

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

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

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Short title: Drought influence simulated ecosystem fluxes

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52 Abstract

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

74

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

77 INTRODUCTION

99

Water availability is the dominant control of roughly 40% of global terrestrial primary 78 productivity (Beer and others, 2010) with concurrent effects on ecosystem respiration 79 (Reichstein and others, 2002a; Schwalm and others, 2010). Recent increases in the global 80 incidence of drought (Dai and others, 2004), and decreased global evapotranspiration (Jung and 81 others, 2010) suggest that current terrestrial ecosystems are finding themselves in more water-82 limited environments (Hartmann, 2011). Such observations are in line with projections of climate 83 change, with higher temperatures and reduced soil moisture, leading to longer and stronger 84 85 seasonal droughts in the coming decades (Giorgi and Lionello, 2008). Process-oriented ecosystem models are critical tools for studying land-atmosphere fluxes 86 and for up-scaling this information to regional and global scales (Raupach and others, 2005). 87 Drought has a large impact on ecosystem state and function, and previous studies have 88 highlighted data-model disagreement for CO₂ fluxes in ecosystems suffering regular drought 89 such as those found in Mediterranean-type climate zones (e.g., Krinner and others, 2005; 90 Morales and others, 2005; Jung and others, 2007). The limited understanding of the hierarchy 91 and the temporal/spatial variation of drivers controlling the ecophysiology/biogeochemistry of 92 Mediterranean ecosystems hamper the accurate representation of H₂O and CO₂ fluxes by models. 93 (Reichstein and others, 2002b; Keenan and others, 2010a; Misson and others, 2010). Thus, it is 94 critical to understand how drought stress influences these fluxes, and how process-oriented 95 96 ecosystem models predict them across different ecosystems. Mediterranean ecosystems constitute a well-suited test-bed for the study and simulation 97 of drought effects, due to the combination of cool, wet winters with hot, dry summers (Joffre and 98

others, 2007). The asynchrony between the supply and demand for water causes annual potential

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

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

In this study we use data from multiple Mediterranean Oak woodland sites to address the following question: How well do process-oriented ecosystem models simulate the temporal variability of CO₂ (i.e., gross primary production and ecosystem respiration) and H₂O vapor fluxes (i.e., evapotranspiration) in Mediterranean oak woodlands across years and under drought or no-drought conditions? Based on previous studies we hypothesize that data-model 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 ₂ 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). 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

study including meteorological drivers were onsite measurements and available from the La

147 Thuile 2007 FLUXNET 2.0v dataset (www.fluxdata.org).

148

149 Model Simulations

150 We performed simulations for all study sites considering differences in leaf habit (i.e., evergreen

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

meteorological forcing input variables along with site-specific ancillary information (Table 1) to

calculate GPP, Reco and ET. All data were drawn from the La Thuile 2007 FLUXNET 2.0v

156 dataset (<u>www.fluxdata.org</u>) and represent onsite measurements.

In this study we evaluated the performance of these models using standard plant 157 functional type parameterizations chosen in accordance with site-specific plant characteristics 158 (i.e., evergreen vs. deciduous) and individual model requirements (Table 1). The model runs 159 were without optimization to avoid enhancing of local agreement between observed- and model-160 calculated fluxes. For all models we used the same data for each site-specific characteristics 161 (e.g., soil texture, nitrogen content, canopy height, maximum leaf area index, soil depth; Table 1) 162 and same forcing variables (e.g., precipitation, longwave/shortwave radiation, air temperature) 163 typically available at the global scale for general model simulations. Specific details about model 164 165 architecture, parameters, and calculation of CO₂ and ET fluxes are found in Table 2. Model outputs and site measurements were averaged into daily sums for GPP, Reco and ET for each 166 year and each site. This modeling exercise provided a total of 105 site-year simulations that were 167 168 analyzed for this study at the daily time-step (Supplementary Figures 1-4).

169

170 Analysis of Ecosystem Drought Conditions

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

$$\text{REW} = \frac{\theta - \theta_{\text{w}}}{\theta_{\text{fc}} - \theta_{\text{w}}} \tag{1}$$

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

180

175

181 Time-series Analysis

182 We explored the spectral properties of the time series of daily GPP, Reco, and ET from

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

information about the periodicities of the time series, and allows us to test for differences in the

spectral properties to identify the frequencies at which there are (if any) substantial data-model

- disagreements. In other words, we are able to evaluate data-model agreement in the frequency
- 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 - mean(x))/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

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,

10-30, 30-200 and 365 days); and b) mean daily flux estimates of GPP, Reco, and ET under no

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

first analysis we were able to identify the time-periods for data model disagreement, and with the

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 ₂ Fluxes and ET
232	Evergreen sites
233	The three-year averages of GPP, Reco and ET for measurements, model outputs, and the

residuals (i.e., measurements minus model outputs) were summarized for evergreen sites (Figure

1). Subsequent analyzes in this study were done using all available data for measurements (n=12

site-years) and simulations (n=60 site-years; Supplementary Figure 1) for evergreen sites. These

sites had an average measured annual sum for GPP of 1518 ± 241 (gC m² vr⁻¹). Reco of 1260 ± 191 237 (gC m² yr⁻¹), and ET of 390 \pm 43 (mm yr⁻¹; Figure 1). Using wavelet analysis we calculated the 238 global wavelet power spectra of GPP, Reco and ET from measurements, model outputs, and 239 240 residuals (3 years of data for each site and model analyzed). For a visual representation of the differences in the power spectra only the measurements and residuals were plotted (Figure 2). In 241 general, the global wavelet power spectra of GPP, Reco and ET from measurements showed high 242 power at 365-days and a lesser seasonal power at ~200-days. Importantly, a similar spectral 243 signature was found in the residuals of these time series showing that model errors were 244 245 associated with these important fluctuations in the measurements. A peak in the global power spectrum means that there were strong systematic oscillations at that specific time-scale. For 246 example, a strong power at 365-days suggests systematic oscillations in the time series at the 247 annual scale, and from Figure 2 one can see that it represents the strongest oscillation but with 248 larger variability across the time series analyzed. 249

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

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

267

268 *Deciduous sites*

Three-year averages of GPP, Reco and ET for measurements, model outputs, and the residuals 269 (i.e., measurements minus model outputs) were summarized for deciduous sites (Figure 4). 270 271 Subsequent analyzes were done using all available data for measurements (n=9 site-years) and simulations (n=45 site-years; Supplementary Figure 2) for deciduous sites. Overall, deciduous 272 sites had an average measured annual sum for GPP of 1972±257 (gC m² yr⁻¹), Reco of 1499±177 273 (gC m² yr⁻¹), and ET of 500 ± 89 (mm yr⁻¹). Similar to evergreen sites, the global wavelet power 274 spectra of GPP, Reco and ET measurements showed strong power at 365-days and a lesser 275 seasonal power at ~200-days for deciduous sites (Figure 5). This means that all the time series 276 showed systematic oscillations that represent year-to-year variability (i.e., 365-days) and intra-277 annual variability that may be linked to plant phenology (i.e., ~200-days). Similarly to every e 278 site, residuals had a comparable spectral signature for all fluxes showing that model errors were 279 associated with these important fluctuations in the measured fluxes, but also showed that there 280 was large variability in the representation of these fluxes at these time-scales. 281

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 ₂ 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 ⁻¹), high photosynthetic photon flux density (47.6 mol m ⁻²
293	day ⁻¹), and warm temperatures (21 °C; Table 1) characterized drought conditions at these sites.
294	These results contrast with higher precipitation (2.8 mm day ⁻¹), lower photosynthetic photon flux
295	density (28.9 mol m ⁻² day ⁻¹) 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 synthetize and find general patterns from these results we applied meta-analysis techniques. For evergreen sites the meta-analysis showed that models agreed with observations 306 in representing mean daily GPP under no drought and under drought conditions (i.e., 95% CI of 307 mean effect size not different from 1; Figure 6a). Models overestimated mean daily Reco under 308 no drought conditions but had even higher overestimation under drought conditions (i.e., 95% CI 309 of mean effect size >1; Figure 6a). Finally, models agreed with observations in representing 310 mean daily ET both under no drought and under drought conditions (i.e., 95% CI of mean effect 311 size not different from 1; Figure 6a). 312

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

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

For deciduous sites the meta-analysis showed that models underestimated the observations in representing mean daily GPP under drought conditions (i.e., 95% CI of mean effect size <1; Figure 6b). In contrast, models overestimated mean daily Reco under drought conditions (i.e., 95% CI of mean effect size >1; Figure 6b). Finally, models agreed with observations in representing mean daily ET both under no drought and under drought conditions (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 for GPP, Reco, and ET at both evergreen and deciduous Mediterranean oak woodland sites. 337 These results support the hypothesis that overall data-model disagreements are substantial at 338 temporal scales between weeks to months (i.e., 10-200 days), but important disagreements were 339 also found at shorter (i.e., 2-10 days) and larger (i.e., 365-days) time scales. Furthermore, the 340 meta-analysis showed that simulated Reco was overestimated under drought conditions for both 341 plant functional types. Previous studies suggest that with appropriate parameterization ecosystem 342 process-oriented models accurately represent ecosystem fluxes in Mediterranean ecosystems 343 (Keenan and others, 2009; Keenan and others, 2010b), but the necessity remains to identify 344 systematic errors with generic parameterizations and evaluate multi-model performance to 345 improve applicability of model outputs at larger spatial scales. 346

347

348 Temporal Variation of Ecosystem Fluxes

In general, we observed that the most important time scales (i.e., with highest spectral power in

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 between 2-10 days for GPP at both evergreen and deciduous sites, which supports previous 352 observations of data-model disagreement at these time scales among multiple models and 353 vegetation types in temperate ecosystems (Dietze and others, 2011). In addition, there was a 354 large underrepresentation of GPP at deciduous sites between 30-200 and 365 days similar to 355 results from other model evaluations (Mahecha and others, 2010). Our results bring attention to 356 the challenge for models to simulate phenological cycles especially for deciduous forests 357 (Richardson and others, 2012). Importantly, the spectral power of ET was systematically 358 359 overrepresented at both vegetation types between 2 and 30 days. This has implications for water balance budgets, and the representation of the temporal variability of water-use-efficiency in 360 these and other semi-arid ecosystems. Thus, there is increasing interest in evaluating this variable 361 in process-oriented ecosystem models (Lawrence and others, 2007; Wang and others, 2011). 362 Our results show systematic errors in Reco for evergreen and deciduous sites that 363 underestimate the oscillations of the time series of Reco at 30-200 days and overestimate the 364 oscillations at 365-days. This is likely a result of an underestimation of the magnitude of Reco in 365 response of water pulses and synoptic events at scales between 30-200 days, but an 366 367 overestimation of the magnitude of Reco at 365-days. The large underestimation of the spectral power for Reco may be a result of the challenge in representing: a) the overall response of Reco 368 to rainfall pulses in Mediterranean ecosystems (Baldocchi and others, 2006); b) the dependence 369 370 of heterotrophic and autotrophic respiration to seasonal variation; which are highly controlled by water availability in Mediterranean ecosystems (Carbone and others, 2011); c) the control of 371 recent photosynthesis on Reco (Vargas and others, 2011); d) changes of the carbon residence 372 373 time in soils or in plants (Trumbore, 2000; Vargas and others, 2009); and e) potential

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

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

Our results support previous observations where ecosystem process-oriented models fail to represent ecosystem fluxes at multiple time scales, and bring attention on the study of the spectral characteristics of the time series as an alternative way for model evaluation (Mahecha and others, 2010; Vargas and others, 2010b; Dietze and others, 2011; Wang and others, 2011). We further hypothesize that model-data disagreement at short time scales may be related to factors controlled by light, the intermediate timescales to drought conditions, and the annual 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 the days for deciduous sites. Thus, the challenge imposed by drought conditions to simulating 397 ecosystem fluxes may affect the annual estimates of productivity and ecosystem carbon balance 398 at water limited ecosystems (Richardson and others, 2010; van der Molen and others, 2011). Our 399 results support the hypothesis of overall data-model disagreement by systematically 400 overestimating daily Reco under drought stress at both plant functional types. The results support 401 that drought has a strong influence on simulating Reco, and therefore it is advisable that model 402 parameters should follow a seasonal course in response to this condition in Mediterranean 403 404 ecosystems (Reichstein and others, 2003). Importantly, daily GPP was underestimated under drought conditions at deciduous sites, which could be a result of the role of stomatal 405 conductance, maximum carboxylation rate (V_{cmax}) and maximum rate of electron transport (J_{max}) 406 influence on leaf scale photosynthesis under drought (Xu and Baldocchi, 2003; Limousin and 407 others, 2010). This may be especially important when taken into account the REW and its 408 409 influence on photosynthesis rates at the canopy scale (Rambal and others, 2003) and model parameters (Keenan and others, 2009; Keenan and others, 2010b). 410 Across sites and years we observed a slight reduction on the mean daily values of GPP 411 412 and Reco under drought conditions but these were associated with large variability (Table 3). Previous studies have shown an important reduction in assimilation (Xu and Baldocchi, 2003; 413

Limousin and others, 2010) and respiration (Reichstein and others, 2003) under drought.

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

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

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

439

440 Implications, Limitations and Future Considerations

441 Historically, model improvements have focused on how drought stress influence photosynthesis, but fewer efforts have been made for the role of drought stress of Reco (van der Molen and 442 others, 2011) and ET (Ichii and others, 2009; Soylu and others, 2011; Thompson and others, 443 2011). Our results show that systematic overestimation in Reco during drought conditions at both 444 evergreen and deciduous Mediterranean oak woodlands, and support previous observations that 445 models need improvements on how drought conditions control Reco (Reichstein and others, 446 2002a). Finally, evergreen sites have lower photosynthetic capacity but longer growing seasons 447 than deciduous sites, which results at similar annual sums of ecosystem fluxes (Baldocchi and 448 449 others, 2010; and this study). Our results show that deciduous sites are more resilient to drought, whereas evergreen sites are more sensitive and decrease substantially ecosystem fluxes under 450 drought. An incorrect representation of ecosystem fluxes may have larger implications under the 451 452 context of climate change where droughts may become more common (Kharin and others, 2007). For example, if plants will encounter more water stress in future years and model outputs 453 overestimate Reco, then plants could be depleted faster from carbon (i.e., carbon starvation) and 454 die faster than in reality. This scenario could be enhanced by the potential underestimation of 455 GPP under drought conditions for deciduous sites limiting the carbon input into the system and 456 generating a positive feedback for carbon depletion and therefore plant mortality. Thus, the 457 omission or misrepresentation of how models response to water deficit will influence predictions 458 about how ecosystems may evolve, adapt and respond to past and future environmental changes. 459 460 Potential modeling experiments and advancements could focus on: a) model sensitivity for water holding capacity, soil drainage and percolation that could affect model design and 461 parameterizations; b) the effect of changes in rooting depth and the ability of roots for extracting 462 463 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 and plant functional types; c) consistently evaluate the autotrophic and heterotrophic contribution 465 of Reco across a wide range of ecosystems and weather conditions including different ranges of 466 drought stress; d) consider the uncertainty for model parameters, initialization and random and 467 systematic errors within measurements under the proposed experiments; e) studies on radiative 468 transfer models and the light absorbed by tree leaves and the understory layer (Kobayashi and 469 others, 2012); and e) hierarchy model comparisons to better identify differences in model-data 470 agreement based on a systematic evaluation of model structures (Vogel and others, 1995). 471 472 This study represents a first attempt to evaluate the overall performance of multiple models for whole ecosystem carbon and water cycling across deciduous and evergreen 473 Mediterranean oak woodlands within FLUXNET. Our results summarize generalities on model-474 data disagreement but these vary for any specific site and any specific model that could be 475 improved by site-specific model parameterizations (Keenan and others, 2009; Keenan and 476 others, 2010b). Therefore, the generality of these multi-model meta-analysis results needs to be 477 tested at more study sites, across different years, and using a larger set of ecosystem process-478 oriented models. It is clear that longer time series are needed in order to account for model-data 479 agreements especially to account for inter-annual variability. Finally, the difficulty in 480 representing responses of ecosystem fluxes in drought prone ecosystems is exacerbated by the 481 biogeochemistry of a vertically stratified canopy with multiple layers of vegetation (e.g., grasses 482 483 and trees), soil hydrology (Sonnentag and others, 2008), and has been identified as a key challenge for the next generation of global climate models (Lawrence and others, 2007). 484 485

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