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

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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

INTRODUCTION

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

Process-oriented ecosystem models are critical tools for studying land-atmosphere fluxes and for up-scaling this information to regional and global scales (Raupach and others, 2005). Drought has a large impact on ecosystem state and function, and previous studies have highlighted data-model disagreement for CO_2 fluxes in ecosystems suffering regular drought such as those found in Mediterranean-type climate zones (e.g., Krinner and others, 2005; Morales and others, 2005; Jung and others, 2007). The limited understanding of the hierarchy and the temporal/spatial variation of drivers controlling the ecophysiology/biogeochemistry of Mediterranean ecosystems hamper the accurate representation of H_2O and CO_2 fluxes by models. (Reichstein and others, 2002b; Keenan and others, 2010a; Misson and others, 2010). Thus, it is critical to understand how drought stress influences these fluxes, and how process-oriented ecosystem models predict them across different ecosystems.

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

5

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 road,

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_2 (i.e., gross primary production and ecosystem respiration) and H_2O 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_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

146 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

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) 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_2 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:

$$REW = \frac{\theta - \theta_w}{\theta_{fc} - \theta_w}$$

175   (1)

176   where θ is soil water content reported in the La Thuile FLUXNET dataset, θ_w is soil water

177   content at permanent wilting point, and θ_{fc} represents water content at field capacity. The values

178   for θ_w and θ_{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     $(x -mean(x))/std(x)$, 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

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_2 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±241 (gC m^2 yr^{-1}), Reco of 1260±191

238   (gC m^2 yr^{-1}), and ET of 390±43 (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 ~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±257 (gC m^2 yr^{-1}), Reco of 1499±177

274 (gC m^2 yr^{-1}), and ET of 500±89 (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 ~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., ~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_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 ^{o}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 ^{o}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

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 mm day^{-1}),

315   high photosynthetic photon flux density (46.7 mol m^{-2} day^{-1}) and warm temperatures (20.8 ^{o}C;

316   Table 1). These results contrast with higher precipitation (3.3 mm day^{-1}), lower photosynthetic

317   photon flux density (24.3 mol m^{-2} day^{-1}), and cool temperatures (11.3 ^{o}C) found under no

318   drought conditions (Table 3). Noteworthy, these patterns were similar to those observed for

319   evergreen sties, 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 were 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

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