

# Drought Influences the Accuracy of Simulated Ecosystem Fluxes: A Model-Data Meta-analysis for Mediterranean Oak Woodlands

**Author/Contributor:**

Vargas, R; Sonnentag, O; Abramowitz, Gabriel; Carrara, A; Chen, J; Ciais, P; Correia, A; Keenan, T; Kobayashi, H; Ourcival, J; Papale, D; Pearson, D; Pereira, J; Piao, S; Rambal, S; Baldocchi, D

**Publication details:**

Ecosystems  
v. 16  
Chapter No. 5  
pp. 749-764  
1432-9840 (ISSN)

**Publication Date:**

2013

**Publisher DOI:**

<http://dx.doi.org/10.1007/s10021-013-9648-1>

**License:**

<https://creativecommons.org/licenses/by-nc-nd/3.0/au/>

Link to license to see what you are allowed to do with this resource.

Downloaded from <http://hdl.handle.net/1959.4/53706> in <https://unsworks.unsw.edu.au> on 2023-01-28

# Drought influences the accuracy of simulated ecosystem fluxes: a model-data meta-analysis for Mediterranean oak woodlands

**Short title:** Drought influence simulated ecosystem fluxes

## Author names

Rodrigo Vargas<sup>1</sup>, Oliver Sonnentag<sup>2</sup>, Gab Abramowitz<sup>3</sup>, Arnaud Carrara<sup>4</sup>, Jing Ming Chen<sup>5</sup>, Philippe Ciais<sup>6</sup>, Alexandra Correia<sup>7</sup>, Trevor F. Keenan<sup>8</sup>, Hideki Kobayashi<sup>9</sup>, Jean-Marc Ourcival<sup>10</sup>, Dario Papale<sup>11</sup>, David Pearson<sup>12</sup>, Joao S. Pereira<sup>7</sup>, Shilong Piao<sup>13</sup>, Serge Rambal<sup>10</sup>, Dennis D. Baldocchi<sup>14</sup>

## Affiliations

<sup>1</sup>Department of Plant and Soil Sciences; Delaware Environmental Institute. University of Delaware, Newark, DE, USA

<sup>2</sup>Département de Géographie, Université de Montréal, Montréal, QC, Canada

<sup>3</sup>Climate Change Research Centre, University of New South Wales, Sydney, Australia

<sup>4</sup>Fundacion CEAM, Paterna, Spain

<sup>5</sup>Department of Geography and Program in Planning, University of Toronto, Toronto, Ontario, Canada

<sup>6</sup>Laboratoire des Sciences du Climat et de l'Environnement, LSCE, Gif sur Yvette, France

<sup>7</sup>Instituto Superior de Agronomia, Technical University of Lisbon, Lisbon, Portugal

<sup>8</sup>Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA

<sup>9</sup>Japan Agency for Marine-Earth Science and Technology, Yokohama, Kanagawa, Japan

<sup>10</sup>CEFE, Centre National de la Recherche Scientifique, Montpellier, France

<sup>11</sup> [DIBAF, University of Tuscia, Viterbo, Italy](#)

<sup>12</sup> Met Office Hadley Centre, FitzRoy Road, Exeter, Devon, EX1 3PB, United Kingdom

<sup>13</sup>Department of Ecology, Peking University, Beijing, China

<sup>14</sup>Department of Environmental Science, Policy and Management, University of California, Berkeley, CA, USA

*\*Corresponding Author*

*Rodrigo Vargas*

*Department of Plant and Soil Sciences; Delaware Environmental Institute. University of Delaware, Newark, DE 19717, USA*

*Email: [rvargas@udel.edu](mailto:rvargas@udel.edu)*

Submitted to *Ecosystems* on March 23<sup>th</sup>, 2012

Submitted revised version on October 26<sup>th</sup>, 2012

Submitted revised version on December 21<sup>st</sup>, 2012

46 Contributions:  
47 R.V. and D.D.B designed the study; R.V. performed data analysis; G.A., J. M.C., P.C., H.K.,  
48 D.Pearson, S.P., O.S., contributed with model results; A.C., A.C., J.M.O., D.Papale, J.S.P., S.R.,  
49 D.D.B., contributed with site observations; R.V. wrote the paper with contributions from G.A., J.  
50 M.C., P.C., H.K., D.Pearson, T.K., S.P., O.S., A.C., A.C., J.M.O., D.Papale, J.S.P., S.R., D.D.B.  
51

52 **ABSTRACT**

53 Water availability is the dominant control of global terrestrial primary productivity with  
54 concurrent effects on evapotranspiration and ecosystem respiration, especially in water-limited  
55 ecosystems. Process-oriented ecosystem models are critical tools for understanding land-  
56 atmosphere exchanges and for up-scaling this information to regional and global scales. Thus, it  
57 is important to understand how ecosystem models simulate ecosystem fluxes under changing  
58 weather conditions. Here, we applied both time-series analysis and meta-analysis techniques to  
59 study how five ecosystem process-oriented models simulated gross primary production (GPP),  
60 ecosystem respiration (Reco), and evapotranspiration (ET). Ecosystem fluxes were simulated for  
61 three years at a daily time step from four evergreen and three deciduous Mediterranean oak  
62 woodlands (21 site-year measurements; 105 site-year-simulations). Mediterranean ecosystems  
63 are important test-beds for studying the interannual dynamics of soil moisture on ecosystem  
64 mass and energy exchange as they experience cool, wet winters with hot, dry summers and are  
65 typically subject to drought. Results show data-model disagreements at multiple temporal scales  
66 for GPP, Reco, and ET at both plant functional types. Overall there was a systematic  
67 underestimation of the temporal variation of Reco at both plant functional types at temporal  
68 scales between weeks and months, and an overestimation at the yearly scale. Modeled Reco was  
69 systematically overestimated during drought for all sites, but daily GPP was systematically  
70 underestimated only for deciduous sites during drought. In contrast, daily estimates of ET  
71 showed good data-model agreement even during drought conditions. This meta-analysis brings  
72 attention to the importance of drought conditions for modeling purposes in representing forest  
73 dynamics in water-limited ecosystems.

74

75 **Key words:** ecosystem models, eddy covariance, FLUXNET, forest survival, model evaluation,  
76 water stress

77 **INTRODUCTION**

78 Water availability is the dominant control of roughly 40% of global terrestrial primary  
79 productivity (Beer and others, 2010) with concurrent effects on ecosystem respiration  
80 (Reichstein and others, 2002a; Schwalm and others, 2010). Recent increases in the global  
81 incidence of drought (Dai and others, 2004), and decreased global evapotranspiration (Jung and  
82 others, 2010) suggest that current terrestrial ecosystems are finding themselves in more water-  
83 limited environments (Hartmann, 2011). Such observations are in line with projections of climate  
84 change, with higher temperatures and reduced soil moisture, leading to longer and stronger  
85 seasonal droughts in the coming decades (Giorgi and Lionello, 2008).

86 Process-oriented ecosystem models are critical tools for studying land-atmosphere fluxes  
87 and for up-scaling this information to regional and global scales (Raupach and others, 2005).  
88 Drought has a large impact on ecosystem state and function, and previous studies have  
89 highlighted data-model disagreement for CO<sub>2</sub> fluxes in ecosystems suffering regular drought  
90 such as those found in Mediterranean-type climate zones (e.g., Krinner and others, 2005;  
91 Morales and others, 2005; Jung and others, 2007). The limited understanding of the hierarchy  
92 and the temporal/spatial variation of drivers controlling the ecophysiology/biogeochemistry of  
93 Mediterranean ecosystems hamper the accurate representation of H<sub>2</sub>O and CO<sub>2</sub> fluxes by models.  
94 (Reichstein and others, 2002b; Keenan and others, 2010a; Misson and others, 2010). Thus, it is  
95 critical to understand how drought stress influences these fluxes, and how process-oriented  
96 ecosystem models predict them across different ecosystems.

97 Mediterranean ecosystems constitute a well-suited test-bed for the study and simulation  
98 of drought effects, due to the combination of cool, wet winters with hot, dry summers (Joffre and  
99 others, 2007). The asynchrony between the supply and demand for water causes annual potential

100 evaporation to exceed annual precipitation (Baldocchi and Xu, 2007), leading to seasonal  
101 droughts which cause large declines in both assimilation and ecosystem respiration (Pereira and  
102 others, 2007; Misson and others, 2010; Schwalm and others, 2010). Soil water availability is the  
103 main factor limiting the metabolism of Mediterranean ecosystems, making them climate change  
104 hotspots (Giorgi, 2006).

105         Oak woodlands are an important forest type in Mediterranean regions of the world (Joffre  
106 and others, 2007). They range from open to dense forest that allows a well developed to sparse  
107 understory comprising mostly of grasses, and are predominantly composed of evergreen and  
108 deciduous trees (Reichstein and others, 2002b; Pereira and others, 2007; Baldocchi and others,  
109 2010). Oak trees in Mediterranean woodlands have developed structural and functional attributes  
110 that enable them to survive on a limited annual water supply by: a) having a generally low to  
111 medium leaf area index, an erectophile leaf inclination angle distribution to reduce thermal load,  
112 or low to medium tree cover to reduce total water loss at the landscape scale (Joffre and others,  
113 2007; Ryu and others, 2010); b) down-regulating photosynthesis, respiration, and stomatal  
114 conductance with decreasing soil water availability (Baldocchi and others, 2010); and c) the  
115 potential of extending their root systems to tap ground water (David and others, 2007; Miller and  
116 others, 2010).

117         In this study we use data from multiple Mediterranean Oak woodland sites to address the  
118 following question: How well do process-oriented ecosystem models simulate the temporal  
119 variability of CO<sub>2</sub> (i.e., gross primary production and ecosystem respiration) and H<sub>2</sub>O vapor  
120 fluxes (i.e., evapotranspiration) in Mediterranean oak woodlands across years and under drought  
121 or no-drought conditions? Based on previous studies we hypothesize that data-model  
122 disagreement may be largest under drought stress (Reichstein and others, 2002b; Schwalm and

123 others, 2010), or at temporal scales between weeks-months where synoptic events (i.e.,  
124 precipitation pulses) drive ecosystem fluxes (Baldocchi and others, 2006) and are challenging for  
125 model performance (Mahecha and others, 2010; Dietze and others, 2011). First, we applied  
126 wavelet analysis as a diagnostic tool to identify the temporal occurrence of data-model  
127 disagreement (Vargas and others, 2010b; Dietze and others, 2011; Wang and others, 2011).  
128 Second, we used meta-analysis techniques as a way to: a) provide quantitative/statistical means  
129 of integrating independent results (i.e., observed fluxes by eddy covariance); and b) identify how  
130 simulated fluxes by different process-oriented models contribute to variation among results and  
131 data-model disagreement (Hedges and others, 1999; Gurevitch and others, 2001).

132

## 133 **METHODS**

### 134 Measurements at Study Sites

135 The study sites included four evergreen and three deciduous Mediterranean oak woodlands  
136 described in Table 1. Flux measurements of CO<sub>2</sub> and water vapor were made at each site using  
137 the eddy covariance technique (Aubinet and others, 2000). We inferred gross primary production  
138 (GPP) and ecosystem respiration (Reco) from half-hourly net ecosystem exchange (NEE)  
139 measurements. Eddy covariance data for this study were drawn from the La Thuile 2007  
140 FLUXNET 2.0v dataset ([www.fluxdata.org](http://www.fluxdata.org)). The La Thuile data set has been harmonized for  
141 gap-filling, quality control of NEE values, and calculation of GPP, Reco, and evapotranspiration  
142 (ET) following standardized protocols (Reichstein and others, 2005; Papale and others, 2006).  
143 Three years (2005-2007) of eddy-covariance data were used at each site (total of 21 site-years;  
144 Supplementary Figures 1, 2), along with continuous meteorological drivers (e.g., solar radiation,  
145 precipitation, soil water content, soil temperature, wind speed). All measurements used in this



146 study including meteorological drivers were onsite measurements and available from the La  
147 Thuile 2007 FLUXNET 2.0v dataset ([www.fluxdata.org](http://www.fluxdata.org)).

148

#### 149 Model Simulations

150 We performed simulations for all study sites considering differences in leaf habit (i.e., evergreen  
151 vs. deciduous). We used five process-oriented ecosystem models (i.e., BEPS, Biome-BGC,  
152 CABLE, ORCHIDEE, JULES; Table 2) based on volunteer participation by attendants at a  
153 FLUXNET workshop during 2009 (Asilomar, California, USA). The models used site  
154 meteorological forcing input variables along with site-specific ancillary information (Table 1) to  
155 calculate GPP, Reco and ET. All data were drawn from the La Thuile 2007 FLUXNET 2.0v  
156 dataset ([www.fluxdata.org](http://www.fluxdata.org)) and represent onsite measurements.

157 In this study we evaluated the performance of these models using standard plant  
158 functional type parameterizations chosen in accordance with site-specific plant characteristics  
159 (i.e., evergreen vs. deciduous) and individual model requirements (Table 1). The model runs  
160 were without optimization to avoid enhancing of local agreement between observed- and model-  
161 calculated fluxes. For all models we used the same data for each site-specific characteristics  
162 (e.g., soil texture, nitrogen content, canopy height, maximum leaf area index, soil depth; Table 1)  
163 and same forcing variables (e.g., precipitation, longwave/shortwave radiation, air temperature)  
164 typically available at the global scale for general model simulations. Specific details about model  
165 architecture, parameters, and calculation of CO<sub>2</sub> and ET fluxes are found in Table 2. Model  
166 outputs and site measurements were averaged into daily sums for GPP, Reco and ET for each  
167 year and each site. This modeling exercise provided a total of 105 site-year simulations that were  
168 analyzed for this study at the daily time-step (Supplementary Figures 1-4).

169

## 170 Analysis of Ecosystem Drought Conditions

171 For subsequent model-data analyzes we assumed ecosystem drought conditions at a daily time  
172 step to occur when the relative extractable soil water (REW) dropped below a threshold of 0.4 as  
173 assumed in previous studies (Bernier and others, 2002). Briefly, REW was calculated from soil  
174 water content at a daily time step:

$$175 \text{ REW} = \frac{\theta - \theta_w}{\theta_{fc} - \theta_w} \quad (1)$$

176 where  $\theta$  is soil water content reported in the La Thuile FLUXNET dataset,  $\theta_w$  is soil water  
177 content at permanent wilting point, and  $\theta_{fc}$  represents water content at field capacity. The values  
178 for  $\theta_w$  and  $\theta_{fc}$  were obtained from site-specific sand and clay contents (Table 1) and equations  
179 provided by Saxton et al (1986).

180

## 181 Time-series Analysis

182 We explored the spectral properties of the time series of daily GPP, Reco, and ET from  
183 measurements and model outputs using the continuous wavelet transform (Torrence and Compo,  
184 1998). Previous studies have reviewed in detail the concepts of wavelet analysis (Torrence and  
185 Compo, 1998), and used this technique for model performance evaluation (Vargas and others,  
186 2010b; Dietze and others, 2011; Wang and others, 2011). Briefly, this technique provides  
187 information about the periodicities of the time series, and allows us to test for differences in the  
188 spectral properties to identify the frequencies at which there are (if any) substantial data-model  
189 disagreements. In other words, we are able to evaluate data-model agreement in the frequency  
190 domain to know when (i.e., at which time scales) there is a data-model agreement or  
191 disagreement.

192 For this analysis we used the Morlet mother wavelet, which is a complex non-orthogonal  
193 wavelet and one of the most-used for geophysical applications (Torrence and Compo, 1998). To  
194 analyze the data we first normalized the time series of observations and model outputs by:  $X' =$   
195  $(x - \text{mean}(x))/\text{std}(x)$ , where  $x$  represents the flux values of the time series of fluxes (e.g., GPP  
196 either from observations ( $X'_{obs}$ ), models ( $X'_{mod}$ ), or residuals (measurements minus model  
197 outputs)). Second, we calculated the global power spectrum using the continuous wavelet  
198 transform of each normalized time series of fluxes or their residuals (Torrence and Compo,  
199 1998). The length of each time series analyzed for observations ( $X'_{obs}$ ), models ( $X'_{mod}$ ), or  
200 residuals was of 3 years. All time-series were analyzed using a daily time step for all 3 years of  
201 measurements at each study site (i.e., 4 evergreen and 3 deciduous sites; 21 site-years), and for  
202 each model simulation for each site (i.e., 5 models and 5 sites; 105 site-years).

203

#### 204 Meta-analysis

205 For this synthesis study we applied meta-analysis techniques (Hedges and others, 1999;  
206 Gurevitch and others, 2001) to determine the generalities of data-model disagreement between  
207 observations of fluxes (i.e., control) and model outputs (i.e., treatments). The meta-analysis was  
208 performed for: a) mean spectral power of GPP, Reco, and ET at different time-periods (i.e., 2-10,  
209 10-30, 30-200 and 365 days); and b) mean daily flux estimates of GPP, Reco, and ET under no  
210 drought and under drought conditions (i.e., REW<0.4). The different time-periods represent  
211 weekly, monthly, seasonally, and yearly oscillations in the time series, respectively. With the  
212 first analysis we were able to identify the time-periods for data model disagreement, and with the  
213 second the effect of drought conditions for daily estimates of ecosystem fluxes.

214 For the meta-analysis, we first calculated the response ratio as the model outputs (either  
215 for the spectral power or the daily  $X'_{mod}$ ) divided by the site observations (either for the spectral  
216 power or the daily  $X'_{obs}$ ) (Hedges and others, 1999). Second, the mean effect size was calculated  
217 as the natural log of the response ratio for each flux (e.g., GPP) and each group (i.e., evergreen  
218 and deciduous) (Hedges and others, 1999). A mean effect size of 1 indicates that the model  
219 outputs were not different from observations, whereas a mean effect size  $>1$  and  $<1$  indicate that  
220 the model outputs overestimated and underestimated the observations, respectively. To  
221 determine if model outputs were different from site observations (i.e., mean effect size  $\neq 1$ ) we  
222 applied a random effects model using the MetaWin software (Rosenberg and others, 2000).  
223 Furthermore, bias-corrected bootstrap 95% confidence intervals (CIs) were calculated for each  
224 mean effect size (Rosenberg and others, 2000). Thus, if the 95% CIs of mean effect size did not  
225 overlap with 1, then differences were considered to be significant at  $P < 0.05$ . We complemented  
226 the meta-analysis by analyzing the root mean square error (RMSE), standard deviation, and  
227 correlation coefficient ( $r$  values) between simulations and measurements for each individual  
228 model and summarize them using Taylor diagrams (Taylor, 2001).

229

## 230 **RESULTS**

### 231 Spectral Properties of CO<sub>2</sub> Fluxes and ET

#### 232 *Evergreen sites*

233 The three-year averages of GPP, Reco and ET for measurements, model outputs, and the  
234 residuals (i.e., measurements minus model outputs) were summarized for evergreen sites (Figure  
235 1). Subsequent analyzes in this study were done using all available data for measurements (n=12  
236 site-years) and simulations (n=60 site-years; Supplementary Figure 1) for evergreen sites. These

237 sites had an average measured annual sum for GPP of  $1518 \pm 241$  ( $\text{gC m}^2 \text{ yr}^{-1}$ ), Reco of  $1260 \pm 191$   
238 ( $\text{gC m}^2 \text{ yr}^{-1}$ ), and ET of  $390 \pm 43$  ( $\text{mm yr}^{-1}$ ; Figure 1). Using wavelet analysis we calculated the  
239 global wavelet power spectra of GPP, Reco and ET from measurements, model outputs, and  
240 residuals (3 years of data for each site and model analyzed). For a visual representation of the  
241 differences in the power spectra only the measurements and residuals were plotted (Figure 2). In  
242 general, the global wavelet power spectra of GPP, Reco and ET from measurements showed high  
243 power at 365-days and a lesser seasonal power at  $\sim 200$ -days. Importantly, a similar spectral  
244 signature was found in the residuals of these time series showing that model errors were  
245 associated with these important fluctuations in the measurements. A peak in the global power  
246 spectrum means that there were strong systematic oscillations at that specific time-scale. For  
247 example, a strong power at 365-days suggests systematic oscillations in the time series at the  
248 annual scale, and from Figure 2 one can see that it represents the strongest oscillation but with  
249 larger variability across the time series analyzed.

250 We were interested in testing how well the model outputs represented the temporal  
251 oscillations of the measurements of GPP, Reco, and ET. Thus, we did a meta-analysis on the  
252 spectral power of model measurements and model outputs at different time-periods (i.e., 2-10,  
253 10-30, 30-200 and 365 days) representing weekly, monthly, seasonally, and yearly oscillations in  
254 the time series. Overall, models underestimated the spectral power of GPP at time-periods of 2-  
255 10 days (95% CI of mean effect size  $< 1$ ; Figure 3a). For Reco, as a generality models  
256 underestimated the spectral power at time-periods of 10-30 and 30-200 days (95% CI of mean  
257 effect size  $< 1$ ; Figure 3b), but overestimated at 2-10 and 365 days (95% CI of mean effect size  
258  $> 1$ ; Figure 3b). In contrast, we found a general overestimation of the spectral power of ET at  
259 time-periods of 2-10 and 10-30 days (95% CI of mean effect size  $> 1$ ; Figure 3c). An

260 underestimation of the spectral power implies a reduction in the magnitude the oscillations of the  
261 time series of a model output in comparison with the observations of each flux. Therefore, an  
262 overestimation of the spectral power represents an increase in the magnitude of the oscillations  
263 of the time series of model outputs in comparison with the measurements of each flux. In other  
264 words, an overestimation of the spectral power of Reco at 365-days suggests a potential  
265 overestimation of this variable when looking at the integrated response of daily simulations at the  
266 annual cycle.

267

#### 268 *Deciduous sites*

269 Three-year averages of GPP, Reco and ET for measurements, model outputs, and the residuals  
270 (i.e., measurements minus model outputs) were summarized for deciduous sites (Figure 4).

271 Subsequent analyzes were done using all available data for measurements (n=9 site-years) and  
272 simulations (n=45 site-years; Supplementary Figure 2) for deciduous sites. Overall, deciduous  
273 sites had an average measured annual sum for GPP of  $1972 \pm 257$  ( $\text{gC m}^2 \text{ yr}^{-1}$ ), Reco of  $1499 \pm 177$   
274 ( $\text{gC m}^2 \text{ yr}^{-1}$ ), and ET of  $500 \pm 89$  ( $\text{mm yr}^{-1}$ ). Similar to evergreen sites, the global wavelet power  
275 spectra of GPP, Reco and ET measurements showed strong power at 365-days and a lesser  
276 seasonal power at  $\sim 200$ -days for deciduous sites (Figure 5). This means that all the time series  
277 showed systematic oscillations that represent year-to-year variability (i.e., 365-days) and intra-  
278 annual variability that may be linked to plant phenology (i.e.,  $\sim 200$ -days). Similarly to evergreen  
279 site, residuals had a comparable spectral signature for all fluxes showing that model errors were  
280 associated with these important fluctuations in the measured fluxes, but also showed that there  
281 was large variability in the representation of these fluxes at these time-scales.

282 For deciduous sites, the meta-analysis revealed that models underestimated the spectral  
283 power of GPP at time-periods of 2-10, 30-200, and 365-days (95% CI of mean effect size <1;  
284 Figure 3a). For Reco, models underestimated the spectral power at time-periods of 10-30 and 30-  
285 200 days (95% CI of mean effect size <1; Figure 3b), but overestimated at 365-days (95% CI of  
286 mean effect size >1; Figure 3b). In contrast, we found a general overestimation of the spectral  
287 power of ET at time-periods of 2-10 and 10-30 days (95% CI of mean effect size >1; Figure 3c),  
288 but an overestimation at 365-days (95% CI of mean effect size >1; Figure 3c).

289

#### 290 Responses of Daily Means of CO<sub>2</sub> Fluxes and ET to Drought Conditions

291 Drought conditions (i.e., REW <0.4) were occurred for 30% of the measured days at evergreen  
292 sites. Low precipitation (0.5 mm day<sup>-1</sup>), high photosynthetic photon flux density (47.6 mol m<sup>-2</sup>  
293 day<sup>-1</sup>), and warm temperatures (21 °C; Table 1) characterized drought conditions at these sites.  
294 These results contrast with higher precipitation (2.8 mm day<sup>-1</sup>), lower photosynthetic photon flux  
295 density (28.9 mol m<sup>-2</sup> day<sup>-1</sup>) and cool temperatures (12.8 °C) characteristic of no drought  
296 conditions (Table 3).

297 Individual model results for daily values of ecosystem fluxes at evergreen sites were  
298 summarized in Supplementary Figure 5. In general, for GPP (Supplementary Figure 5a, b) and  
299 Reco (Supplementary Figure 5d, e) the correlation coefficient decreased, and the RMSE and  
300 standard deviation increased under drought conditions. In contrast, the correlation coefficient,  
301 RMSE and standard deviation for daily values of ET tend was more consistent between drought  
302 and no drought conditions (Supplementary Figure 5e, f). Importantly, we did not find that any  
303 single model that consistently over- or under- represented ecosystem fluxes across all sites  
304 (Supplementary Figures 1, 2, 5).

305 To synthesize and find general patterns from these results we applied meta-analysis  
306 techniques. For evergreen sites the meta-analysis showed that models agreed with observations  
307 in representing mean daily GPP under no drought and under drought conditions (i.e., 95% CI of  
308 mean effect size not different from 1; Figure 6a). Models overestimated mean daily Reco under  
309 no drought conditions but had even higher overestimation under drought conditions (i.e., 95% CI  
310 of mean effect size  $>1$ ; Figure 6a). Finally, models agreed with observations in representing  
311 mean daily ET both under no drought and under drought conditions (i.e., 95% CI of mean effect  
312 size not different from 1; Figure 6a).

313 Drought conditions (i.e., REW  $<0.4$ ) occurred for 41% of the measured days at deciduous  
314 sites. Drought conditions at these sites were characterized by low precipitation ( $0.7 \text{ mm day}^{-1}$ ),  
315 high photosynthetic photon flux density ( $46.7 \text{ mol m}^{-2} \text{ day}^{-1}$ ) and warm temperatures ( $20.8 \text{ }^\circ\text{C}$ ;  
316 Table 1). These results contrast with higher precipitation ( $3.3 \text{ mm day}^{-1}$ ), lower photosynthetic  
317 photon flux density ( $24.3 \text{ mol m}^{-2} \text{ day}^{-1}$ ), and cool temperatures ( $11.3 \text{ }^\circ\text{C}$ ) found under no  
318 drought conditions (Table 3). Noteworthy, these patterns were similar to those observed for  
319 evergreen sites, but deciduous sites present lower sensitivity to drought.

320 Individual model results for daily values of ecosystem fluxes at deciduous sites were  
321 summarized in Supplementary Figure 4. In general, for GPP (Supplementary Figure 6a, b) and  
322 Reco (Supplementary Figure 6d, e) the correlation coefficient decreased, and the RMSE and  
323 standard deviation increased under drought conditions. In contrast, the correlation coefficient,  
324 RMSE and standard deviation of daily values of ET tend to be more consistent between drought  
325 and no drought conditions (Supplementary Figure 6e, f). We also did not find that any single  
326 model consistently over- or under- represented ecosystem fluxes across all sites (Supplementary  
327 Figure 3, 4, 6).



328 For deciduous sites the meta-analysis showed that models underestimated the  
329 observations in representing mean daily GPP under drought conditions (i.e., 95% CI of mean  
330 effect size  $<1$ ; Figure 6b). In contrast, models overestimated mean daily Reco under drought  
331 conditions (i.e., 95% CI of mean effect size  $>1$ ; Figure 6b). Finally, models agreed with  
332 observations in representing mean daily ET both under no drought and under drought conditions  
333 (i.e., 95% CI of mean effect size not different from 1; Figure 6b).

334

## 335 **DISCUSSION**

336 Our results show that overall there were data-model disagreements at multiple temporal scales  
337 for GPP, Reco, and ET at both evergreen and deciduous Mediterranean oak woodland sites.  
338 These results support the hypothesis that overall data-model disagreements are substantial at  
339 temporal scales between weeks to months (i.e., 10-200 days), but important disagreements were  
340 also found at shorter (i.e., 2-10 days) and larger (i.e., 365-days) time scales. Furthermore, the  
341 meta-analysis showed that simulated Reco was overestimated under drought conditions for both  
342 plant functional types. Previous studies suggest that with appropriate parameterization ecosystem  
343 process-oriented models accurately represent ecosystem fluxes in Mediterranean ecosystems  
344 (Keenan and others, 2009; Keenan and others, 2010b), but the necessity remains to identify  
345 systematic errors with generic parameterizations and evaluate multi-model performance to  
346 improve applicability of model outputs at larger spatial scales.

347

### 348 Temporal Variation of Ecosystem Fluxes

349 In general, we observed that the most important time scales (i.e., with highest spectral power in  
350 Figure 2) were those between 30-200 and at 365-days for GPP, Reco and ET at both evergreen

351 and deciduous sites. Our results show an overall underrepresentation of the spectral power  
352 between 2-10 days for GPP at both evergreen and deciduous sites, which supports previous  
353 observations of data-model disagreement at these time scales among multiple models and  
354 vegetation types in temperate ecosystems (Dietze and others, 2011). In addition, there was a  
355 large underrepresentation of GPP at deciduous sites between 30-200 and 365 days similar to  
356 results from other model evaluations (Mahecha and others, 2010). Our results bring attention to  
357 the challenge for models to simulate phenological cycles especially for deciduous forests  
358 (Richardson and others, 2012). Importantly, the spectral power of ET was systematically  
359 overrepresented at both vegetation types between 2 and 30 days. This has implications for water  
360 balance budgets, and the representation of the temporal variability of water-use-efficiency in  
361 these and other semi-arid ecosystems. Thus, there is increasing interest in evaluating this variable  
362 in process-oriented ecosystem models (Lawrence and others, 2007; Wang and others, 2011).

363 Our results show systematic errors in Reco for evergreen and deciduous sites that  
364 underestimate the oscillations of the time series of Reco at 30-200 days and overestimate the  
365 oscillations at 365-days. This is likely a result of an underestimation of the magnitude of Reco in  
366 response of water pulses and synoptic events at scales between 30-200 days, but an  
367 overestimation of the magnitude of Reco at 365-days. The large underestimation of the spectral  
368 power for Reco may be a result of the challenge in representing: a) the overall response of Reco  
369 to rainfall pulses in Mediterranean ecosystems (Baldocchi and others, 2006); b) the dependence  
370 of heterotrophic and autotrophic respiration to seasonal variation; which are highly controlled by  
371 water availability in Mediterranean ecosystems (Carbone and others, 2011); c) the control of  
372 recent photosynthesis on Reco (Vargas and others, 2011); d) changes of the carbon residence  
373 time in soils or in plants (Trumbore, 2000; Vargas and others, 2009); and e) potential

374 confounded parameterization during drought stress (Reichstein and others, 2003), or that  
375 parameters are not representative of specific time scales (Mahecha and others, 2010).

376 Mediterranean oak woodlands have complex heterogeneous canopies that represent a  
377 challenge to accurately estimate leaf area index (Ryu and others, 2010) and understory net  
378 ecosystem exchange (Misson and others, 2007), especially for open canopy sites. These sites  
379 may have an understory of grasses and forbs with different photosynthesis rates and phenology  
380 (Joffre and others, 2007) that were not explicitly considered in the generic parameterizations of  
381 the process-oriented models used in this study. For example, the understory could be a large  
382 contributor to GPP, Reco or ET along the year or may be dependent to seasonality (Misson and  
383 others, 2007) driving interannual variability in ecosystem fluxes (Ma and others, 2007). In  
384 addition, most land surface and process-oriented models assume that a vegetated canopy can be  
385 abstracted as a turbid medium, but they fail to simulate radiation environments in heterogeneous  
386 landscapes (Mariscal and others, 2004).

387 Our results support previous observations where ecosystem process-oriented models fail  
388 to represent ecosystem fluxes at multiple time scales, and bring attention on the study of the  
389 spectral characteristics of the time series as an alternative way for model evaluation (Mahecha  
390 and others, 2010; Vargas and others, 2010b; Dietze and others, 2011; Wang and others, 2011).  
391 We further hypothesize that model-data disagreement at short time scales may be related to  
392 factors controlled by light, the intermediate timescales to drought conditions, and the annual  
393 scales potentially to antecedent conditions and inter-annual weather variability.

394

395 Ecosystem Fluxes and Drought Stress

396 Drought conditions were present for 30% of the measured days for evergreen sites and 41% of  
397 the days for deciduous sites. Thus, the challenge imposed by drought conditions to simulating  
398 ecosystem fluxes may affect the annual estimates of productivity and ecosystem carbon balance  
399 at water limited ecosystems (Richardson and others, 2010; van der Molen and others, 2011). Our  
400 results support the hypothesis of overall data-model disagreement by systematically  
401 overestimating daily Reco under drought stress at both plant functional types. The results support  
402 that drought has a strong influence on simulating Reco, and therefore it is advisable that model  
403 parameters should follow a seasonal course in response to this condition in Mediterranean  
404 ecosystems (Reichstein and others, 2003). Importantly, daily GPP was underestimated under  
405 drought conditions at deciduous sites, which could be a result of the role of stomatal  
406 conductance, maximum carboxylation rate ( $V_{cmax}$ ) and maximum rate of electron transport ( $J_{max}$ )  
407 influence on leaf scale photosynthesis under drought (Xu and Baldocchi, 2003; Limousin and  
408 others, 2010). This may be especially important when taken into account the REW and its  
409 influence on photosynthesis rates at the canopy scale (Rambal and others, 2003) and model  
410 parameters (Keenan and others, 2009; Keenan and others, 2010b).

411         Across sites and years we observed a slight reduction on the mean daily values of GPP  
412 and Reco under drought conditions but these were associated with large variability (Table 3).  
413 Previous studies have shown an important reduction in assimilation (Xu and Baldocchi, 2003;  
414 Limousin and others, 2010) and respiration (Reichstein and others, 2003) under drought.  
415 However, there are also lag effects at the seasonal scale where assimilation and respiration  
416 increase at the time when soil water content starts to decrease (Baldocchi and others, 2010;  
417 Vargas and others, 2010a). Thus, lag effects between wet and dry seasons and their influence on

418 REW and ecosystem fluxes are important and explain the large variability observed in the mean  
419 calculation of these fluxes divided by drought conditions (Table 3).

420         The potential access to ground water by the trees through deep roots is an important  
421 adaptation that influence plant function (David and others, 2007; Miller and others, 2010). A  
422 deeper rooting depth may result in access to more soil, and a potential access to ground water  
423 that may have a direct effect on stomata conductance and an indirect effect on Reco.  
424 Furthermore, oak trees that have access to ground water may perform hydraulic lift and  
425 redistribute water to shallow soil layers stimulating microbial activity and potentially  
426 heterotrophic soil respiration. Recently there have been efforts improving how to simulate water  
427 table depth and how roots utilize the water as the water table fluctuates in order to improve  
428 evapotranspiration estimates (Ichii and others, 2009; Soylu and others, 2011; Thompson and  
429 others, 2011), and could have implications for representation of other ecosystem fluxes. Finally,  
430 Reco may be challenging to represent under drought conditions especially after light rain pulse  
431 events that could rapidly increase heterotrophic respiration. These light rain pulse events may not  
432 be sufficient to reduce drought conditions as water may not permeate and increase soil water  
433 content at deeper soil depths (Thomey and others, 2011). Furthermore, heterotrophic respiration  
434 may be substantially increased after these light rain pulses due to organic matter breakdown by  
435 photodegradation during the dry and hot summers (Brandt and others, 2009). Thus,  
436 understanding pulse dynamics in these ecosystems has been an important topic to understand  
437 shifts in contribution of ecosystem fluxes (Baldocchi and others, 2006; Thomey and others,  
438 2011).

439

440 Implications, Limitations and Future Considerations

441 Historically, model improvements have focused on how drought stress influence photosynthesis,  
442 but fewer efforts have been made for the role of drought stress of Reco (van der Molen and  
443 others, 2011) and ET (Ichii and others, 2009; Soylu and others, 2011; Thompson and others,  
444 2011). Our results show that systematic overestimation in Reco during drought conditions at both  
445 evergreen and deciduous Mediterranean oak woodlands, and support previous observations that  
446 models need improvements on how drought conditions control Reco (Reichstein and others,  
447 2002a). Finally, evergreen sites have lower photosynthetic capacity but longer growing seasons  
448 than deciduous sites, which results at similar annual sums of ecosystem fluxes (Baldocchi and  
449 others, 2010; and this study). Our results show that deciduous sites are more resilient to drought,  
450 whereas evergreen sites are more sensitive and decrease substantially ecosystem fluxes under  
451 drought. An incorrect representation of ecosystem fluxes may have larger implications under the  
452 context of climate change where droughts may become more common (Kharin and others, 2007).  
453 For example, if plants will encounter more water stress in future years and model outputs  
454 overestimate Reco, then plants could be depleted faster from carbon (i.e., carbon starvation) and  
455 die faster than in reality. This scenario could be enhanced by the potential underestimation of  
456 GPP under drought conditions for deciduous sites limiting the carbon input into the system and  
457 generating a positive feedback for carbon depletion and therefore plant mortality. Thus, the  
458 omission or misrepresentation of how models response to water deficit will influence predictions  
459 about how ecosystems may evolve, adapt and respond to past and future environmental changes.

460 Potential modeling experiments and advancements could focus on: a) model sensitivity  
461 for water holding capacity, soil drainage and percolation that could affect model design and  
462 parameterizations; b) the effect of changes in rooting depth and the ability of roots for extracting  
463 water across the soil-water compartment (e.g., root weighted soil moisture, access of water by

464 deep roots) or soil depth and their relationship with soil texture across Mediterranean ecosystems  
465 and plant functional types; c) consistently evaluate the autotrophic and heterotrophic contribution  
466 of Reco across a wide range of ecosystems and weather conditions including different ranges of  
467 drought stress; d) consider the uncertainty for model parameters, initialization and random and  
468 systematic errors within measurements under the proposed experiments; e) studies on radiative  
469 transfer models and the light absorbed by tree leaves and the understory layer (Kobayashi and  
470 others, 2012); and e) hierarchy model comparisons to better identify differences in model-data  
471 agreement based on a systematic evaluation of model structures (Vogel and others, 1995).

472         This study represents a first attempt to evaluate the overall performance of multiple  
473 models for whole ecosystem carbon and water cycling across deciduous and evergreen  
474 Mediterranean oak woodlands within FLUXNET. Our results summarize generalities on model-  
475 data disagreement but these vary for any specific site and any specific model that could be  
476 improved by site-specific model parameterizations (Keenan and others, 2009; Keenan and  
477 others, 2010b). Therefore, the generality of these multi-model meta-analysis results needs to be  
478 tested at more study sites, across different years, and using a larger set of ecosystem process-  
479 oriented models. It is clear that longer time series are needed in order to account for model-data  
480 agreements especially to account for inter-annual variability. Finally, the difficulty in  
481 representing responses of ecosystem fluxes in drought prone ecosystems is exacerbated by the  
482 biogeochemistry of a vertically stratified canopy with multiple layers of vegetation (e.g., grasses  
483 and trees), soil hydrology (Sonnentag and others, 2008), and has been identified as a key  
484 challenge for the next generation of global climate models (Lawrence and others, 2007).

485

486 ACKNOWLEDGEMENTS

487 This work used data produced in the La Thuile 2007 FLUXNET workshop. We thank Deb  
488 Agarwal, Dario Papale, Markus Reichstein, and Catharine van Ingen for their work in the  
489 organization of the La Thuile data set. We acknowledge financial support for database  
490 development and maintenance from CarboeuropelP, FAO-GTOS-TCO, iLEAPS, the Max  
491 Planck Institute for Biogeochemistry, the National Science Foundation, the University of Tuscia,  
492 the US Department of Energy, the Berkeley Water Center, the Lawrence Berkeley National  
493 Laboratory, Microsoft Research eScience, and Oak Ridge National Laboratory, University of  
494 Virginia. J.P. and A.C. thanks João Banza for collecting flux tower measurements and Teresa do  
495 Paço for reviewing and correcting evapotranspiration fluxes in Évora experimental site. R.V.  
496 acknowledges support from Ciencia Básica CONACyT (152671). D. Pearson was supported by  
497 the Joint UK DECC/Defra Met Office Hadley Centre Climate Programme (GA01101). D. Papale  
498 acknowledges the support from GHG-Europe FP7 European project. This manuscript was  
499 improved by comments of two anonymous reviewers and Dr. Thomas Hickler.

500

501



502 REFERENCES

- 503 Aubinet, M., Grelle, A., Ibrom, A., Rannik, U., Moncrieff, J., Foken, T., Kowalski, A.S., Martin, P.H.,  
504 Berbigier, P., Bernhofer, C., Clement, R., Elbers, J., Granier, A., Grunwald, T., Morgenstern, K.,  
505 Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R., Vesala, T., 2000. Estimates of the annual  
506 net carbon and water exchange of forests: The EUROFLUX methodology. *Adv Ecol Res* 30, 113-  
507 175.
- 508 Baldocchi, D., Tang, J.W., Xu, L.K., 2006. How switches and lags in biophysical regulators affect spatial-  
509 temporal variation of soil respiration in an oak-grass savanna. *Journal of Geophysical Research-*  
510 *Biogeosciences* 111, doi:10.1029/2005JG000063.
- 511 Baldocchi, D., Xu, L., 2007. What limits evaporation from Mediterranean oak woodlands – The supply of  
512 moisture in the soil, physiological control by plants or the demand by the atmosphere? *AdWR* 30,  
513 2113-2122.
- 514 Baldocchi, D.D., Ma, S.Y., Rambal, S., Misson, L., Ourcival, J.M., Limousin, J.M., Pereira, J., Papale,  
515 D., 2010. On the differential advantages of evergreenness and deciduousness in mediterranean  
516 oak woodlands: a flux perspective. *Ecol. Appl.* 20, 1583-1597.
- 517 Ball, J.T., Berry, J.A., 1982. The  $C_i/C_s$  ratio: a basis for predicting stomatal control of photosynthesis.  
518 *Carnegie Institute Washington Year Book*, pp. 88–92.
- 519 Ball, J.T., Berry, J.A., Woodrow, I.E., 1987. A model predicting stomatal conductance and its  
520 contribution to the control of photosynthesis under different environmental conditions. In:  
521 *Binggins, I.J. (Ed.), Progress in Photosynthesis Research, Vol. IV, Martinus Nijhoff, Dordrecht.,*  
522 *pp. 221–224.*
- 523 Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rodenbeck, C., Arain, M.A.,  
524 Baldocchi, D., Bonan, G.B., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M.,  
525 Luysaert, S., Margolis, H., Oleson, K.W., Rouspard, O., Veenendaal, E., Viovy, N., Williams,  
526 C., Woodward, F.I., Papale, D., 2010. Terrestrial Gross Carbon Dioxide Uptake: Global  
527 Distribution and Covariation with Climate. *Sci* 329, 834-838.

528 Bernier, P.Y., Breda, N., Granier, A., Raulier, F., Mathieu, F., 2002. Validation of a canopy gas exchange  
529 model and derivation of a soil water modifier for transpiration for sugar maple (*Acer saccharum*  
530 Marsh.) using sap flow density measurements. *For. Ecol. Manage.* 163, 185-196.

531 Best, M.J., Pryor, M., Clark, D.B., Rooney, G.G., Essery, R.L.H., Menard, C.B., Edwards, J.M., Hendry,  
532 M.A., Porson, A., Gedney, N., Mercado, L.M., Sitch, S., Blyth, E., Boucher, O., Cox, P.M.,  
533 Grimmond, C.S.B., Harding, R.J., 2011. The Joint UK Land Environment Simulator (JULES),  
534 model description - Part 1: Energy and water fluxes. *Geosci Model Dev* 4, 677-699.

535 Brandt, L.A., Bohnet, C., King, J.Y., 2009. Photochemically induced carbon dioxide production as a  
536 mechanism for carbon loss from plant litter in arid ecosystems. *Journal of Geophysical Research-*  
537 *Biogeosciences* 114, -.

538 Carbone, M.S., Still, C.J., Ambrose, A.R., Dawson, T.E., Williams, A.P., Boot, C.M., Schaeffer, S.M.,  
539 Schimel, J.P., 2011. Seasonal and episodic moisture controls on plant and microbial contributions  
540 to soil respiration. *Oecologia* 167, 265-278.

541 Casals, P., Gimeno, C., Carrara, A., Lopez-Sangil, L., Sanz, M., 2009. Soil CO<sub>2</sub> efflux and extractable  
542 organic carbon fractions under simulated precipitation events in a Mediterranean Dehesa. *Soil*  
543 *Biol. Biochem.* 41, 1915-1922.

544 Clark, D.B., Mercado, L.M., Sitch, S., Jones, C.D., Gedney, N., Best, M.J., Pryor, M., Rooney, G.G.,  
545 Essery, R.L.H., Blyth, E., Boucher, O., Harding, R.J., Huntingford, C., Cox, P.M., 2011. The  
546 Joint UK Land Environment Simulator (JULES), model description - Part 2: Carbon fluxes and  
547 vegetation dynamics. *Geosci Model Dev* 4, 701-722.

548 Collatz, G.J., Ball, J.T., Grivet, C., Berry, J.A., 1991. Physiological and environmental regulation of  
549 stomatal conductance, photosynthesis and transpiration: A model that includes a laminar  
550 boundary layer. *Agr Forest Meteorol* 54, 107-136.

551 Dai, A.G., Trenberth, K.E., Qian, T.T., 2004. A global dataset of Palmer Drought Severity Index for  
552 1870-2002: Relationship with soil moisture and effects of surface warming. *Journal of*  
553 *Hydrometeorology* 5, 1117-1130.

554 David, T.S., Henriques, M.O., Kurz-Besson, C., Nunes, J., Valente, F., Vaz, M., Pereira, J.S., Siegwolf,  
555 R., Chaves, M.M., Gazarini, L.C., David, J.S., 2007. Water-use strategies in two co-occurring  
556 Mediterranean evergreen oaks: surviving the summer drought. *Tree Physiology* 27, 793-803.

557 Dietze, M.C., Vargas, R., Richardson, A.D., Stoy, P.C., Barr, A.G., Anderson, R.S., Arain, M.A., Baker,  
558 I.T., Black, T.A., Chen, J.M., Ciais, P., Flanagan, L.B., Gough, C.M., Grant, R.F., Hollinger, D.,  
559 Izaurrealde, R.C., Kucharik, C.J., Lafleur, P., Liu, S.G., Lokupitiya, E., Luo, Y.Q., Munger, J.W.,  
560 Peng, C.H., Poulter, B., Price, D.T., Ricciuto, D.M., Riley, W.J., Sahoo, A.K., Schaefer, K.,  
561 Suyker, A.E., Tian, H.Q., Tonitto, C., Verbeeck, H., Verma, S.B., Wang, W.F., Weng, E.S., 2011.  
562 Characterizing the performance of ecosystem models across time scales: A spectral analysis of  
563 the North American Carbon Program site-level synthesis. *Journal of Geophysical Research-*  
564 *Biogeosciences* 116.

565 Ducoudré, N.I., Laval, K., Perrier, A., 1993. SECHIBA, a new set of parameterizations of the hydrologic  
566 exchanges at the land-atmosphere interface within the LMD atmospheric circulation model. *J.*  
567 *Clim.* 6, 248-273.

568 Farquhar, G., Von Caemmerer, S., Berry, J., 1980. A biochemical model of photosynthetic CO<sub>2</sub>  
569 assimilation in leaves of C<sub>3</sub> species. *Planta* 149, 78–90.

570 Friend, A.D., Schugart, H.H., Running, S.W., 1993. A physiology-based gap model of forest dynamics.  
571 *Ecology* 74, 792-797.

572 Giorgi, F., 2006. Climate change hot-spots. *Geophys. Res. Lett.* 33, L08707,  
573 doi:08710.01029/02006GL025734.

574 Giorgi, F., Lionello, P., 2008. Climate change projections for the Mediterranean region. *Global Planet.*  
575 *Change* 63, 90-104.

576 Gurevitch, J., Curtis, P.S., Jones, M.H., 2001. Meta-analysis in ecology. *Adv. Ecol. Res.* 32, 199-247.

577 Hartmann, H., 2011. Will a 385 million year-struggle for light become a struggle for water and for  
578 carbon? - How trees may cope with more frequent climate change-type drought events. *Global*  
579 *Change Biol.* 17, 642-655.

580 Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental  
581 ecology. *Ecology* 80, 1150-1156.

582 Ichii, K., Wang, W.L., Hashimoto, H., Yang, F.H., Votava, P., Michaelis, A.R., Nemani, R.R., 2009.  
583 Refinement of rooting depths using satellite-based evapotranspiration seasonality for ecosystem  
584 modeling in California. *Agr Forest Meteorol* 149, 1907-1918.

585 Joffre, R., Rambal, S., Damesin, C., 2007. Functional Attributes in Mediterranean-type Ecosystems. In:  
586 Pugnaire, F.I. (Ed.), *Functional Plant Ecology*, pp. 285-312.

587 Ju, W.M., Chen, J.M., Black, T.A., Barr, A.G., Liu, J., Chen, B.Z., 2006. Modelling multi-year coupled  
588 carbon and water fluxes in a boreal aspen forest. *Agr Forest Meteorol* 140, 136-151.

589 Jung, M., Le Maire, G., Zaehle, S., Luysaert, S., Vetter, M., Churkina, G., Ciais, P., Viovy, N.,  
590 Reichstein, M., 2007. Assessing the ability of three land ecosystem models to simulate gross  
591 carbon uptake of forests from boreal to Mediterranean climate in Europe. *Biogeosciences* 4, 647-  
592 656.

593 Jung, M., Reichstein, M., Ciais, P., Seneviratne, S.I., Sheffield, J., Goulden, M.L., Bonan, G., Cescatti,  
594 A., Chen, J., de Jeu, R., Dolman, A.J., Eugster, W., Gerten, D., Gianelle, D., Gobron, N., Heinke,  
595 J., Kimball, J., Law, B.E., Montagnani, L., Mu, Q., Mueller, B., Oleson, K., Papale, D.,  
596 Richardson, A.D., Roupsard, O., Running, S., Tomelleri, E., Viovy, N., Weber, U., Williams, C.,  
597 Wood, E., Zaehle, S., Zhang, K., 2010. Recent decline in the global land evapotranspiration trend  
598 due to limited moisture supply. *Nature* 467, 951-954.

599 Keenan, T., Garcia, R., Friend, A.D., Zaehle, S., Gracia, C., Sabate, S., 2009. Improved understanding of  
600 drought controls on seasonal variation in Mediterranean forest canopy CO<sub>2</sub> and water fluxes  
601 through combined in situ measurements and ecosystem modelling. *Biogeosciences* 6, 1423-1444.

602 Keenan, T., Sabate, S., Gracia, C., 2010a. The importance of mesophyll conductance in regulating forest  
603 ecosystem productivity during drought periods. *Global Change Biol.* 16, 1019-1034.

604 Keenan, T., Sabate, S., Gracia, C., 2010b. Soil water stress and coupled photosynthesis–conductance  
605 models: Bridging the gap between conflicting reports on the relative roles of stomatal, mesophyll  
606 conductance and biochemical limitations to photosynthesis. *Agr Forest Meteorol* 150, 443-453.

607 Kharin, V.V., Zwiers, F.W., Zhang, X.B., Hegerl, G.C., 2007. Changes in temperature and precipitation  
608 extremes in the IPCC ensemble of global coupled model simulations. *J. Clim.* 20, 1419-1444.

609 Kobayashi, H., Baldocchi, D.D., Ryu, Y., Chen, Q., Ma, S.Y., Osuna, J.L., Ustin, S.L., 2012. Modeling  
610 energy and carbon fluxes in a heterogeneous oak woodland: A three-dimensional approach. *Agr  
611 Forest Meteorol* 152, 83-100.

612 Kowalczyk, E.A., Wang, Y.P., Law, R.M., Davies, H.L., McGregor, J.L., Abramowitz, G., 2006. The  
613 CSIRO Atmosphere Biosphere Land Exchange (CABLE) model for use in climate models and as  
614 an offline model. CSIRO Marine and Atmospheric Research Paper 013, CSIRO, Australia, pp.  
615 [http://www.cmar.csiro.au/e-print/open/kowalczyka\\_2006a.pdf](http://www.cmar.csiro.au/e-print/open/kowalczyka_2006a.pdf).

616 Krinner, G., Viovy, N., de Noblet-Ducoudre, N., Ogee, J., Polcher, J., Friedlingstein, P., Ciais, P., Sitch,  
617 S., Prentice, I.C., 2005. A dynamic global vegetation model for studies of the coupled  
618 atmosphere-biosphere system. *Global Biogeochem. Cycles* 19, -.

619 Lawrence, D.M., Thornton, P.E., Oleson, K.W., Bonan, G.B., 2007. The partitioning of  
620 evapotranspiration into transpiration, soil evaporation, and canopy evaporation in a GCM:  
621 Impacts on land-atmosphere interaction. *Journal of Hydrometeorology* 8, 862-880.

622 Leuning, R., Kelliher, F.M., Depury, D.G.G., Schulze, E.D., 1995. Leaf nitrogen, photosynthesis,  
623 conductance and transpiration: scaling from leaves to canopies. *Plant Cell and Environment* 18,  
624 1183-1200.

625 Limousin, J.M., Misson, L., Lavoit, A.V., Martin, N.K., Rambal, S., 2010. Do photosynthetic limitations  
626 of evergreen *Quercus ilex* leaves change with long-term increased drought severity? *Plant Cell  
627 Environ* 33, 863-875.

628 Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. *Funct. Ecol.* 8, 315-323.

629 Ma, S.Y., Baldocchi, D.D., Xu, L.K., Hehn, T., 2007. Inter-annual variability in carbon dioxide exchange  
630 of an oak/grass savanna and open grassland in California. *Agr Forest Meteorol* 147, 157-171.

631 Mahecha, M.D., Reichstein, M., Jung, M., Seneviratne, S.I., Zaehle, S., Beer, C., Braakhekke, M.C.,  
632 Carvalhais, N., Lange, H., Le Maire, G., Moors, E., 2010. Comparing observations and process-  
633 based simulations of biosphere-atmosphere exchanges on multiple timescales. *Journal of*  
634 *Geophysical Research-Biogeosciences* 115, G02003.

635 Mariscal, M.J., Martens, S.N., Ustin, S.L., Chen, J.Q., Weiss, S.B., Roberts, D.A., 2004. Light-  
636 transmission profiles in an old-growth forest canopy: Simulations of photosynthetically active  
637 radiation by using spatially explicit radiative transfer models. *Ecosystems* 7, 454-467.

638 Miller, G.R., Chen, X.Y., Rubin, Y., Ma, S.Y., Baldocchi, D.D., 2010. Groundwater uptake by woody  
639 vegetation in a semiarid oak savanna. *Water Resour. Res.* 46, -.

640 Misson, L., Baldocchi, D.D., Black, T.A., Blanken, P.D., Brunet, Y., Yuste, J.C., Dorsey, J.R., Falk, M.,  
641 Granier, A., Irvine, M.R., Jarosz, N., Lamaud, E., Launiainen, S., Law, B.E., Longdoz, B.,  
642 Loustau, D., Mckay, M., Paw, K.T., Vesala, T., Vickers, D., Wilson, K.B., Goldstein, A.H., 2007.  
643 Partitioning forest carbon fluxes with overstory and understory eddy-covariance measurements: A  
644 synthesis based on FLUXNET data. *Agr Forest Meteorol* 144, 14-31.

645 Misson, L., Rocheteau, A., Rambal, S., Ourcival, J.M., Limousin, J.M., Rodriguez, R., 2010. Functional  
646 changes in the control of carbon fluxes after 3 years of increased drought in a Mediterranean  
647 evergreen forest? *Global Change Biol.* 6, 2461-2475.

648 Monteith, J.L., 1965. Evaporation and the environment. *Symposium of the Society of Exploratory*  
649 *Biology* 19, 205-234.

650 Morales, P., Sykes, M.T., Prentice, I.C., Smith, P., Smith, B., Bugmann, H., Zierl, B., Friedlingstein, P.,  
651 Viovy, N., Sabate, S., Sanchez, A., Pla, E., Gracia, C.A., Sitch, S., Arneth, A., Ogee, J., 2005.  
652 Comparing and evaluating process-based ecosystem model predictions of carbon and water fluxes  
653 in major European forest biomes. *Global Change Biol.* 11, 2211-2233.

654 Papale, D., Reichstein, M., Aubinet, M., Canfora, E., Bernhofer, C., Kutsch, W., Longdoz, B., Rambal,  
655 S., Valentini, R., Vesala, T., Yakir, D., 2006. Towards a standardized processing of Net  
656 Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty  
657 estimation. *Biogeosciences* 3, 571-583.

658 Pereira, J.S., Mateus, J.A., Aires, L.M., Pita, G., Pio, C., David, J.S., Andrade, V., Banza, J., David, T.S.,  
659 Paco, T.A., Rodrigues, A., 2007. Net ecosystem carbon exchange in three contrasting  
660 Mediterranean ecosystems - the effect of drought. *Biogeosciences* 4, 791-802.

661 Rambal, S., Joffre, R., Ourcival, J.M., Cavender-Bares, J., Rocheteau, A., 2004. The growth respiration  
662 component in eddy CO<sub>2</sub> flux from a *Quercus ilex* mediterranean forest. *Global Change Biol.* 10,  
663 1460-1469.

664 Rambal, S., Ourcival, J.M., Joffre, R., Mouillot, F., Nouvellon, Y., Reichstein, M., Rocheteau, A., 2003.  
665 Drought controls over conductance and assimilation of a Mediterranean evergreen ecosystem:  
666 scaling from leaf to canopy. *Global Change Biol.* 9, 1813-1824.

667 Raupach, M.R., Rayner, P.J., Barrett, D.J., DeFries, R.S., Heimann, M., Ojima, D.S., Quegan, S.,  
668 Schimmlus, C.C., 2005. Model-data synthesis in terrestrial carbon observation: methods, data  
669 requirements and data uncertainty specifications. *Global Change Biol.* 11, 378-397.

670 Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C.,  
671 Buchmann, N., Gilmanov, T., Granier, A., Grunwald, T., Havrankova, K., Ilvesniemi, H., Janous,  
672 D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F.,  
673 Ourcival, J.M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G.,  
674 Vaccari, F., Vesala, T., Yakir, D., Valentini, R., 2005. On the separation of net ecosystem  
675 exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global*  
676 *Change Biol.* 11, 1424-1439.

677 Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentini, R., Banza, J., Casals, P., Cheng, Y.F.,  
678 Grunzweig, J.M., Irvine, J., Joffre, R., Law, B.E., Loustau, D., Miglietta, F., Oechel, W.,  
679 Ourcival, J.M., Pereira, J.S., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M., Romanya,

680 J., Rossi, F., Tedeschi, V., Tirone, G., Xu, M., Yakir, D., 2003. Modeling temporal and large-  
681 scale spatial variability of soil respiration from soil water availability, temperature and vegetation  
682 productivity indices. *Global Biogeochem. Cycles* 17.

683 Reichstein, M., Tenhunen, J.D., Rouspard, O., Ourcival, J.M., Rambal, S., Dore, S., Valentini, R., 2002a.  
684 Ecosystem respiration in two Mediterranean evergreen Holm Oak forests: drought effects and  
685 decomposition dynamics. *Funct. Ecol.* 16, 27-39.

686 Reichstein, M., Tenhunen, J.D., Rouspard, O., Ourcival, J.M., Rambal, S., Miglietta, F., Peressotti, A.,  
687 Pecchiari, M., Tirone, G., Valentini, R., 2002b. Severe drought effects on ecosystem CO<sub>2</sub> and  
688 H<sub>2</sub>O fluxes at three Mediterranean evergreen sites: revision of current hypotheses? *Global*  
689 *Change Biol.* 8, 999-1017.

690 Richardson, A.D., Anderson, R.S., Arain, M.A., Barr, A.G., Bohrer, G., Chen, G.S., Chen, J.M., Ciais, P.,  
691 Davis, K.J., Desai, A.R., Dietze, M.C., Dragoni, D., Garrity, S.R., Gough, C.M., Grant, R.,  
692 Hollinger, D.Y., Margolis, H.A., McCaughey, H., Migliavacca, M., Monson, R.K., Munger, J.W.,  
693 Poulter, B., Raczka, B.M., Ricciuto, D.M., Sahoo, A.K., Schaefer, K., Tian, H.Q., Vargas, R.,  
694 Verbeeck, H., Xiao, J.F., Xue, Y.K., 2012. Terrestrial biosphere models need better  
695 representation of vegetation phenology: results from the North American Carbon Program Site  
696 Synthesis. *Global Change Biol.* 18, 566-584.

697 Richardson, A.D., Black, T.A., Ciais, P., Delbart, N., Friedl, M.A., Gobron, N., Hollinger, D.Y., Kutsch,  
698 W.L., Longdoz, B., Luyssaert, S., Migliavacca, M., Montagnani, L., Munger, J.W., Moors, E.,  
699 Piao, S.L., Rebmann, C., Reichstein, M., Saigusa, N., Tomelleri, E., Vargas, R., Varlagin, A.,  
700 2010. Influence of spring and autumn phenological transitions on forest ecosystem productivity.  
701 *Philosophical Transactions of the Royal Society B-Biological Sciences* 365, 3227-3246.

702 Rosenberg, M.S., Adams, D.C., Gurevitch, J., 2000. *MetaWin: statistical software for meta-analysis,*  
703 *version 2.0.* Sinauer Associates, Sunderland, Massachusetts, USA.

704 Ruimy, A., Dedieu, G., Saugier, B., 1996. TURC: A diagnostic model of continental gross primary  
705 productivity and net primary productivity. *Global Biogeochem. Cycles* 10, 269-285.



706 Running, S.W., Coughlan, J.C., 1988. A general model of forest ecosystem processes for regional  
707 applications. 1. Hydrologic balance, canopy gas-exchange and primary production processes.  
708 Ecol. Model. 42, 125-154.

709 Ryu, Y., Sonnentag, O., Nilson, T., Vargas, R., Kobayashi, H., Rebecca, W., Baldocchi, D.D., 2010. How  
710 to quantify tree leaf area index in an open savanna ecosystem: A multi-instrument and multi-  
711 model approach. Agr Forest Meteorol 150, 63-76.

712 Saxton, K.E., Rawls, W.J., Romberger, J.S., Papendick, R.I., 1986. Estimating Generalized Soil-Water  
713 Characteristics from Texture. Soil Sci. Soc. Am. J. 50, 1031-1036.

714 Schwalm, C.R., Williams, C.A., Schaefer, K., Arneeth, A., Bonal, D., Buchmann, N., Chen, J., Law, B.E.,  
715 Lindroth, A., Luysaert, S., Reichstein, M., Richardson, A.D., 2010. Assimilation exceeds  
716 respiration sensitivity to drought: A FLUXNET synthesis. Global Change Biol. 16, 657-670.

717 Sonnentag, O., Chen, J.M., Roulet, N.T., Ju, W., Govind, A., 2008. Spatially explicit simulation of  
718 peatland hydrology and carbon dioxide exchange: Influence of mesoscale topography. Journal of  
719 Geophysical Research-Biogeosciences 113.

720 Soyulu, M.E., Istanbuluoglu, E., Lenters, J.D., Wang, T., 2011. Quantifying the impact of groundwater  
721 depth on evapotranspiration in a semi-arid grassland region. HESS 15, 787-806.

722 Taylor, K.E., 2001. Summarizing multiple aspects of model performance in a single diagram. J Geophys  
723 Res-Atmos 106, 7183-7192.

724 Tedeschi, V., Rey, A., Manca, G., Valentini, R., Jarvis, P.G., Borghetti, M., 2006. Soil respiration in a  
725 Mediterranean oak forest at different developmental stages after coppicing. Global Change Biol.  
726 12, 110-121.

727 Thomey, M.L., Collins, S.L., Vargas, R., Johnson, J.E., Brown, R.F., Natvig, D.O., Friggens, M.T., 2011.  
728 Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan  
729 Desert grassland. Global Change Biol. 17, 1505-1515.

730 Thompson, S.E., Harman, C.J., Konings, A.G., Sivapalan, M., Neal, A., Troch, P.A., 2011. Comparative  
731 hydrology across AmeriFlux sites: The variable roles of climate, vegetation, and groundwater.  
732 *Water Resour. Res.* 47.

733 Tirone, G., Dore, S., Matteucci, G., Greco, S., Valentini, R., 2003. Evergreen Mediterranean forests.  
734 carbon and water fluxes, balances, ecological and ecophysiological determinants. In: Valentini, R.  
735 (Ed.), *Fluxes of Carbon, Water and Energy of European Forests*. Springer-Verlag, Berlin, pp.  
736 125-149.

737 Torrence, C., Compo, G.P., 1998. A practical guide to wavelet analysis. *Bulletin of the American*  
738 *Meteorological Society* 79, 61-78.

739 Trumbore, S., 2000. Age of soil organic matter and soil respiration: Radiocarbon constraints on  
740 belowground C dynamics. *Ecol. Appl.* 10, 399-411.

741 van der Molen, M.K., Dolman, A.J., Ciais, P., Eglin, T., Gobron, N., Law, B.E., Meir, P., Peters, W.,  
742 Phillips, O.L., Reichstein, M., Chen, T., Dekker, S.C., Doubkova, M., Friedl, M.A., Jung, M., van  
743 den Hurk, B.J.J.M., de Jeu, R.A.M., Kruijt, B., Ohta, T., Rebel, K.T., Plummer, S., Seneviratne,  
744 S.I., Sitch, S., Teuling, A.J., van der Werf, G.R., Wang, G., 2011. Drought and ecosystem carbon  
745 cycling. *Agr Forest Meteorol* 151, 765-773.

746 Vargas, R., Baldocchi, D.D., Allen, M.F., Bahn, M., Black, T.A., Collins, S.L., Yuste, J.C., Hirano, T.,  
747 Jassal, R.S., Pumpanen, J., Tang, J.W., 2010a. Looking deeper into the soil: biophysical controls  
748 and seasonal lags of soil CO<sub>2</sub> production and efflux. *Ecol. Appl.* 20, 1569-1582.

749 Vargas, R., Baldocchi, D.D., Bahn, M., Hanson, P.J., Hosman, K.P., Kulmala, L., Pumpanen, J., Yang,  
750 B., 2011. On the multi-temporal correlation between photosynthesis and soil CO<sub>2</sub> efflux:  
751 reconciling lags and observations. *New Phytol.* 191, 1006-1017.

752 Vargas, R., Detto, M., Baldocchi, D.D., Allen, M.F., 2010b. Multiscale analysis of temporal variability of  
753 soil CO<sub>2</sub> production as influenced by weather and vegetation. *Global Change Biol.* 16, 1589-  
754 1605.

755 Vargas, R., Trumbore, S.E., Allen, M.F., 2009. Evidence of old carbon used to grow new fine roots in a  
756 tropical forest. *New Phytol.* 182, 710-718.

757 Vogel, C.A., Baldocchi, D.D., Luhar, A.K., Rao, S., 1995. A comparison of a hierarchy of models for  
758 determining energy balance components over vegetation canopies. *JApMe* 34, 2182-2196.

759 Wang, Y.P., Kowalczyk, E., Leuning, R., Abramowitz, G., Raupach, M.R., Pak, B., van Gorsel, E.,  
760 Luhar, A., 2011. Diagnosing errors in a land surface model (CABLE) in the time and frequency  
761 domains. *Journal of Geophysical Research-Biogeosciences* 116, -.

762 White, M.A., Thornton, P.E., Running, S.T., Nemani, R.R., 2000. Parameterization and sensitivity  
763 analysis of the BIOME-BGC terrestrial ecosystem model: net primary production controls. *Earth*  
764 *Interactions* 4, 1-85.

765 Xu, L.K., Baldocchi, D.D., 2003. Seasonal trends in photosynthetic parameters and stomatal conductance  
766 of blue oak (*Quercus douglasii*) under prolonged summer drought and high temperature. *Tree*  
767 *Physiology* 23, 865-877.

768

769

770