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ECOSYSTEMS

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

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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 3 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

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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 (for example, 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 comprised 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 load, or low to medium tree cover to reduce total water loss at the landscape scale (Joffre and others 2007; Ryu and others 2010); (b) downregulating 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 (that is, gross primary production and ecosystem respiration) and H_2O vapor fluxes (that is, 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 and months where synoptic events (that is, 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 (that is, 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 data set (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 (for example, 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 data set (www.fluxdata.org).

Model Simulations

We performed simulations for all study sites considering differences in leaf habit (that is, evergreen vs. deciduous). We used five process-oriented ecosystem models (that is, 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 data set (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 (that is, evergreen vs. deciduous) and individual model requirements (Table 1, 2). 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 characteristic (for example, soil texture, nitrogen content, canopy height, maximum leaf area index, soil depth; Table 1) and same forcing variables (for example, 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, 2, 3, 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). In brief, REW was calculated from soil water content at a daily time step:

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

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 and others (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

Table 1. Characteristics of the Seven Mediterranean Oak Woodlands Used for the Modeling Exercise in This Study

Variable	Castelporziano	Évora	Las Majadas	Puechabon	Roccarespampani 1	Roccarespampani 2	Tonzi Ranch
Location	41.705200 12.376100	38.476501 –8.024550	39.941502 –5.773360	43.741402 3.595830	42.408100 11.930000	42.390301 11.920900	38.431599 −120.966003
Elevation (m.a.s.l.)	68	243	260	270	234	234	177
Annual air temperature (°C)	15	16	16	14	15	15	16
Precipitation (mm y^{-1})	927	577	691	820	905	921	651
Aboveground							
Leaf habit	Evergreen	Evergreen	Evergreen	Evergreen	Deciduous	Deciduous	Deciduous
Dominant tree	*Quercus ilex*	*Quercus ilex*	*Quercus ilex*	*Quercus ilex*	*Quercus cerris*	*Quercus cerris*	*Quercus douglasii*
Maximum LAI	3.5	0.5	0.5	2.8	3.0	3.9	0.8
Canopy height (m)	10–15	7.3	7	5	14	16.50	9.41
Canopy architecture	Close	Open	Open	Close	Close	Close	Open
Foliage nitrogen (%)	1.4	1.38	1.32	1.26	2	2.00	1.84
Leaf C:N	32.1	34.08	34.1	35.7	21	21	25.2
Measurement height (m)	18	29	15	12.2	20	20	23.4
Soil							
Sand (%)	89.6	83	80	26	35.61	35.61	43
Silt (%)	5	9	10.7	35.2	32.34	32.34	43
Clay (%)	5.4	8	9.3	38.8	32.05	32.05	14
N (%)	–	0.12	–	0.48	0.21	0.21	0.11
C (%)	0.32	1.6	3.32	7.4	3.8	3.9	1.09
Soil pH	6.21	5.6	5.6	7.3	6.6	6.6	–
Soil bulk density	0.9	1.3	1.5	–	1.3	1.3	1.6
Soil depth (m)	>1	0.3	>1	0.5	0.7	0.7	0.75
Soil type	Haplic arenosols	Sandy Cambisol	Stagnic Alisols	Rhodo-chromic luvisol	Luvisoil	Luvisoil	Auburn
Reference	(Tirone and others 2003)	(Pereira and others 2007)	(Casals and others 2009)	(Rambal and others 2003; Rambal and others 2004)	(Tedeschi and others 2006)	(Tedeschi and others 2006)	(Ma and others 2007)

Data taken from the FLUXNET database available at (www.fluxdata.org).

Table 2. Description of the Main Ecosystem Processes in Participating Models

	BEPS	BIOME BGC	CABLE	JULES	ORCHIDEE
Photosynthesis	Farquhar's model (Farquhar and others 1980)	Farquhar's model (Farquhar and others 1980)	Farquhar's model (Farquhar and others 1980)	Model based on (Collatz and others 1991)	Farquhar's model (Farquhar and others 1980)
Stomatal conductance	(Ball and others 1987) based on (Ball and Berry 1982)	Modified Ball-Berry-Leuning stomatal model (Leuning and others 1995) by (Running and Coughlan 1988)	Ball-Berry-Leuning stomatal model (Leuning and others 1995)	(Ball and others 1987) based on (Ball and Berry 1982)	(Ball and others 1987) based on (Ball and Berry 1982)
Autotrophic respiration	Growth is represented by a fraction of photosynthesis, maintenance respiration depends on tissue mass and temperature.	Growth respiration is a proportion of total new carbon allocated to growth. Maintenance respiration is calculated as a function of tissue mass, tissue N concentration, and tissue temperature.	Growth respiration is a proportion of total new carbon allocated to growth.	Growth respiration is a proportion of total new carbon allocated to growth. Maintenance respiration depend on the mean leaf N concentration (Friend and others 1993)	Based on (Ruimy and others 1996), growth respiration is a fixed part of allocated photosynthates (30%). Maintenance respiration calculated as a function of temperature, biomass and C:N ratio
Heterotrophic respiration	Modified Arrhenius dependence on temperature (Lloyd and Taylor 1994) and soil moisture.	Modified Arrhenius dependence on temperature (Lloyd and Taylor 1994).	Modified Arrhenius dependence on temperature (Lloyd and Taylor 1994) and soil moisture.	A Q_{10} model and the dependence on soil moisture (Clark and others 2011).	Modified Arrhenius dependence on temperature (Lloyd and Taylor 1994) and soil moisture.
Evapotranspiration	Penman–Monteith equation (Monteith 1965)	Penman–Monteith equation (Monteith 1965)	Penman–Monteith equation (Monteith 1965)	Based on a surface resistance representing restrictions in availability of water (Best and others 2011)	Bulk formula to formulate surface fluxes (Ducoudré and others 1993)
Water balance	Five soil layers	Single soil layer	Six soil layers	Four soil layers	Two soil layers
Phenology	Prescribed	Prescribed	Prescribed	Prescribed	Prescribed
Model main reference	(Ju and others 2006)	(White and others 2000)	(Kowalczyk and others 2006)	(Best and others 2011)	(Krinner and others 2005)

and others 2011; Wang and others 2011). In brief, 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 (that is, 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:

$$X' = (x - \text{mean}(x))/\text{std}(x),$$

where x represents the flux values of the time series of fluxes (for example, 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 (that is, four evergreen and three deciduous sites; 21 site-years), and for each model simulation for each site (that is, 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 (that is, control) and model outputs (that is, treatments). The meta-analysis was performed for: (a) mean spectral power of GPP, Reco, and ET at different time-periods (that is, 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 (that is, REW < 0.4). The different time-periods represent weekly, monthly, seasonal, 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 (for example, GPP) and each group (that is, evergreen and deciduous) (Hedges and others 1999). A mean effect size of one indicates that the model outputs were not different from observations, whereas a mean effect size greater than 1 and less than 1 indicates that the model outputs overestimated and underestimated the observations, respectively. To determine if model outputs were different from site observations (that is, mean effect size $\neq 1$) 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 (SD), 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 3-year averages of GPP, Reco, and ET for measurements, model outputs, and the residuals (that is, 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. 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 approximately 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 spec-

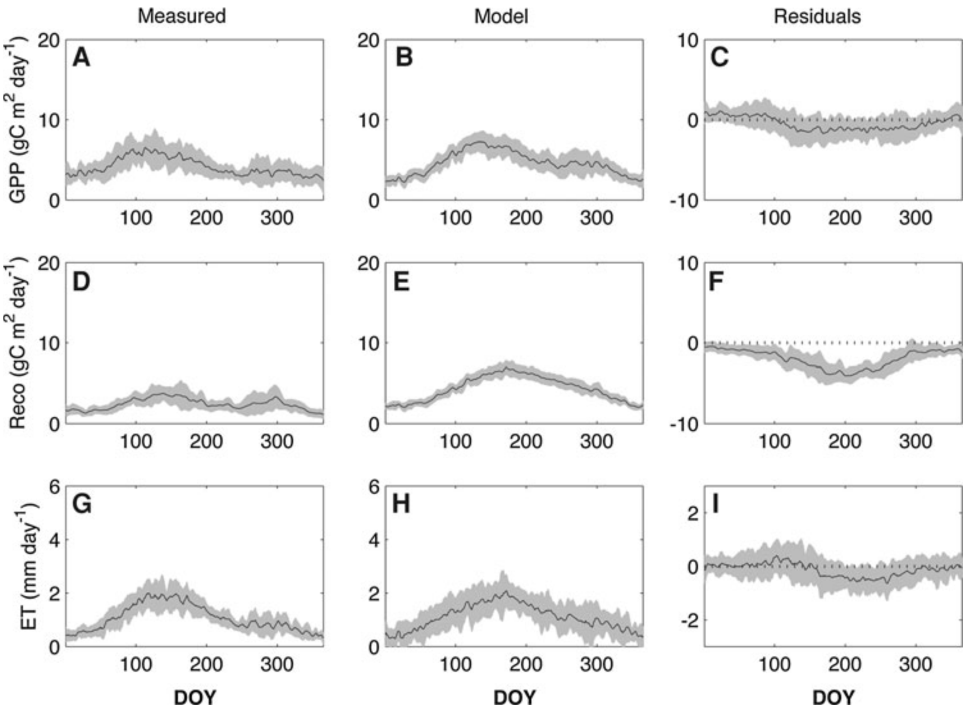

Figure 1. Time series of the annual average cycle for site measurements, model output, and residuals (that is, [measurements—model output]) for evergreen Mediterranean oak woodlands. *Solid line* represents mean and *gray area* ±1 SD. The annual average cycles were done using flux data from 3 years at four sites (n = 12 site years). Subsequent analyzes for this study were done with all the available data.

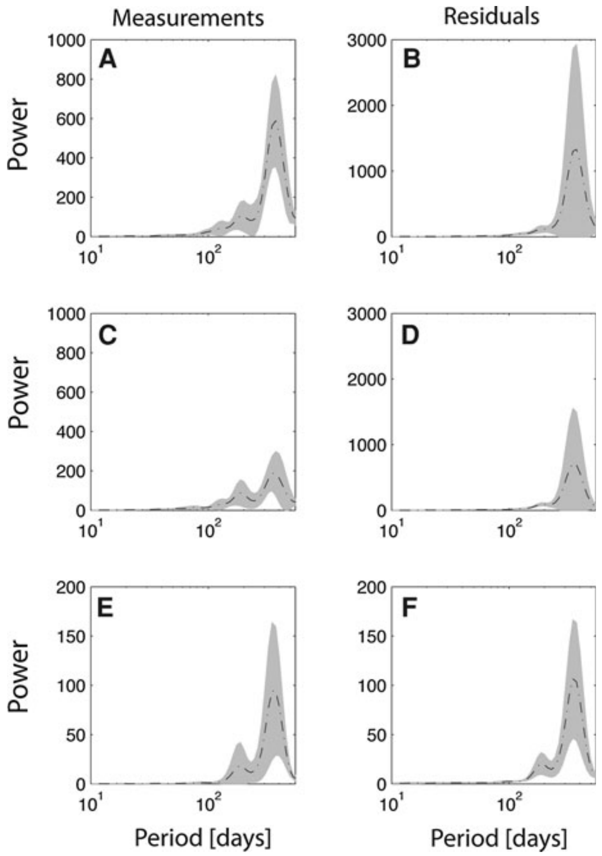

Figure 2. Spectral properties of the ensemble of site measurements and model residuals for GPP (**A**, **B**), Reco (**C**, **D**), and ET (**E**, **F**) at evergreen sites. *Dashed line* represents mean and *gray area* ±1 SD.

trum 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 (that is, 2–10, 10–30, 30–200, and 365 days) representing weekly, monthly, seasonal, 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 of 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

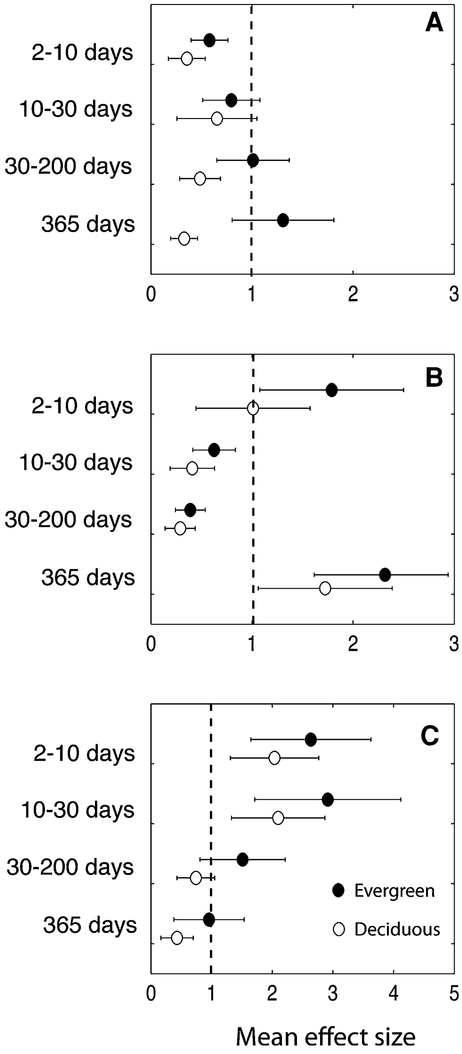

Figure 3. Mean effect size (observations vs. models) of the spectral power for GPP (**A**), Reco (**B**), and ET (**C**) at different time periods for evergreen and deciduous sites. Means and 95% confidence intervals are depicted.

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 (that is, 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. 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 approximately 200-days for deciduous sites (Figure 5). This means that all the time series showed systematic oscillations that represent year-to-year variability (that is, 365-days) and intra-annual variability that may be linked to plant phenology (that is, ~200-days). Similarly to evergreen sites' 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 (that is, REW < 0.4) 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°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°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 SD increased under drought conditions. In contrast, the correlation coefficient, RMSE, and SD for daily values of ET were more consistent between drought and no

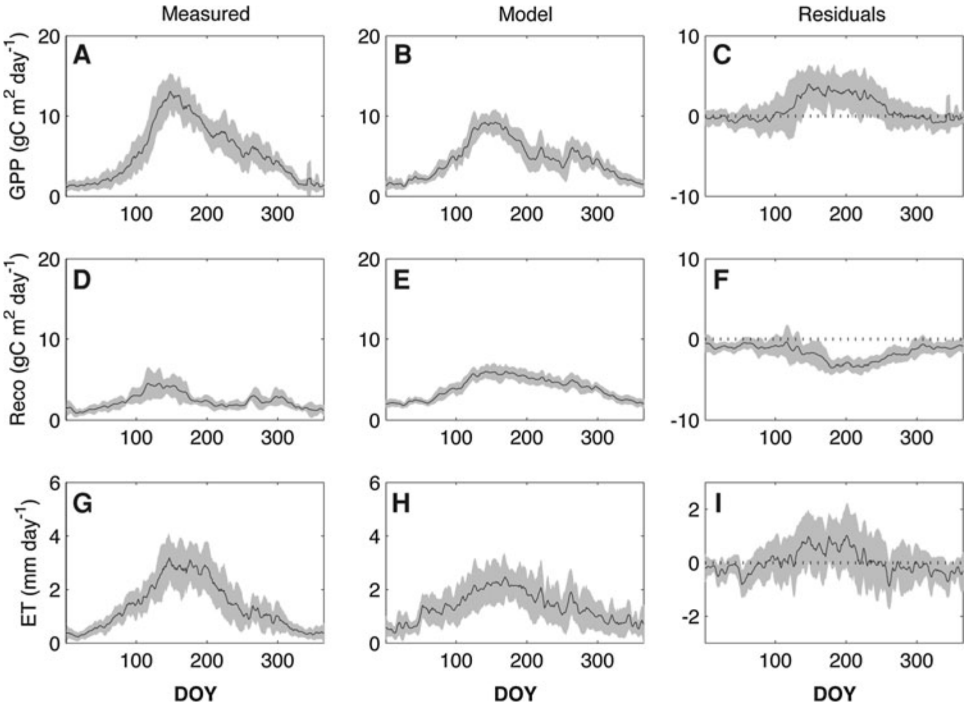

Figure 4. Time series of the annual average cycle for site measurements, model output, and residuals (that is, [measurements—model output]) for deciduous Mediterranean oak woodlands. *Solid line* represents mean and *gray area* ±1 SD. The annual average cycles were done using flux data from 3 years at three sites (n = 9 site years). Subsequent analyzes for this study were done with all the available data.

drought conditions (supplementary Figure 5E, F). Importantly, no single model consistently over- or under-represented ecosystem fluxes across all sites (supplementary Figures 1, 2, 5).

To synthesize 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 (that is, 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 overestimations under drought conditions (that is, 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 (that is, 95% CI of mean effect size not different from 1; Figure 6A).

Drought conditions (that is, 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 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 SD increased under drought conditions. In contrast, the correlation coefficient, RMSE and SD of daily values of ET 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 Figures 3, 4, 6).

For deciduous sites the meta-analysis showed that models underestimated the observations in representing mean daily GPP under drought conditions (that is, 95% CI of mean effect size <1; Figure 6B). In contrast, models overestimated mean daily Reco under drought conditions (that is, 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 (that is, 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

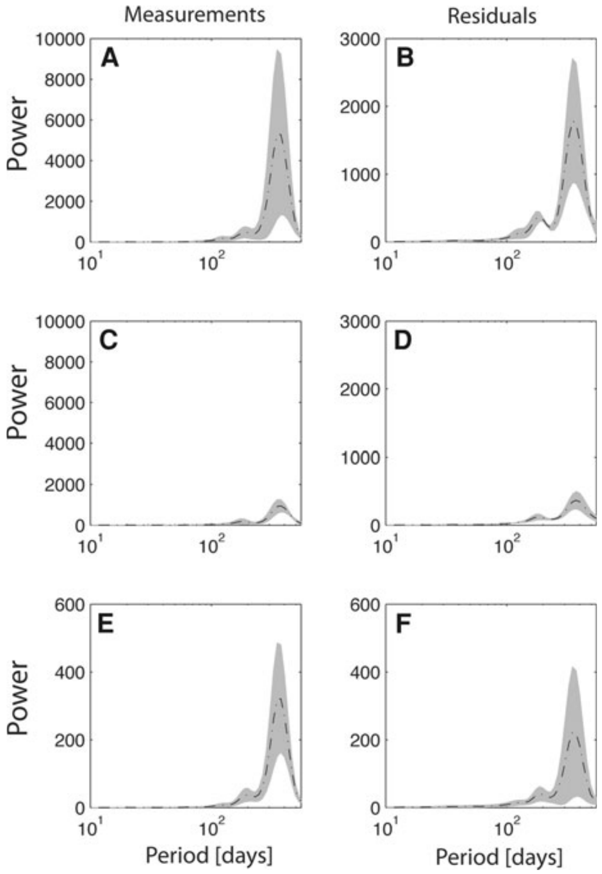

Figure 5. Spectral properties of the ensemble of site measurements and model residuals for GPP (**A**, **B**), Reco (**C**, **D**), and ET (**E**, **F**) at deciduous sites. *Dashed line* represents mean and *gray area* ±1 SD.

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 and months (that is, 10–200 days), but important disagreements were also found at shorter (that is, 2–10 days) and longer (that is, 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), 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 (that is, with highest spectral power in Figure 2) were those between 30–200 and at 365-days for GPP, Reco, and ET at both evergreen and deciduous sites. Our results show an overall underrepresentation of the spectral power between 2 and 10 days for GPP at both evergreen and deciduous sites, which supports previous observations of data-model disagreement at these time scales among multiple models and vegetation types in temperate ecosystems (Dietze and others 2011). In addition, there was a large underrepresentation of GPP at deciduous sites between 30–200 and 365 days similar to results from other model evaluations (Mahecha and others 2010). Our results bring attention to the challenge for models to simulate phenological cycles especially for deciduous forests during the growing seasons and its transitions (Richardson and others 2012). Importantly, the spectral power of ET was systematically 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 these and other semi-arid ecosystems. Thus, there is increasing interest in evaluating this variable in

Table 3. Mean Daily Values of Air Temperature (Ta), Precipitation (Precip), Photosynthetic Photon Flux Density (PPFD), Gross Primary Productivity (GPP), Ecosystem Respiration (Reco), Evapotranspiration (ET), and Relative Extractable Water (REW) at Evergreen and Deciduous Sites Under Drought or No Drought Conditions

Vegetation type	Condition	Ta (°C)	Precip (mm day^{-1})	PPFD (mol m^{-2} d^{-1})	GPP (gC m^{-2} day^{-1})	Reco (gC m^{-2} day^{-1})	ET (mm day^{-1})	REW
Evergreen	Drought	21 (5.8)	0.5 (3.2)	47.6 (14.7)	5.2 (3.5)	4.4 (3.4)	1.3 (1.0)	0.3 (0.04)
	No drought	12.8 (5.9)	2.8 (9.0)	28.9 (17.7)	5.7 (3.4)	4.9 (3.3)	1.4 (1.0)	0.6 (0.14)
Deciduous	Drought	20.8 (5.0)	0.7 (3.3)	46.7 (15.5)	5.1 (5.2)	3.5 (2.7)	1.4 (1.4)	0.2 (0.13)
	No drought	11.3 (4.8)	3.3 (7.9)	24.3 (15.6)	5.3 (5.0)	3.6 (2.7)	1.4 (1.3)	0.6 (0.14)

Numbers in parentheses represent ±1 SD.

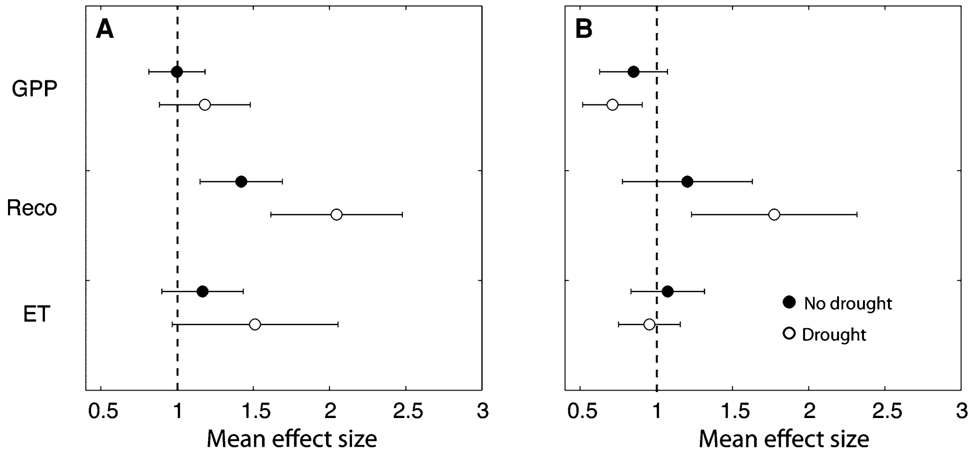

Figure 6. Mean effect size (observations vs. models) for daily means of GPP, Reco, and ET under drought and no drought conditions at evergreen (**A**) and deciduous (**B**) sites. Means and 95% confidence limits are depicted.

process-oriented ecosystem models (Lawrence and others 2007; Wang and others 2011).

Our results show systematic errors in Reco for evergreen and deciduous sites that underestimate the oscillations of the time series of Reco at 30–200 days and overestimate the oscillations at 365-days. This is likely a result of an underestimation of the magnitude of Reco in response to water pulses and synoptic events at scales between 30 and 200 days, but an 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 to rainfall pulses in Mediterranean ecosystems (Baldocchi and others 2006); (b) the dependence of heterotrophic and autotrophic respiration on seasonal variations, which are highly controlled by water availability in Mediterranean ecosystems (Carbone and others 2011); (c) the control of recent photosynthesis on Reco (Vargas and others 2011); (d) changes in the carbon residence 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 challenge to accurately estimate leaf area index (Ryu and others 2010) and understory net ecosystem exchange (Misson and others 2007), especially for open canopy sites. These sites may have an understory of grasses and forbs with different photosynthesis rates and phenologies (Joffre and others 2007) that were not explicitly considered in the generic parameterizations of the process-oriented models used in this study. For example, the understory could be a large contributor to GPP, Reco, or ET along the year or may be dependent on seasonality (Misson and others 2007) driving interannual variability in ecosystem fluxes (Ma and others 2007). In addition, most land surface and process-oriented models assume that a vegetated canopy can be abstracted as a turbid medium, but they fail to simulate radiation environments in heterogeneous landscapes (Mariscal and others 2004).

Our results support previous observations where ecosystem process-oriented models fail to represent ecosystem fluxes at multiple time scales, and bring attention to 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.

Ecosystem Fluxes and Drought Stress

Drought conditions were present for 30% of the measured days for evergreen sites and 41% of the days for deciduous sites, and these dates were centered along the growing season. Thus, the challenge imposed by drought conditions to simulating ecosystem fluxes may affect the annual estimates of productivity and ecosystem carbon balance at water limited ecosystems (Richardson and others 2010; van der Molen and others 2011). Our results support the hypothesis of overall data-model disagreement by systematically overestimating daily Reco under drought stress at both plant functional types. The results support that drought has a strong influence on simulating Reco, and therefore it is advisable that model parameters should follow a seasonal course in response to this condition in Mediterranean 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 conductance, maximum carboxylation rate (V_{cmax}) and maximum rate of electron transport (J_{max}) influence on leaf scale photosynthesis under drought (Xu and Baldocchi 2003; Limousin and others 2010). This may be especially important when REW is taken into account and its influence on photosynthesis rates at the canopy scale (Rambal and others 2003) and model parameters (Keenan and others 2009, 2010b).

Across sites and years we observed a slight reduction in the mean daily values of GPP 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; 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 increase at the time when soil water content starts to decrease (Baldocchi and others 2010; Vargas and others 2010a), supporting that the larger data-model disagreement is during drought events across the growing season. 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 influences 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 stomatal 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 at improving how to simulate water table depth and how roots utilize the water as the water table fluctuates 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 contributions of ecosystem fluxes (Baldocchi and others 2006; Thomey and others 2011).

Implications, Limitations, and Future Considerations

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

Potential modeling experiments and advancements could focus on: (a) model sensitivity to water holding capacity, soil drainage, and percolation that could affect model design and parameterizations; (b) the effect of changes in rooting depth and the ability of roots to extract water across the soil–water compartment (for example, 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, 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 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 (for example, 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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