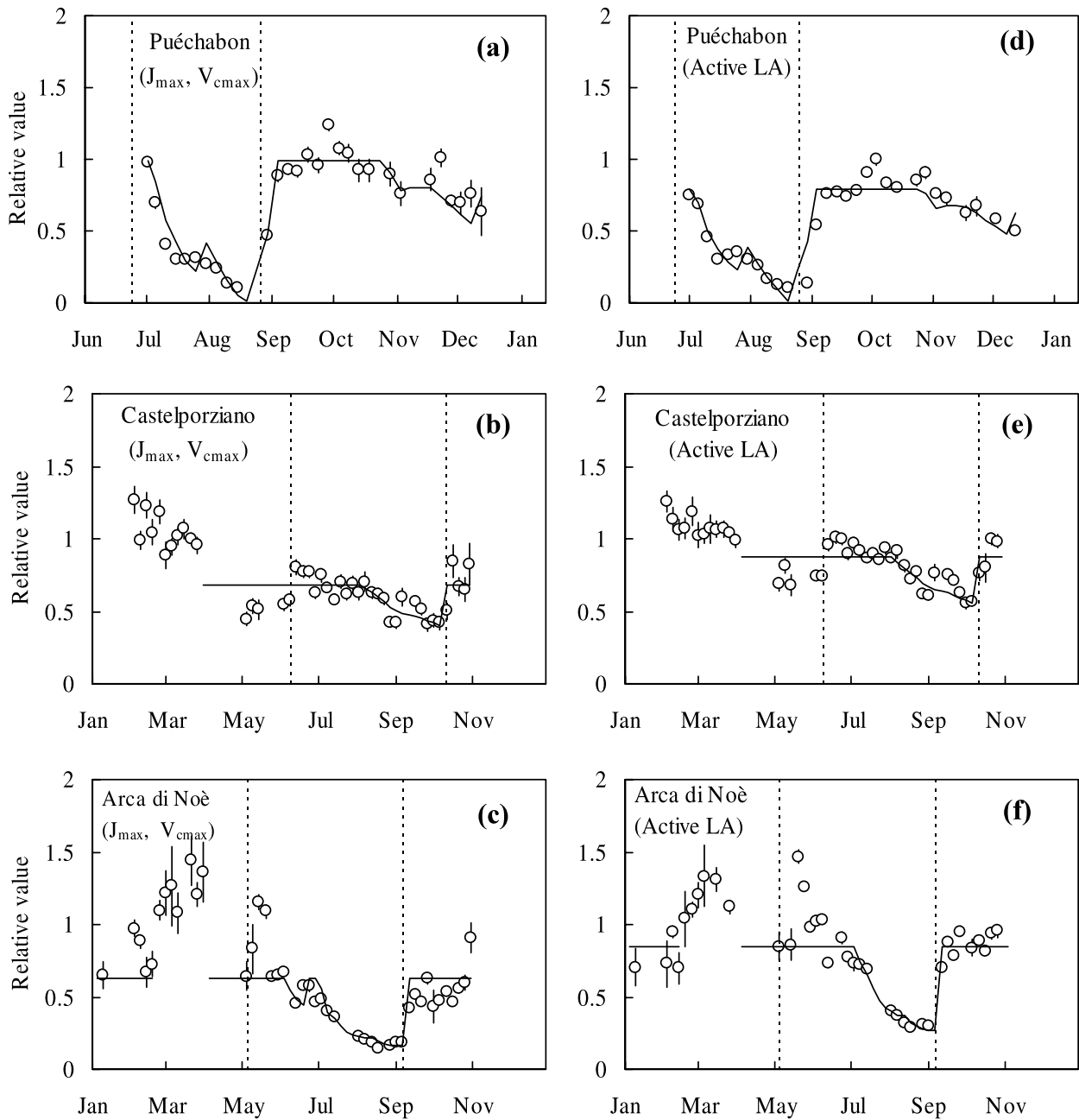
#### 4. Discussion

[30] It has been shown recently that the classical approach of modeling drought effects on canopy gas exchange (classical stomatal control, [cf. Schulze, 1986; Ball *et al.*, 1987; Tenhunen *et al.*, 1990; Chaves, 1991; Sala and Tenhunen, 1996]) is not able to describe ecosystem flux data from drought-stressed Mediterranean sites since this approach inevitably overestimates water use efficiency during drought [Reichstein *et al.*, 2002b]. Particularly, it was evident that the mismatch was not due to the specific Ball-Berry approach but a general problem of the assumption that fluxes are only affected by classical stomatal control, without any changes in other parameters. Reichstein *et al.* [2002b] hypothesized that the most likely changes to consider during drought are namely (1) changes in mesophyll photosynthetic capacity [cf. Harley and Tenhunen, 1991; Lawlor, 1995], (2) the induction of stomatal patchiness (i.e., nonnormal distribution of stomatal apertures [cf. Beyschlag *et al.*, 1992; Beyschlag and Eckstein, 1998; Buckley *et al.*, 1999]). The first hypothesis has meanwhile received support from leaf-level studies [Xu and Baldocchi, 2003].

[31] Thus the assumption that not only overall leaf stomatal conductance (modeled via the Ball-Berry coefficient  $m$ ) but also other parameters are affected by the drought was tested by inverting the fine-scale canopy gas

exchange model PROXEL<sub>NEE</sub>. This study stresses the strength of a two-criteria or multicriteria inverse modeling approach to analyze ecosystem flux data. While parameter estimates were not constrained (i.e., not identifiable) if only either carbon or water fluxes were considered, well-constrained parameter estimates were obtained by considering simultaneously both carbon dioxide and water exchange. Additionally, the bootstrap method applied here renders estimates of parameter uncertainty that are valid independent of assumptions about the distribution of the residuals. To our knowledge, this is the first study detecting drought effects on ecosystem gas exchange via such a multicriteria approach, but we see large potential for detecting other stress and disturbance effects as, for instance, chilling or air pollution effects.

[32] The results of the model inversion strongly indicate that “leaf activity” decreases in response to drought since the best model results (smallest model errors) for both CO<sub>2</sub> and H<sub>2</sub>O exchange are obtained when either photosynthetic capacities or the proportion of active leaf area progressively decline through the drought period while the optimized Ball-Berry coefficient does not exhibit a clear trend in response to drought. The relative changes in both “activity” parameters (capacity or active leaf area) are extremely similar and closely related to soil water content as soil water availability decreased. At high soil water content, the leaf activity is virtually independent of soil water content and shows a larger scatter, indicating that it is more constrained by other factors. Most apparent are the high “activity parameters” estimated for the early spring which suggests that “physiological phenology” (here defined as seasonal changes in physiological properties) is an impor-

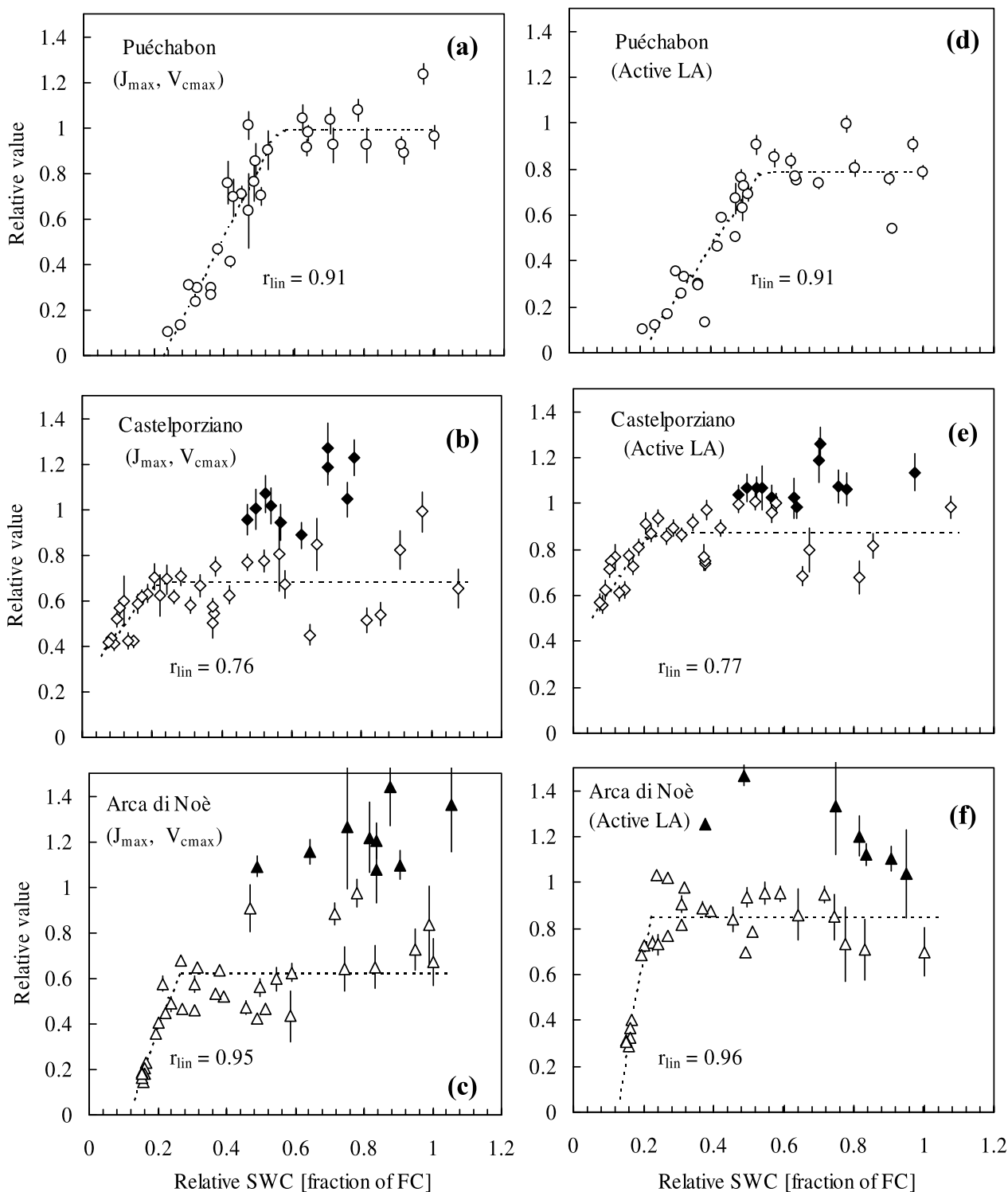


**Figure 5.** Time courses of (a–c) fitted relative photosynthetic capacities ( $J_{max}$ ;  $V_{cmax}$ ) and (d–f) (alternatively) of active leaf area (LA) at the three sites. For the photosynthetic capacities a  $y$  value of 1.0 corresponds to a  $V_{cmax}$  of  $41 \mu\text{mol m}^{-2} \text{s}^{-1}$  and a  $J_{max}$  of  $141 \mu\text{mol m}^{-2} \text{s}^{-1}$  (both at  $25^\circ\text{C}$ , Sun leaves). Lines are the respective time courses, when the functional dependencies (of capacities or active leaf area) on soil water content in Figure 6 are used. Error bars denote approximately  $\pm 1$  SE for the parameter estimates if larger than the symbol. Dashed lines circumscribe the summer drought period for each site.

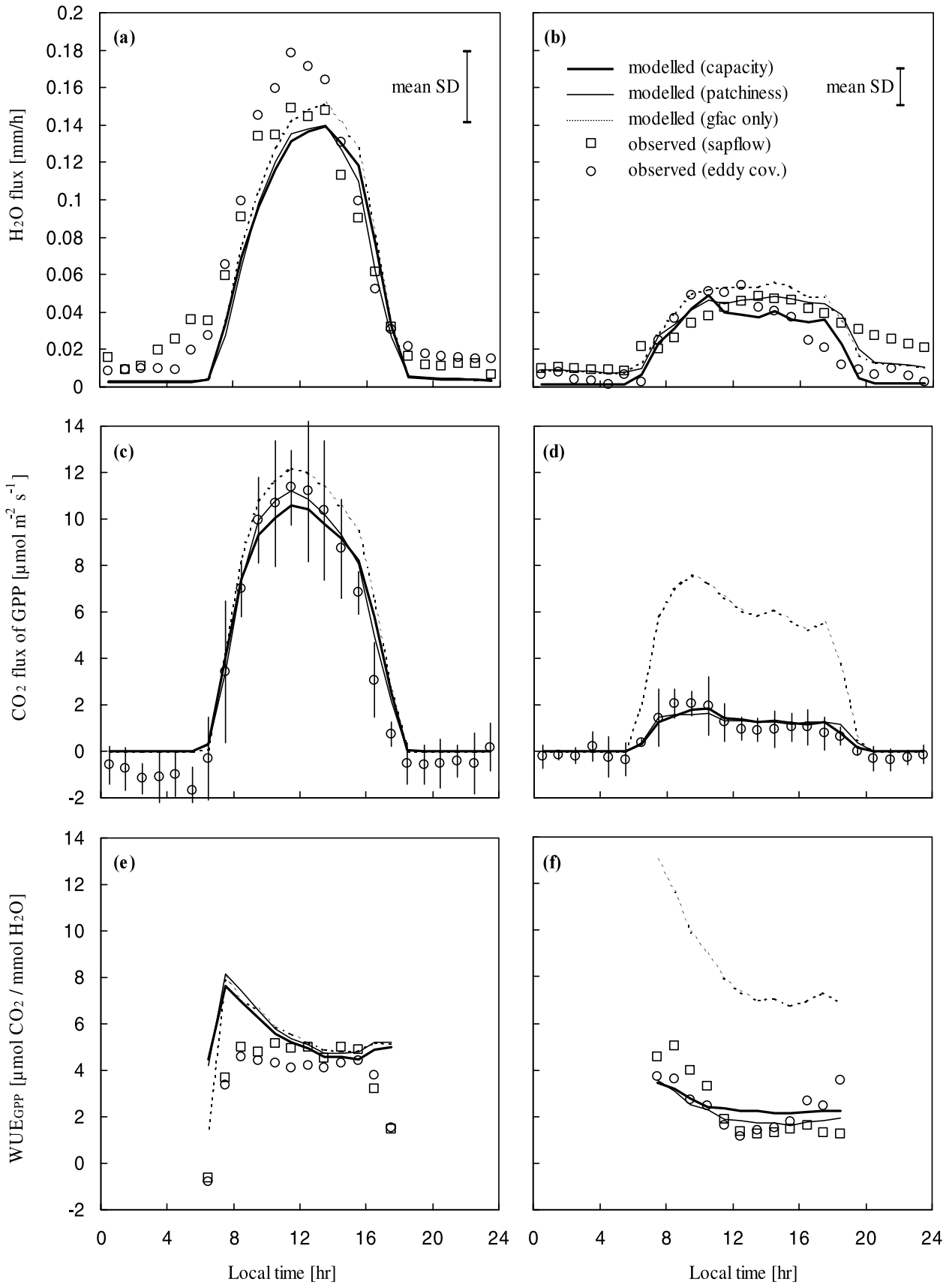
tant variable in determining ecosystem gas exchange over the course of the year, in addition to structural phenological changes in leaf area index.

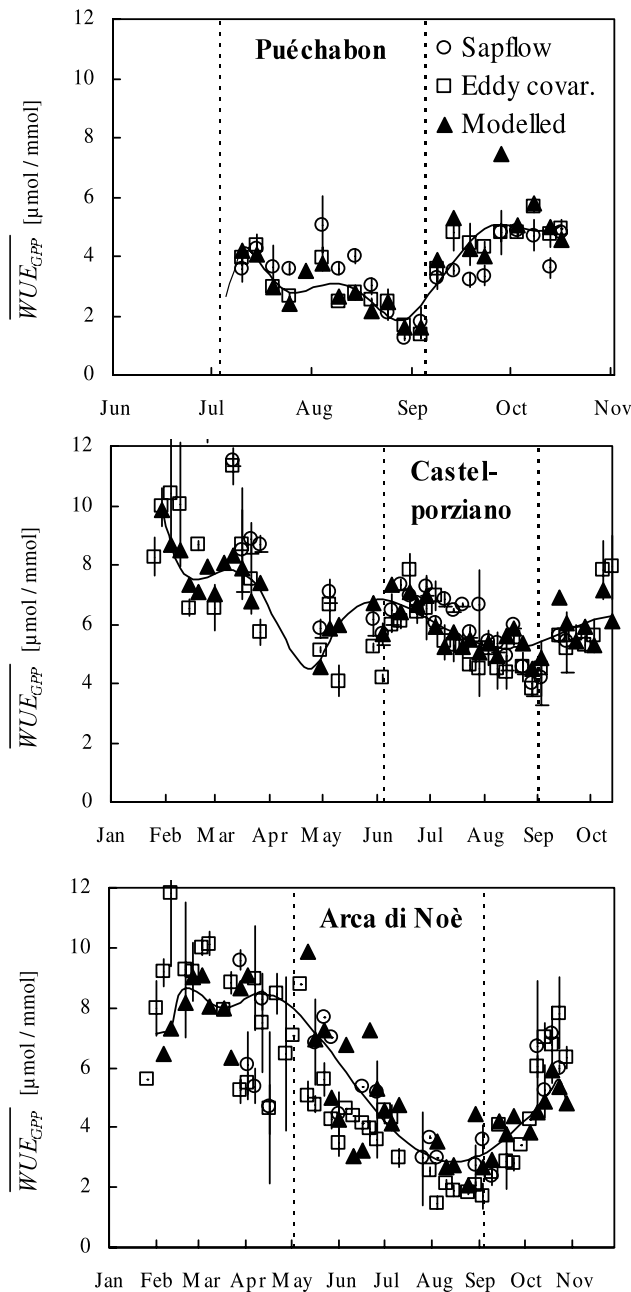
[33] However, from the flux data, it could not be demonstrated that one of the activity approaches considered in the modeling (capacity approach or patchiness approach) was superior since both approaches are equally successful in describing the seasonal and diurnal trends of canopy gas

exchange. This problem of identifying subprocesses is a well-recognized problem with the inversion of complex models [Mous, 1993; Abbaspour et al., 1997]. Similar problems arose at the leaf level, which led to controversial interpretation of leaf-level gas exchange data, and further progress will require new observations of stomatal behavior or isotopic studies [see Beyschlag and Eckstein, 1998]. Nevertheless, our modeling study suggests that both effects



**Figure 6.** Relationship between (a–c) fitted relative photosynthetic capacities ( $V_{cmax}$ ;  $J_{max}$ ) or (d–f) proportion of active leaf area (LA) and relative soil water content (RSWC) for the three sites. In Figures 6a–6c a y value of 1.0 corresponds to a  $V_{cmax}$  of  $41 \mu\text{mol m}^{-2} \text{s}^{-1}$  and a  $J_{max}$  of  $141 \mu\text{mol m}^{-2} \text{s}^{-1}$  (both at  $25^\circ\text{C}$ , Sun leaves). Curves are linear functions with upper threshold (saturation), fitted to unfilled symbols. Also indicated are the correlation coefficients between RSWC and the respective parameter (for the linearly increasing part of the function), which differed with high significance from zero ( $P < 0.01$ ). Filled symbols denote winter-spring transition (February–April). Error bars denote approximately  $\pm 1$  SE, if larger than the symbol.





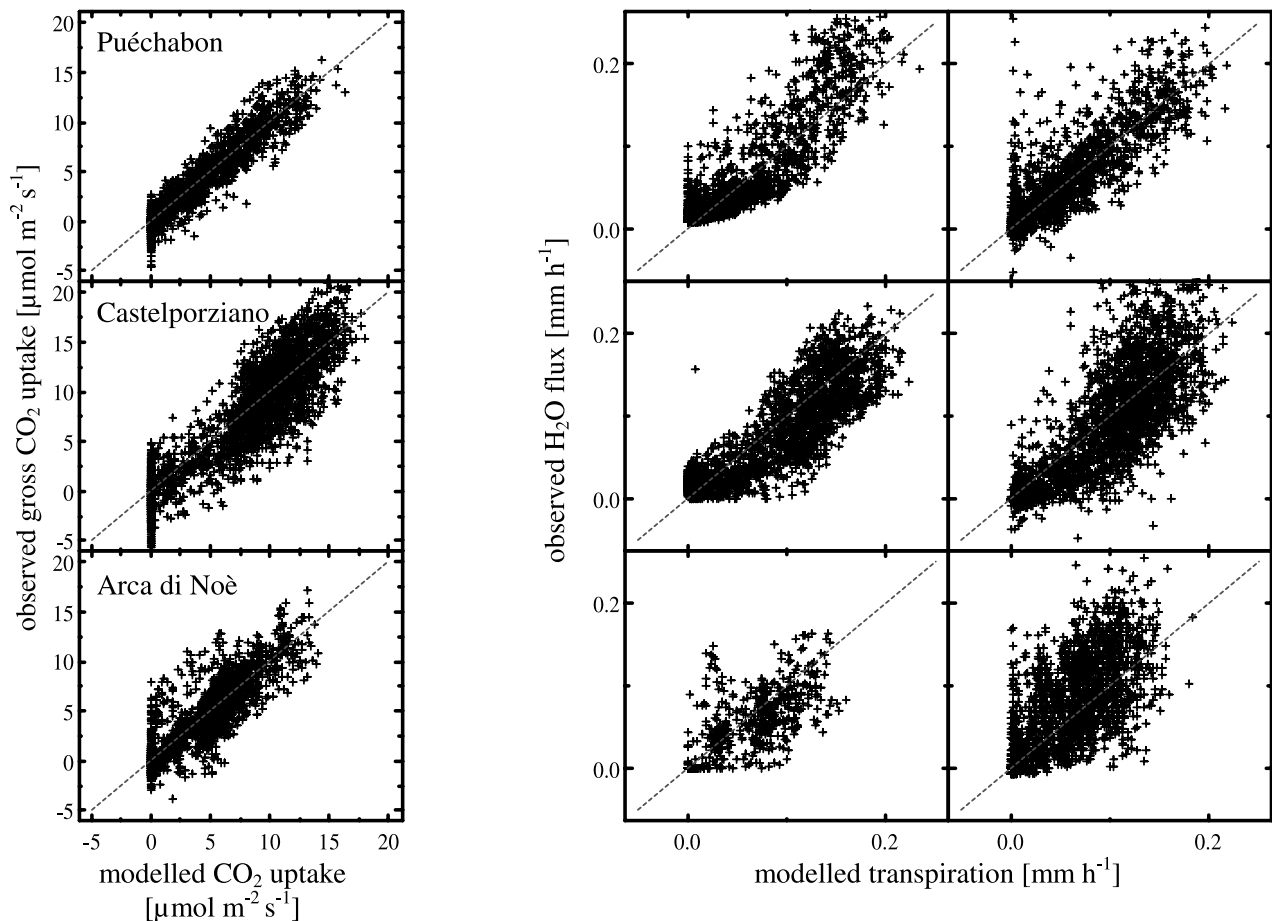
**Figure 8.** Time courses of 5-day medians of water use efficiency of gross carbon uptake ( $WUE_{GPP}$ , observed from sapflow and eddy covariance data, and modeled) at the three sites. Error bars are  $\pm 1$  SE of the observed data. Solid curve is a least squares spline to the modeled time course of  $WUE_{GPP}$ . Dashed lines circumscribe the summer drought period for each site.

may be superimposed. Predicted active leaf area greater than 1.0 in early spring may reflect phenology of tree, understory or forest floor species with potentially higher leaf area indices or higher physiological capacities during that period. The spring period after leaf flushing is known as a period with higher activity in leaves of Mediterranean trees. On the other hand, large drought-induced reductions of photosynthetic capacities of more than 70%, as estimated for the Puéchabon and Arca di Noè site, seem unlikely since in drought-adapted species only minor changes in mesophyll capacities have been found in laboratory studies [Kaiser, 1987; Chaves, 1991; Cornic, 1994]. Instead, patchy stomatal closure over a large portion of the leaf surface has been observed for Mediterranean species as a consequence of drought [Beyschlag *et al.*, 1992; Beyschlag and Eckstein, 1998] and also for *Quercus ilex* L. [Genty and Meyer, 1995] so that Rouspard *et al.* [1996] concluded that stomatal closure is probably the main factor reducing  $CO_2$  availability in the chloroplasts during drought (p. 252).

[34] Despite the difficulties in quantifying the relative importance of capacity changes versus patchy stomatal closure from ecosystem flux data, the crucial result of this exercise is that for all sites the canopy responses to drought can successfully be described with reasonable and simple assumptions about changes in leaf activity. This is in contrast to the conventional approach of only adjusting (uniform) leaf stomatal conductance, (e.g., Ball-Berry approach), which failed to describe the observed decline in carbon uptake [Reichstein *et al.*, 2002b]. As mentioned earlier, the latter approach is incorporated in virtually all leading models of canopy gas exchange, although problems have already been apparent [Baldochi, 1997]. Thus the new approach presented here is considered a significant step forward in modeling the simultaneous drought effects on canopy carbon and water exchange, particularly as soil water content is an excellent predictor for the leaf activity changes at all sites when drought occurs. At the same time, the results hint at the potential importance of patchy stomatal closure for canopy gas exchange, which according to Beyschlag and Eckstein [1998] is still largely unknown (p. 292). More mechanistic descriptions of the effects of patchy stomatal closure on canopy gas exchange will require further investigations into the spatial and diurnal distribution of stomatal control within canopies. It is noteworthy that the patchiness might not only occur at the leaf level, but also at the canopy level (i.e., that whole parts of the canopy cease their gas exchange, while other part are still active). Such phenomena may be investigated in the future by high-resolution canopy infrared photography.

[35] It should be stressed that the biogeochemical and ecological implications of our finding that drought effects on canopy carbon assimilation are stronger than expected by

**Figure 7.** (opposite) Average diurnal courses of (a, b) modeled and observed transpiration, (c, d) gross carbon uptake, and (e, f) water use efficiency of gross carbon uptake under (right) well-watered conditions 25.9–15.10 and (left) during severe drought 15.8–4.9 at the Puéchabon site. The model's "patchiness" and "capacity" involved the hypothesis that active leaf area or photosynthetic capacities, respectively, vary through the drought according to the optimization results in Figure 5. For comparison, the results from the model with the "Ball-Berry-coefficient-only"-hypothesis are also shown as dashed lines [cf. Reichstein *et al.*, 2002b]. For observed carbon fluxes, the standard deviations for each hour are given. For water fluxes, the average standard deviation (mean SD) for eddy covariance fluxes is given in the upper right corner. For sapflow, mean SD was slightly lower.

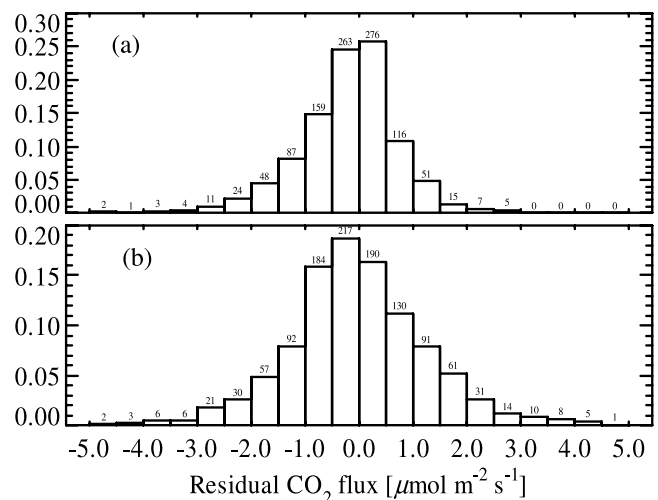


**Figure 9.** Scatterplot matrix of hourly observed versus modeled CO<sub>2</sub> and H<sub>2</sub>O fluxes. (left) ecosystem gross carbon uptake, (center) sapflow versus modeled transpiration, and (right) eddy covariance evapotranspiration versus modeled transpiration for (top) Puéchabon, (middle) Castelporziano, and (bottom) Arca di Noè site.

current models are potentially manifold since assimilation is the trophic basis in ecosystems and many processes (e.g., plant growth, litter fall, soil carbon dynamics) directly or indirectly depend on it. Current canopy and ecosystem models likely underestimate the effect of increasing drought stress under climate change in Mediterranean and subtropical ecosystems and consequently will tend to overestimate canopy carbon sequestration under drought. This bias can be avoided by including drought effects via patchy stomatal closure or photosynthetic capacities, as shown here. It is proposed to include these or similar formulations in biogeochemical models of ecosystems where drought effects are likely to occur. This will be most crucial for Mediterranean and subtropical biomes, but might be also important in tropical and temperate regions, where also significant drought effects on ecosystem fluxes have been detected [Baldocchi, 1997; Williams *et al.*, 1998] so that even implications of the drought effects found in the current study for carbon balances in global models may be expected.

**5. Conclusion**

[36] In conclusion, this study confirms the recent hypothesis that drought effects on canopy gas exchange might be better modeled via changes in photosynthetic capacities or



**Figure 10.** Histograms of residuals of gross carbon uptake fluxes for the Puéchabon site for (a) nighttime and (b) daytime.

**Table 2.** Model-Data Comparison Statistics for Hourly Fluxes of Gross Ecosystem CO<sub>2</sub> Uptake and Modeled Transpiration (Versus Sapflow and Versus Eddy Evapotranspiration Measurements) at the Three Sites<sup>a</sup>

Statistic <sup>b</sup>	Gross CO <sub>2</sub> Uptake			Transpiration Compared With Sapflow			Transpiration Compared With Eddy Covariance		
	Puéchabon	Castelporziano	Arca di Noè	Puéchabon	Castelporziano	Arca di Noè	Puéchabon	Castelporziano	Arca di Noè
<i>Day and Nighttime Fluxes Considered</i>									
MEF	0.912	0.804	0.791	0.818	0.764	0.710	0.769	0.672	0.537
r <sup>2</sup>	0.913	0.808	0.791	0.832	0.804	0.766	0.779	0.673	0.596
<i>y = ax + b</i>									
a	1.014	1.042	0.981	1.077	0.872	0.817	0.939	1.036	1.039
b	-0.158	-0.636	0.136	0.002	0.001	0.002	0.007	-0.005	0.012
N	2228	2618	2262	1815	2336	850	2226	2631	2547
MAE	0.839	2.031	1.152	0.017	0.022	0.013	0.017	0.030	0.027
MEDAE	0.609	1.633	0.738	0.010	0.015	0.005	0.010	0.021	0.017
RMSE	1.141	2.592	1.703	0.026	0.029	0.022	0.025	0.042	0.039
Merr	-0.117	-0.313	0.070	0.006	-0.009	-0.005	0.005	-0.002	0.014
<i>Only Day-Time Fluxes Considered</i>									
MEF	0.873	0.611	0.689	0.763	0.607	0.231	0.690	0.500	0.187
r <sup>2</sup>	0.873	0.619	0.689	0.781	0.677	0.417	0.697	0.503	0.324
<i>y = ax + b</i>									
a	0.993	1.092	0.986	1.144	0.924	0.649	0.929	1.081	0.841
b	-0.007	-1.207	0.082	-0.006	-0.006	0.017	0.008	-0.011	0.029
N	1256	1991	1435	1227	1692	440	1256	2003	1645
MAE	0.975	2.184	1.291	0.022	0.028	0.024	0.021	0.037	0.037
MEDAE	0.716	1.812	0.871	0.014	0.025	0.018	0.015	0.030	0.030
RMSE	1.300	2.742	1.821	0.031	0.034	0.030	0.030	0.048	0.047
Merr	-0.044	-0.285	0.005	0.005	-0.014	-0.009	0.003	-0.002	0.018

<sup>a</sup>Units for model statistics (*b*, MAE, MEDAE, RMSE, ME<sub>err</sub>) are  $\mu\text{mol m}^{-2} \text{s}^{-1}$  with carbon fluxes and  $\text{mm h}^{-1}$  with water fluxes. Results are divided into daytime and nighttime combined and daytime only.

<sup>b</sup>Abbreviations: MEF, modeling efficiency; *r*<sup>2</sup>, coefficient of determination; *y = ax + b*, linear regression parameters observed (*y*) versus modeled (*x*); *N*, number of observations; MAE, mean absolute error; MEDAE, median absolute error; RMSE, root mean squared error; ME<sub>err</sub>, mean error. See section 2 for definitions.

patchy stomatal closure rather than via “classical” stomatal control. Further data sets should be analyzed in order to explore if these patterns can be generalized. Moreover, this study demonstrates the large potential of multicriteria inverse modeling of ecosystem gas exchange data, as obtained for instance in eddy covariance flux networks. Within a data-assimilation framework, this potential should be exploited for calibration of process-based models that are applied for estimation of carbon and water balances.

[37] **Acknowledgments.** We would like to thank two anonymous reviewers for their helpful comments on the manuscript. Financial support for this work was given by the projects MEDEFU (ENV 4-CT98-0455), EUROFLUX (ENV4-CT95-0078), CARBOEUROFLUX (ENV-CT97-0694), and MIND (EVK2-2001-00296) within the fourth and fifth European Community Framework Programme.

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