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

Short title: Drought influence simulated ecosystem fluxes

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

ABSTRACT

Water availability is the dominant control of global terrestrial primary productivity with concurrent effects on evapotranspiration and ecosystem respiration, especially in water-limited ecosystems. Process-oriented ecosystem models are critical tools for understanding land-atmosphere exchanges and for up-scaling this information to regional and global scales. Thus, it is important to understand how ecosystem models simulate ecosystem fluxes under changing weather conditions. Here, we applied both time-series analysis and meta-analysis techniques to study how five ecosystem process-oriented models simulated gross primary production (GPP), 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 woodlands (21 site-year measurements; 105 site-year-simulations). Mediterranean ecosystems are important test-beds for studying the interannual dynamics of soil moisture on ecosystem mass and energy exchange as they experience cool, wet winters with hot, dry summers and are typically subject to drought. Results show data-model disagreements at multiple temporal scales for GPP, Reco, and ET at both plant functional types. Overall there was a systematic underestimation of the temporal variation of Reco at both plant functional types at temporal 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 underestimated only for deciduous sites during drought. In contrast, daily estimates of ET 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 dynamics in water-limited ecosystems.

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

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

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 and others, 2007). They range from open to dense forest that allows a well developed to sparse understory comprising mostly of grasses, and are predominantly composed of evergreen and 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 that enable them to survive on a limited annual water supply by: a) having a generally low to 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, 2007; Ryu and others, 2010); b) down-regulating photosynthesis, respiration, and stomatal conductance with decreasing soil water availability (Baldocchi and others, 2010); and c) the potential of extending their root systems to tap ground water (David and others, 2007; Miller and others, 2010).

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 CO_2 (i.e., gross primary production and ecosystem respiration) and H_2O 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

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

METHODS

Measurements at Study Sites

The study sites included four evergreen and three deciduous Mediterranean oak woodlands described in Table 1. Flux measurements of CO_2 and water vapor were made at each site using the eddy covariance technique (Aubinet and others, 2000). We inferred gross primary production (GPP) and ecosystem respiration (Reco) from half-hourly net ecosystem exchange (NEE) measurements. Eddy covariance data for this study were drawn from the La Thuile 2007 FLUXNET 2.0v dataset (www.fluxdata.org). The La Thuile data set has been harmonized for gap-filling, quality control of NEE values, and calculation of GPP, Reco, and evapotranspiration (ET) following standardized protocols (Reichstein and others, 2005; Papale and others, 2006). Three years (2005-2007) of eddy-covariance data were used at each site (total of 21 site-years; Supplementary Figures 1, 2), along with continuous meteorological drivers (e.g., solar radiation, 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 Thuile 2007 FLUXNET 2.0v dataset (www.fluxdata.org).

Model Simulations

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, CABLE, ORCHIDEE, JULES; Table 2) based on volunteer participation by attendants at a 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 dataset (www.fluxdata.org) and represent onsite measurements.

In this study we evaluated the performance of these models using standard plant functional type parameterizations chosen in accordance with site-specific plant characteristics (i.e., evergreen vs. deciduous) and individual model requirements (Table 1). The model runs were without optimization to avoid enhancing of local agreement between observed- and model-calculated fluxes. For all models we used the same data for each site-specific characteristics (e.g., soil texture, nitrogen content, canopy height, maximum leaf area index, soil depth; Table 1) and same forcing variables (e.g., precipitation, longwave/shortwave radiation, air temperature) typically available at the global scale for general model simulations. Specific details about model architecture, parameters, and calculation of CO_2 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 year and each site. This modeling exercise provided a total of 105 site-year simulations that were analyzed for this study at the daily time-step (Supplementary Figures 1-4).

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:

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

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).

Time-series Analysis

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, 1998). Previous studies have reviewed in detail the concepts of wavelet analysis (Torrence and Compo, 1998), and used this technique for model performance evaluation (Vargas and others, 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 disagreement.

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

Meta-analysis

For this synthesis study we applied meta-analysis techniques (Hedges and others, 1999; Gurevitch and others, 2001) to determine the generalities of data-model disagreement between observations of fluxes (i.e., control) and model outputs (i.e., treatments). The meta-analysis was 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 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.

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

RESULTS

Spectral Properties of CO_2 Fluxes and ET

Evergreen sites

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 m^2 yr^{-1}), Reco of 1260±191 (gC m^2 yr^{-1}), and ET of 390±43 (mm yr^{-1}; Figure 1). Using wavelet analysis we calculated the global wavelet power spectra of GPP, Reco and ET from measurements, model outputs, and 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 general, the global wavelet power spectra of GPP, Reco and ET from measurements showed high power at 365-days and a lesser seasonal power at ~200-days. Importantly, a similar spectral signature was found in the residuals of these time series showing that model errors were 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 example, a strong power at 365-days suggests systematic oscillations in the time series at the annual scale, and from Figure 2 one can see that it represents the strongest oscillation but with larger variability across the time series analyzed.

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

Deciduous sites

Three-year averages of GPP, Reco and ET for measurements, model outputs, and the residuals (i.e., measurements minus model outputs) were summarized for deciduous sites (Figure 4). 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 sites had an average measured annual sum for GPP of 1972±257 (gC m^2 yr^{-1}), Reco of 1499±177 (gC m^2 yr^{-1}), and ET of 500±89 (mm yr^{-1}). Similar to evergreen sites, the global wavelet power spectra of GPP, Reco and ET measurements showed strong power at 365-days and a lesser seasonal power at ~200-days for deciduous sites (Figure 5). This means that all the time series showed systematic oscillations that represent year-to-year variability (i.e., 365-days) and intra-annual variability that may be linked to plant phenology (i.e., ~200-days). Similarly to evergreen site, residuals had a comparable spectral signature for all fluxes showing that model errors were associated with these important fluctuations in the measured fluxes, but also showed that there was large variability in the representation of these fluxes at these time-scales.

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

Responses of Daily Means of CO_2 Fluxes and ET to Drought Conditions

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

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

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 in representing mean daily GPP under no drought and under drought conditions (i.e., 95% CI of mean effect size not different from 1; Figure 6a). Models overestimated mean daily Reco under no drought conditions but had even higher overestimation under drought conditions (i.e., 95% CI of mean effect size >1; Figure 6a). 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 6a).

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 ^{o}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 ^{o}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 summarized in Supplementary Figure 4. In general, for GPP (Supplementary Figure 6a, b) and Reco (Supplementary Figure 6d, e) the correlation coefficient decreased, and the RMSE and standard deviation increased under drought conditions. In contrast, the correlation coefficient, 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 model consistently over- or under- represented ecosystem fluxes across all sites (Supplementary 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).

DISCUSSION

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

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
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

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

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

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

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 of Reco across a wide range of ecosystems and weather conditions including different ranges of drought stress; d) consider the uncertainty for model parameters, initialization and random and systematic errors within measurements under the proposed experiments; e) studies on radiative transfer models and the light absorbed by tree leaves and the understory layer (Kobayashi and others, 2012); and e) hierarchy model comparisons to better identify differences in model-data agreement based on a systematic evaluation of model structures (Vogel and others, 1995).

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 Mediterranean oak woodlands within FLUXNET. Our results summarize generalities on model-data disagreement but these vary for any specific site and any specific model that could be improved by site-specific model parameterizations (Keenan and others, 2009; Keenan and others, 2010b). Therefore, the generality of these multi-model meta-analysis results needs to be tested at more study sites, across different years, and using a larger set of ecosystem process-oriented models. It is clear that longer time series are needed in order to account for model-data agreements especially to account for inter-annual variability. Finally, the difficulty in representing responses of ecosystem fluxes in drought prone ecosystems is exacerbated by the biogeochemistry of a vertically stratified canopy with multiple layers of vegetation (e.g., grasses 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).

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