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Comment

Interactive comment on “Improved understanding of drought controls on seasonal variation in Mediterranean forest canopy CO₂ and water fluxes through combined in situ measurements and ecosystem modelling” by T. Keenan et al.

T. Keenan

t.keenan@creaf.uab.es

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Response to Anonymous Referee #1

First of all we would like to thank the reviewer for the informative comments on our manuscript that significantly improved the previous version. Answers and comments to each point raised by the reviewer are given in detail below.

Referee 1). What concerns me most about the work is its focus on effects of soil moisture deficit on stomata conductance and photosynthetic capacity - and then to base this

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Discussion Paper



effort on a simulated soil water balance with no attempt of its evaluation. Moreover, calculation of the water balance is seemingly simplified using a number of assumptions regarding runoff and drainage. It is unclear whether/how e.g., rooting depth and the total volume of soil exploited by vegetation is considered (Table 1 suggests maybe yes, but the text certainly does not allow to judge how the soil water balance calculations were done exactly – please clarify). To my knowledge, the study sites all have soil water measurements although perhaps not on a continuous basis. Even if these data were not easily accessible via the Fluxnet web interface: what prevented you from either (a) digging into the published papers from these sites or (b) approaching the site PIs about availability of soil moisture data? For four locations this surely wouldn't have been an undue effort.

You may, of course, retort that measurements of soil water are not necessarily representative for the entire flux site because of the well-known spatial heterogeneity that is a problem for all below-ground measurements (soil moisture, heat flux, etc). There is a point to be made here, and I do not wish to say that your modelled soil moisture values shouldn't be used. But evaluation against measurements will demonstrate whether you capture seasonality, degree and speed of drying/rewetting – and this can normally be done even with data from a limited number of soil sensors. Without demonstrating that the modelled soil moisture patterns are reasonable the overall analysis is weak.

Authors: Thank you for pointing out this oversight. We have obtained deep soil water column measurements during the studied period for both the total soil column at Puechabon (4.5m) and the top 1m soil at Collelongo. This has allowed for the validation of our soil water reconstruction at these two sites. At both sites the reconstruction very accurately captures the timing, slope and magnitude of the seasonal cycles of soil water content (Fig. 1). The data at Puechabon compared very well with the reconstruction (the reconstruction was scaled to a new soil water holding capacity of 210mm, the current estimate of Puechabon soil water holding capacity (Serge Rambal, personal communication)). At Collelongo, the results were similar, except in autumn 1998,

[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)[Discussion Paper](#)

where the reconstruction overestimated the soil water content. This is probably because the Collelongo measurements relate to the top 1m of soil, whereas Collelongo soil depth is estimated to be 4m. Therefore, in dry periods with low photosynthetic activity (conditions corresponding to the three overestimated measurements), the top soil layer will dry out more quickly than deeper soil. It is worth mentioning that changing the absolute value of the soil water deficit under stress would not alter our conclusions regarding the relative effects of soil water on the conductance-assimilation relationship and photosynthetic capacity, only the slope of the relationships.

Soil water content is a key factor in our analysis, and for that reason we felt it important to make an effort to reconstruct total soil water content for the soil column, instead of using the soil water measurements (generally taken with respect to only the first 15-25cm soil) available from the FLUXNET web site. In Mediterranean forests, the seasonal cycle of shallow surface soil water content generally has a weak relation to the total available water in the soil column (which is why we did not use it for validation purposes). This is even more relevant given the deep rooting systems of many Mediterranean forests, which have evolved as a mechanism for resisting water stressed periods. This coupled with issues of soil heterogeneity led us to choose a reconstruction approach.

We have included these data in the revised manuscript, along with an improved description and evaluation of the soil water reconstruction technique used.

Referee 2). The analysis seeks to demonstrate that reduced conductance cannot fully explain effects of soil moisture deficit on canopy assimilation; it is required to introduce an additionally reduced photosynthetic capacity into the models. Can you comment how this goes together with the notion of stomata optimizing carbon gain at a certain water loss? You seem to suggest that carbon gain is actually reduced further than suggested by stomata closure alone? Wouldn't that mean that the plant actually maintains the stomata more open than necessary, and the optimum theory wouldn't hold? Maybe I am missing the point here, but further discussion along these lines would be useful.

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Discussion Paper



Authors: Theoretically it makes sense for the plant to divert resources away from photosynthetic capacity and maintain a relatively constant C_i/C_a ratio as the soil dries, which is what we find. However, our approach is an empirical fix, and we did not take into account the effect of other potential factors which may play a role, e.g. a changing mesophyll conductance. This has been clarified in the revised text with further discussion. Please see Friend, 1995 Ecological Modelling 77, 233-255 for further discussion regarding modeled stomatal responses and the optimum theory.

Referee 3). page 2288/line 6, "Recent studies have suggested. . ." It is certainly true that often stomata closure is being looked at the chief cause of reduced photosynthesis under drought conditions. However, here (as in some other places in the text) the authors seem to forget that effects of severe soil water deficit e.g., on Rubisco activity have been intensively studied for decades. They also have been addressed in previous (often plant-based or site-specific) modelling studies, although it is true that only a small number of studies that are applicable over larger regions have focused on this issue.

Authors: We have included additional material in the revised manuscript to highlight past studies on soil water stress effects on non-stomatal limitations to photosynthesis, and put them in the context of the present work.

Referee 4). Introduction/general: Soil water deficit may indeed become an increasingly frequent feature of Mediterranean ecosystems in future. However, vegetation response via reduced photosynthesis and transpiration is only one aspect of the overall ecosystem response; eventually, existing vegetation types will be replaced by other growth forms, including desertification being discussed for some areas (also, vegetation changes can be amplified by transiently enhanced uncontrolled fires).

Authors: This is quite true, but we did not say that photosynthesis/transpiration were the only factors likely to be affected by such change. They are important, however (together with respiration), in governing whole-plant abilities to thrive under given conditions. That is the reason to get this right in a DGVM such as ORCHIDEE. We need to get the

[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)[Discussion Paper](#)

physiology right to get the competitive interactions right, and hence be able to better predict vegetation change. This has been clarified in the revised manuscript.

Referee 5). Page 2291/canopy conductance: the assumption of negligible soil evaporation is only valid when soils are dry. Soil evaporation is driven by radiation with the slope of the relationship becoming very low when the top soil layer dries. Therefore, assuming surface conductance being equal to canopy conductance is not always true when the canopy is dry but the soil sufficiently well watered. Also, the difference between forest canopy transpiration and conductance, transpiration & conductance of the entire vegetation (including understorey), and total evapotranspiration and surface conductance it is not clearly made in the manuscript (there is some vague mentioning of understorey vegetation in the discussion later-on). This must be addressed at least in form of discussion/uncertainties.

Authors: The influence of soil evaporation is likely to be negligible if the canopy leaf area is high (Daikoku et al., Influence of evaporation from the forest floor on evapotranspiration from the dry canopy (2008) Hydrological Processes, 20, 4083 – 4096). Golden days filter out wetter periods. Also, we are primarily interested in the dry season, when soil evap. is not likely to be a problem for our analysis.

As pointed out, different species and/or strong undergrowth activity at a particular site could complicate the interpretation of the results. Differing seasonal dynamics and responses of, for example, dominant tree species' phenology versus understorey phenology/activity could lead to the invalid interpretation of the gross canopy fluxes. Unfortunately, for most sites in the FLUXNET network, little information is available regarding the proportion of the fluxes which is attributable to each species in mixed forests, or the understorey, and even less on the seasonal variability of this proportion.

For this reason we chose only sites which were strongly dominated by one species, and with no evidence of major contributions from understorey activity. We also checked for high flux activity outside of the growing season of the dominant species, which

[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)[Discussion Paper](#)

would indicate the presence of an active understorey. Mediterranean forests typically have a low contribution from the understorey to total fluxes, due to the fact that the dominant species has greater access to soil water reserves because of their deep rooting capabilities.

Site by site comments on the potential confounding effects of an understorey: Collesongo: Monospecific *Fagus sylvatica*, no understorey. Puechabon: Almost monospecific *Quercus ilex* (>85%), understorey: *Buxus sempervirens* (has been qualitatively found to have a very small impact on fluxes) (<http://daac.ornl.gov/FLUXNET/>) Blodgett: Monospecific *Pinus ponderosa* plantation. Two independent model estimates of the tower footprint both indicate that roughly 90% of the footprint was within the *Pinus ponderosa* plantation (Baker et al., 1999; Goldstein et al., 2000). Understorey has been reported to be sparse (understorey was cleared in 1999 as a management exercise.). By the end of the period included in this study, total one-sided leaf area index (LAI) was 2.49, comprising 72% *P. ponderosa* in the overstorey and 28% understorey shrubs (*A. manzanita* 22% and *C. cordulatus* 6%) (Misson et al., 2006). Roccarespampani: Monospecific *Quercus cerris*, understorey: deciduous shrubs. We were not able to ascertain the contribution of the understorey to total fluxes at Roccarespampani, but assume it was limited to early spring and late autumn. We used only flux data from the active period of *Quercus cerris* for the calculation of model parameters. We assume that the understorey would not contribute to the fluxes during drought periods as it would be inactive during summer due to shallow rooting capacity (higher soil layers will dry out faster than deep soil).

We propose adding a paragraph to the Discussion section as follows: “We assume all latent heat and CO₂ flux measurements to result from the fluxes of water and CO₂ across the canopy surfaces of the dominant species at each site. We recognise that this may not always be true. Other tree species on a site, or an active understorey, could potentially make large contributions to the total measured fluxes. Therefore, we focused on highly monospecific stands, and excluded sites at which strong contributions

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Discussion Paper



from understorey activity had been reported. This cannot guarantee, however, that the results are unaffected by the presence of non-dominant species, but we assume that any bias introduced is minimal.”

Referee 6). Page 2293, line 12: eddy flux measurements do not observe net photosynthesis. Presumably you used the gap-filled & portioned flux time series that are available as Fluxnet level 4 data. In seasonally dry ecosystems it is crucial to account for effects of soil water deficit and of rewetting on soil respiration. If that is not done well, the derived canopy assimilation rate will be wrong. Have you uncritically taken the provided Fluxnet GPP data (derived from standardised methods)? Have you checked whether the seasonality of respiration responds to temperature as well as soil water? I don't want to imply that the Fluxnet data is wrong (and the standardising methods to my knowledge certainly DO have a soil water dependency of respiration), but it would still be advisable to cross-check the downloaded data (e.g., visually, by plotting time series of respiration together with meteorology; or by comparing to original papers from the sites, etc) before using it for your modelling purposes. And since only four sites are involved this could have been done easily.

Authors: Before using the FLUXNET data, we confirmed that ecosystem respiration was responsive to soil water content. The ecosystem respiration dropped sharply during the summer period at all sites. As stated in the text (Section 2.1): “FLUXNET datasets include measurements of carbon dioxide and water fluxes at half-hourly time steps (Wofsy et al., 1993). We used the level-4 datasets, in which flux separation techniques for splitting the observed net carbon fluxes into assimilation and respiration have been employed (Reichstein et al., 2005). Gap-filled data were excluded.”

Referee 7). What kind of photosynthesis parameterizations were done in GOTILWA and ORCHIDEE to be applied at the sites? Did you have to specify values of J_{max} , V_{max} for leaves or canopy? If so, how were these derived? How did you determine values of other site-level variables (page 2298; e.g., growth/maintenance respiration, allocation patterns, fractional cover of a PFT)? From published literature?

[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)[Discussion Paper](#)

Authors: Previously published parameter values were used in each model at each site. This (and any changes in applied parameters from previously published values) will be clarified in the revised manuscript.

Referee 8). Page 2300: reference should be to fig. 3a and 3b (not 2a and 2b).

Authors: O.K., this error has been rectified in the text.

Referee 9). Fig 3 and related analysis: I may have overlooked something: in the Figure it looks like m and G_{s0} were determined on a half-hourly (or hourly) basis, no? What is the rationale of doing so? I would expect changes in slope m , or offset G_{s0} in response to changes in soil water deficit to be visible on a day-to-day basis (rather from one half hour to the next).

Authors: Midday (hourly) values were used. This was done in order to calculate the m and G_{s0} values which correspond to the time of day of high production. 'Mid-day' should be added to the figure caption.

Referee 10). Fig. 4: how was A_n normalised? And can you be more specific as to why you have chosen A_n only within a certain range of C_i/C_a (ca. 0.6 to 0.8)? Presumably, you wanted to select periods when you could be sure that stomatal limitation would be small (and therefore other limitations are visible)? During periods of severe soil water deficit I would have expected that a C_i/C_a of 0.6 and above is only found in the morning hours, when v_{pd} is still very low, is that so? In Figure 1 it would be helpful, to include calculated diurnal course of G_c in addition to the shown A_n and E_a .

Authors: A_n was normalized to the observed average assimilation rate under well watered conditions (> 0.8 Relative soil water holding capacity) of the selected data at each site. This explanation should be added to the figure caption. The reviewer is correct in their assumption as to why we selected the C_i/C_a range. This is (perhaps poorly) explained as follows in the text (Page 9, Lines 5-10), but will be further clarified in the revised version: "Evidence for any reductions in photosynthetic capacity under soil

[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)[Discussion Paper](#)

moisture stress were assessed by comparing rates of photosynthesis at different soil moisture contents but over a restricted range of leaf C_i concentrations ($220 < C_i < 300$), radiation ($> 250 \text{ W m}^{-2}$), and temperature ($< 25 \text{ }^\circ\text{C}$). Any differences in rates of assimilation under otherwise non-limiting conditions could then be attributed to non-stomatal soil water effects, rather than changes in the rate of supply of CO_2 to the intercellular spaces, light limitation, or any temperature effects.” The value of C_i/C_a was site and stress dependent. It dropped below 0.6 later in the day under strongly stressed conditions. G_c will be added to the data shown in Fig. 1.

Referee 11). Fig 5: show the range of golden days values of A_n and E_a from the measurements; can you also indicate st.dev of the model values? Authors: O.K.

Referee 12). Table 3: I am not very well versed in the use of MEF. But in many cases, values appear to be negative (which indicates relatively poor model-observation match) even in cases when r^2 are quite good. In the text overall you do not discuss MEF a lot; but if MEF is indeed more sensitive than r^2 , I would have liked to see the results on these values being used in more detail.

Authors: The modelling efficiency statistic (MEF) is similar to r^2 , which is interpreted as the proportion of variation explained by the fitted line whereas the MEF statistic is the proportion of variation explained by the line $Y = f(X_1, \dots, X_p)$. This statistic has been extensively used in hydrology models (Byers et al., 1989, Loague and Green, 1991 and Zacharias et al., 1996), but has also been used in biological models. It is related to the RMSE according to: $\text{MEF} = 1 - \text{RMSE}^2/s^2$ where s^2 is the variance of the observations. A value near one indicates a close match between observations and model predictions. A value of zero indicates that the model predicts individual observations no better than the average of the observations. Values less than zero indicate that the observation average would be a better predictor than the model results. The MEF will be thus introduced in the text along with the r^2 where appropriate.

Referee 13). In the end it was not clear to me why two models have been compared,

[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)[Discussion Paper](#)

what was the exact purpose of this comparison, and why were these two models chosen. This could be made clearer – For instance, is there a generally better performance to be expected from models that represent tree cohorts (like GOTILWA), and if so, why? Obviously, one advantage of Orchidee is the extrapolation to larger regions but other dynamic vegetation models that are based on forest gap dynamics can do as well. Is GOTILWA applicable for larger regions?

Authors: GOTILWA+ (Growth Of Trees Is Limited by WAtEr) was developed in the Mediterranean region. ORCHIDEE (ORganizing Carbon and Hydrology In Dynamic EcosystEms) was developed as a global dynamic vegetation model, but has been shown to perform poorly in the Mediterranean. There was thus a strong opportunity to learn from each other in comparing the two model responses in Mediterranean conditions. This study is also the first step towards a wider scale application. We have clarified this for the reader in the revised text.

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Interactive
Comment

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Discussion Paper



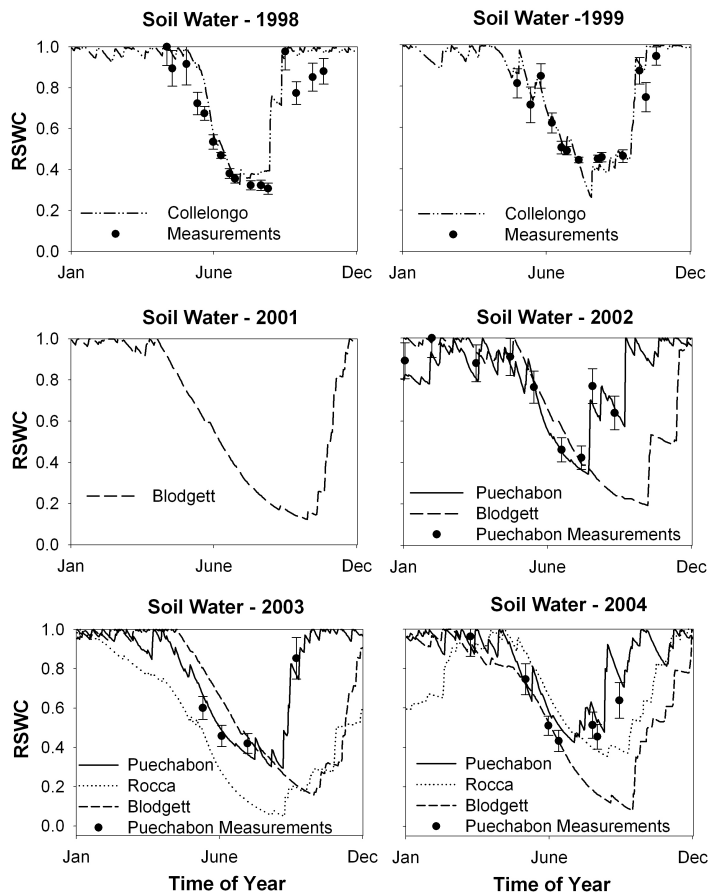


Fig. 1. Fig. 1. Reconstructed daily relative soil water content (RSWC) for the simulated periods at each of the studied sites, separated by year. Measurements show soil water observations at Puechabon and Col