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Carbon–Water Flux Coupling Under Progressive Drought

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Abstract.

Water-use efficiency, defined as the ratio of carbon assimilation over evapotranspiration (ET), is a key metric to assess ecosystem functioning in response to environmental conditions. It remains unclear which factors control this ratio during periods of extended water-limitation, and current semi-empirical water-use efficiency models fail to reproduce observed ET dynamics for these periods. Here, we use dry-down events occurring at eddy-covariance flux tower sites in the FLUXNET database as natural experiments to assess if and how decreasing soil-water availability modifies water-use efficiency on ecosystem scale. We demonstrate that an attenuating soil-water availability factor in junction with a previously discovered additive radiation term is necessary to accurately predict ET flux magnitudes and dry-down lengths of these water-limited periods. In an analysis of the attenuation, 20–33% of the observed decline in ET was due to the previously unconsidered soil-water availability effect. We conclude by noting the rates of ET decline differ significantly between FLUXNET sites with tall and short vegetation types and discuss the dependency of this rate on the variability of seasonal dryness.

1 Introduction

The interaction of the global carbon and water cycle has emerged as a critical topic in Earth system science (Ito and Inatomi, 2012; Hartmann et al., 2013). In terrestrial ecosystems, transpiration and photosynthesis are closely linked by gas diffusion in plant stomata (Cowan and Farquhar, 1977; Ball et al., 1987), while the lack of water is one of the principal limiting factors for the productivity of terrestrial ecosystems. Ecosystems can experience perpetual water-limitation, seasonal water stress or irregularly occurring droughts. Climate change is expected to exacerbate existing water scarcities, with a particular increase of drought events expected in semi-arid and subtropical regions (Dominguez et al., 2012). Drought events are important for biogeochemistry because they have been identified as prime-sources for the variability of carbon and water fluxes at ecosystem-level (Zscheischler et al., 2014). This can mainly be attributed to a decline of the gross primary productivity (GPP) under severe water limitation (Ma et al., 2012; Stocker et al., 2018). Despite the importance, predictions of ecosystem responses to intermittent and severe decreases of water availability remain tenuous as multiple, interlocking processes are involved (van der

Molen et al., 2011). Furthermore, systematic studies on drought events are hampered by the limited frequency with which they occur at any given location.

The water-use efficiency (WUE) of plants is a central metric for understanding the mechanisms and trade-offs involved during periods of water limitation. It is defined as the ratio of carbon assimilation and water loss through transpiration, therefore

5   reflecting how liberal or sparing plants expend their bounded water resources. From a physiological perspective, limited water availability poses a dilemma for plants. If they maintained stomatal conductance, they would risk cavitation, effectively halting the translocation of sugars and nutrients (Manzoni et al., 2013; Sperry and Love, 2015). They therefore have to restrict stomatal conductance, accepting restricted carbon assimilation (Schulze, 1986) and elevated leaf-temperatures further limiting photosynthesis (Salvucci and Crafts-Brandner, 2004). This response is triggered also by the soil- and leaf-water potential, mediated

10   by the formation of abscisic acid (Davies and Zhang, 1991) and results in a relative decrease of transpiration and an increase in water-use efficiency (Schroeder et al., 2001; Anderegg et al., 2017). Intercomparison studies show that global biosphere models try to capture this effect with different model formulations, as the exact magnitudes and interactions of relevant processes remain uncertain (De Kauwe et al., 2013; Verhoef and Egea, 2014).

On leaf-scale, analytical models can accurately predict stomatal conductance and WUE based on assumptions of optimality

15   (Katul et al., 2010; Medlyn et al., 2011). For whole ecosystems and based on flux tower data, research has focussed on how water-use efficiency varies with atmospheric water vapor deficit (VPD), assuming well-watered conditions (Zhou et al., 2014, 2015). Embedded in this is the premise that the parameter uWUE, reflecting the *underlying water-use efficiency* of an ecosystem is constant in time. Ecosystem-level analyses of the effect of soil-water limitation on stomatal conductance and WUE are further complicated by the fact that atmospheric and soil droughts typically co-occur, making a separation of their respective effects

20   difficult (Knauer et al., 2015). A preceding study further demonstrated that an additional radiation term improves predicting transpiration from GPP and VPD at ecosystem-level (Boese et al., 2017). Yet these water-use efficiency models may not perform well during droughts, where water limitation is expected to alter ecosystem functioning qualitatively (Farooq et al., 2009). To assess this, dry-down events can be used as natural experiments during which the ecosystem experiences progressive soil-water depletion and thus stress. Dry-down events are periods of many consecutive dry days during which ET declines

25   approximately exponentially with time reflecting an approximate linear relationship between ET and soil moisture (Williams and Albertson, 2004; Teuling et al., 2006).

In this study we use a large global archive of flux tower observations containing 31 sites with 47 dry-down events to scrutinize water-use efficiency formulations during periods of increasing water limitation. Here, we pay particular attention to systematic biases of ET predictions that impact the predicted dry-down speed. To this end, we show how a simple parameterization based

30   on an effective water-balance-based variable helps in improving predictions under progressive drought.

2 Detection of Dry-Down Events & Structure of the Analysis

2.1 Data & preprocessing

Observations of gross primary productivity (GPP) and evapotranspiration (ET) were taken from the La Thuille (open and fair use data policy sites) and Berkeley (Tier 1 data policy sites) collections of the FLUXNET (Baldocchi et al., 2001). Further,
5 we used the global radiation (Rg), vapor pressure deficit (VPD) and precipitation (P) measured at the corresponding eddy-covariance (EC) sites. Day-time values of GPP, ET and VPD were derived by aggregating observations with potential radiation larger than 10 W m^{-2}.

The EC data were pre-processed according to the established methods to assure consistent quality of the observations. Eddy-covariance GPP values were obtained with the flux partitioning method of Reichstein et al. (2005). For our analyses,
10 we included data fulfilling a set of minimum conditions: GPP > 0.1 gC d^{-1} m^{-2}, ET > 0.05 mm d^{-1} and VPD > 0.001 kPa. This reduces the proportionally large impact of random measurement errors when the observed fluxes are low. As proposed by Beer et al. (2009), we excluded the data for days with a precipitation event and the three following days. This can reduce contributions by evaporation to the observed evapotranspiration, because physical evaporation typically decreases rapidly after rain events due to the depletion of water stored on leaves (Miralles et al., 2010) and the topsoil (Wythers et al., 1999). Thus,
15 the observed evapotranspiration after three successively rain-free days can be expected to approximate transpiration.

2.2 Dry-down event selection

Determining whether a given period should be considered to be a dry-downevent (DDE) was pivotal for our analysis. We define a dry-down event as an extended rain free period of at least 15 days which shows evidence of increasing water-limitation on ET. Water limitation on ET was detected by negative trends of ET and evaporative fraction (ET/Rn). We estimated the start
20 of a dry-down event as the point in time where daily ET was not primarily limited any more by atmospheric demand. See the supplementary materials for details.

A list of the 47 identified dry-down events detected at the 31 respective sites can be found in the supplementary materials.

2.3 Derivation of soil-water availability proxy

Empirical studies that investigate the effects of water availability on ecosystem fluxes across many sites are limited by the
25 availability of consistent estimates of soil-water data-sets. Even fine-grained measurements cannot remedy a central problem with soil-water observations, namely the quantity does not necessarily reflect the water-stress actually experienced by the plants. This is a particularly severe limitation for studies that aim to associate observed patterns in ecosystem-level fluxes with related changes in the available soil-water. The absence of rainfall in conjunction with the observed decrease of ET can offer a valuable opportunity to establish a water-balance based proxy variable in analogy to the "relative extractable water" that is
30 frequently used in ecosystem or land surface models.

The amount of water stored in the root zone depends on the mass balance of input by precipitation, output by evapotranspiration and storage changes. As we filtered for precipitation-free periods, we can assume that the amount of stored water depended solely on the output by observed evapotranspiration. During the exponential decays of dry-down events, the evapotranspiration rate of each time step is defined as a direct product of the available soil-water. At the beginning of a given dry-down event, we

5   assumed that the remaining soil-water, S_{rem}, was equal to an integral of the exponential decay of evapotranspiration:

$$S_{\mathrm{rem0}} = \int\limits_{t=0}^{\infty} \mathrm{ET}_t \tag{1}$$

where ET_t denotes the evapotranspiration predicted by a fitted exponential decay model. For each successive time step, we then subtracted the respective evapotranspiration from the prior S_{rem}:

$$S_{\mathrm{rem}t+1} = S_{\mathrm{rem}t} - \mathrm{ET}_t \tag{2}$$

10   If the ET observations had missing values, we used the ET predicted by the exponential decay model instead. Finally, we rescaled the S_{rem} from its value in mm by dividing it by S_{rem0}, yielding a variable bounded by 0 and 1.

The advantage of this water availability measure is that it can be estimated consistently for dry-down events across diverse ecosystems solely from flux tower data, and that it is constrained by the water balance. A main disadvantage is that the measure depends on the assumption that the initial ET value marks the onset of water limitation, which might not always be the case.

15   ## 2.4   Models

For our analysis, we started with the WUE model proposed by Zhou et al. (2015). This model can be inverted to yield predictions of ET, as a function of GPP and VPD:

$$\mathrm{ET}_t = \frac{\mathrm{GPP}_t \cdot \mathrm{VPD}_t^{0.5}}{\mathrm{uWUE}}, \tag{3}$$

where uWUE denotes the site-specific *underlying water-use efficiency* assumed to be constant in time. For increased clarity,
20   variables are labelled with a subscript t, indicating that they vary with time. Recently, Boese et al. (2017) found that radiation is an important driver of transpiration, independent of gross primary productivity. Therefore, we formulated an amended version of the model by Zhou et al., further referred to as "Rad":

$$\mathrm{ET}_t = \frac{\mathrm{GPP}_t \cdot \mathrm{VPD}_t^{0.5}}{\mathrm{uWUE}} + r \cdot Rg_t, \tag{4}$$

where Rg denotes incoming solar radiation and r denotes a site-specific parameter controlling the sensitivity of additional
25   ET to Rg.

Both models do not explicitly account for the limiting effect of soil-water availability on transpiration. Indirectly, however, this effect is partly contained in the GPP: With decreasing soil-water content, plants may contract their stomata to avoid water loss. This would inevitably lead to a reduction of CO2 diffusion into the leaf and subsequently an inhibition of photosynthesis. To model an *explicit* effect of the soil-water availability on transpiration, we used a stress scalar s adopted from Keenan et al.
5 (2010):

$$s = \left(\frac{S_{\mathrm{rem}_t}}{\max(S_{\mathrm{rem}_t})} \right)^q, \tag{5}$$

where q denotes a site-specific shape parameter that modifies the response of s to S_{rem}. For both the Zhou and the +Rg models the resulting evapotranspiration was then calculated as the product of the unattenuated model predictions with the attenuating factor s reflecting soil-water limitation (SWL) as

10 $$\mathrm{ET}_t = s \cdot \left(\frac{\mathrm{GPP}_t \cdot \mathrm{VPD}_t^{0.5}}{\mathrm{uWUE}} \right) \tag{6}$$

for the Zhou+SWL model and as

$$\mathrm{ET}_t = s \cdot \left(\frac{\mathrm{GPP}_t \cdot \mathrm{VPD}_t^{0.5}}{\mathrm{uWUE}} + r \cdot Rg_t \right) \tag{7}$$

for the +Rg+SWL model.

2.5 Model calibration and evaluation

15 All models were inverted against ET observations by contrasting measured with predicted values in a cost function. The parameters were estimated with a two-step algorithm to avoid local minima: First a pseudo-random search within defined bounds followed by a Levenberg-Marquardt gradient-based search (Moré, 1978). In both steps, the cost was defined by the sum of squared deviations.

We evaluated the models with multiple different metrics. A variant of the Nash-Sutcliffe model efficiency (MEF) was used
20 as the primary criterion to assess the accuracy of the predictions (Nash and Sutcliffe, 1970). It is defined as:

$$\mathrm{MEF} = 1 - \frac{\sum \left(Y_{\mathrm{prd}} - Y_{\mathrm{obs}} \right)^2}{\sum \left(Y_{\mathrm{obs}} - \overline{Y_{\mathrm{obs}}} \right)^2}, \tag{8}$$

where Y_{obs} denotes the observations of a variable Y and Y_{prd} denotes the predictions. This metric is related to the R^2, however it has the advantage that the bias of a model is integrated. To avoid that very large negative values have a disproportional impact on averages calculated across sites, we rescaled negative MEF with:

25 $$\mathrm{MEF}_{\mathrm{bounded}} = \begin{cases} \mathrm{MEF} \geq 0 : \mathrm{MEF} \\ \mathrm{MEF} < 0 : e^{2 \cdot \mathrm{MEF}} - 1 \end{cases} \tag{9}$$

which yields a $\text{MEF}_{\text{bounded}}$that exponentially approaches -1 in the negative infinite limit. In the following, we refer to $\text{MEF}_{\text{bounded}}$ as MEF for simplicity.

To assess differences of metrics between models, calibration schemes or classes of site characteristics, we used bootstrapping to derive 95% confidence intervals for the respective metric (Efron, 1979).

5   To assess the ability of the models to reproduce the over-all trends during dry-down events, we also calculated coefficients of the exponential decay (Teuling et al., 2006). We assume that a dry-down event follows an approximately exponential behavior of the form

$$\text{ET}_t = \text{ET}_{t=0} \cdot e^{-k \cdot t} \tag{10}$$

The coefficient k denotes the slope of the exponential function. If this form is assumed to be the general form for dry-
10   down events, then k reflects the rate at which ET decreases. A higher value of k would then indicate a faster rate at which ET decreases over time. This parameter can be used as an index for assessing whether water-use efficiency models correctly reproduce the rate at which ET declines during a dry-down event. For many droughts in the FLUXNET database, ET exhibits a distinctly exponential decrease indicating that availability of soil-water becomes the predominant control of the flux (Fig. 1).

2.6   Experimental design

15   Water-use efficiency models aim to represent the general coupling between transpiration and gross primary productivity. Different variants can include additional covariates such as radiation or the estimated reduction of transpiration due to scarcity of soil-water (see preceding sections). An adequate model would be expected to accurately predict water-use efficiency under widely varying environmental conditions. For periods of water-limitation the included attenuation factors are hypothesized to be sufficient to correctly reflect the successively increasing soil-water stress. However, we cannot preclude that some processes
20   are restricted to periods of sufficient water availability or that the same processes have altered sensitivities during water scarcity. To test for such dependencies, we conducted our analyses with two different calibration and two different evaluation schemes; the relevant *unstressed* (US) and *dry-down* (DD) periods are exemplarily highlighted in Fig. 1.

The main part of the analysis was conducted along two different *calibration schemes*:

1. In the first, all models were calibrated to the full record of suitable observations evapotranspiration for each site, com-
25   bining unstressed and dry-down periods. The models were then evaluated only during dry-down events. We refer to this calibration scheme as **FLcal**.

2. In the second form, the models were for each site calibrated only to periods classified as dry-down events. The evaluation was accordingly done only during these dry-down events. We refer to this calibration scheme as **DDcal**.

Similarly, the models were evaluated in two different *evaluation schemes*:

30   1. In the first, both the Zhou and +Rg model were calibrated to the full record of suitable observations of the site and evaluated for periods without water-limitation, or "unstressed". This evaluation scheme is referred to as **USevl**.
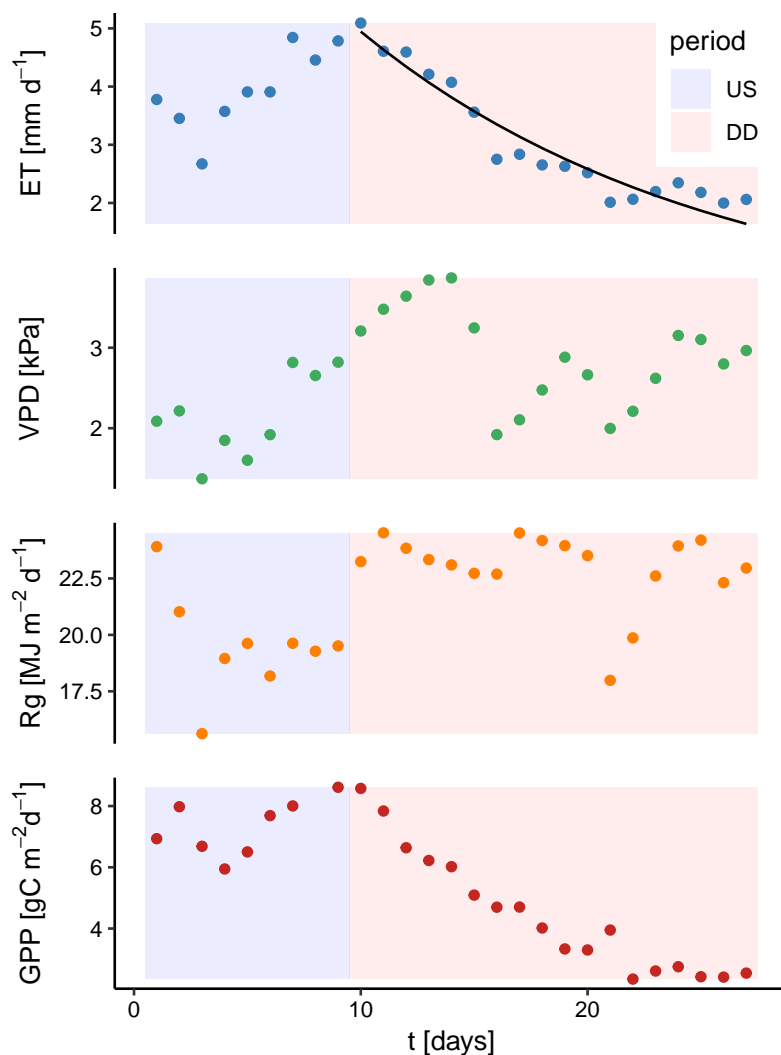
Figure 1. Temporal behavior of relevant ecosystem variables during an *unstressed* period (US) and a *dry-down* event (DD) at the FLUXNET site US-Arc. While ET and GPP show a distinct and exponential decay during the dry-down event, the variables reflecting the atmospheric demand (solar radiation, Rg and the vapor pressure deficit, VPD) remain high. The black line denotes an exponential fit to the decreasing ET.

2. The second scheme used the same parameter estimates, however, the models were now evaluated exclusively during dry-down periods. We refer to this evaluation scheme as **DDevl**.

The parameters that were calibrated in the different schemes were uWUE for all models, *r* for the variants including the additive radiation term and *q* for the +SWL model variants integrating the water availability proxy S_{rem}. To assess the vari-
5 ability of the predicted lengths of dry-down events between sites, we classified all sites according to their reported biome types into two classes reflecting vegetation height: *Short* included all FLUXNET sites with the biome types GRA (grassland) and

CRO (crops). *Tall* included all FLUXNET sites with the vegetation types EBF (evergreen broad-leaf forest), DBF (deciduous broad-leaf forest), ENF (evergreen needle-leaf forest), MF (mixed forest), WSA (woody savanna), OSH (open shrubland), CSH (closed shrubland) and SAV (savanna). Due to the preponderance of forest ecosystems vegetation in the *tall* class, our distinction can elucidate the different water-use strategies of plant types with shallower and deeper root networks (Jackson et al., 1996).

Furthermore, we also explored whether the lengths of included dry-down events depended on hydro-climatic properties of the sites. For this, we used a *water-availability index* (WAI), which is a metric derived as a simple water-balance model with one storage component (Teuling et al., 2006) driven by daily precipitation and potential evapotranspiration obtained from CRUNCEP reanalyses (Tramontana et al., 2016).

First, each site was initialized with $\mathrm{WAI} = 100\,\mathrm{mm}$ of plant-available soil-water. For each subsequent time step, the output of plant-available water from the ecosystem (w_{out_t}) was calculated as:

$$w_{\mathrm{out}_t} = \min\left(\mathrm{PET}_t, k \cdot \mathrm{WAI}_{t-1}\right), \tag{11}$$

where PET denotes the potential evapotranspiration, k denotes the maximum fraction of soil-water available for evapotranspiration without limitation of atmospheric demand. The water-availability index for each time step (WAI_t) was then calculated as:

$$\mathrm{WAI}_t = min(100, \mathrm{WAI}_{t-1} - w_{\mathrm{out}_t} + P_t), \tag{12}$$

where P_t denotes the amount of precipitation for each day.

While this index does not incorporate important site-specific characteristics of soil and vegetation, it can serve as climatic measure of water-availability that incorporates basic principles of soil-water dynamics such as memory-effects and the co-limitation of supply and demand. After deriving mean-seasonal cycles of WAI at each site, we used the interquantile difference $q(0.99) - q(0.2)$ as a measure of the *seasonal dryness* that a site typically experiences for a sufficient fraction of each year.

2.7 Fraction of radiation-associated transpiration

The augmented water-use efficiency model described in Eq. 4 can be used to partition the total predicted transpiration into diffusion- and radiation-associated transpiration due to the additive formulation. It is then possible to calculate the fraction of transpiration which was statistically associated with radiation as

$$\mathrm{ET}_{\mathrm{frac}_t} = \frac{r \cdot Rg_t}{\frac{\mathrm{GPP}_t \cdot \sqrt{\mathrm{VPD}_t}}{\mathrm{uWUE}} + r \cdot Rg_t} \tag{13}$$

where $\mathrm{ET}_{\mathrm{frac}_t}$ denotes the fraction of radiation-associated transpiration. The parameters *r* and uWUE are before estimated for the respective site.

2.8 Attenuation

Dry-down events were defined and identified by their characteristic decay of evapotranspiration. For many dry-down events, the decline of ET was accompanied with similarly exponential declines of GPP. Due to the strong remaining dependency of ET on GPP, this in itself can explain a certain share of the observed ET decline.

5 However, in this analysis we posit that an additional attenuating effect may play a role in the temporal dynamic of declining ET. To quantify the magnitude of this effect, we calculate the total fractional reduction of ET as

$$d = \frac{\sum (1-s) \mathrm{ET}_{\mathrm{rad}t}}{\sum \mathrm{ET}_{\mathrm{rad}t}} \tag{14}$$

where the denominator is the summed predicted ET without limitation factors and the numerator is the sum of daily ET reductions due to the vector s (Eq. 5).

10 As for previously introduced analyses, this metric can be calculated for the two different calibration schemes FLcal and DDcal.

3 Results

As a first test for the validity of water-use efficiency under water-limitation, we evaluated the Zhou and the +Rg model inside and outside dry-down events with a bounded Nash-Sutcliffe Model Efficiency (MEF). The calibration was conducted for each
15 site separately with all available and adequate observations, irrespective of the soil-water status (FLcal). Both models showed significantly and strongly reduced MEF when the models were evaluated during the dry-down events rather than periods without water limitation (Fig. 2). During these periods, the +Rg model still outperformed the Zhou model.

To diagnose the origin of the differences in MEF, we assessed the magnitude of the model residuals over the course of DDEs. Aggregated across all dry-down events, model residuals declined systematically with increasing drought (Fig. 3). For
20 the Zhou model, the absolute residuals were biggest at the beginning of the events. Based on the characteristic dynamic of the model residuals we surmized that the effect of soil-water limitation was not adequately represented in the two model variants. Specifically, both models tended to underestimate ET at the beginning of the dry-down events, when soil-water can be assumed to be in ample supply. Towards the end, when soil-water has become considerably more limited, the +Rg model tended to overestimate ET.

25 To address these discrepancies, we employed the soil-water proxy variable S_{rem}. Assuming that it reflects the availability of soil-water, we provided each model with a mechanism to attenuate transpiration in response to decreases in S_{rem}. Consequently, the original as well as the amended models were reassessed for the two calibration schemes (Fig. 4). Irrespective of whether model parameters were estimated based on the full time series (FLcal) or only based on dry-down event data points (DDcal), the reference Zhou model shows the lowest mean MEF when averaged over sites. Notably, however, was that for the mean MEF
30 across sites, no significant improvement resulted from adding the effect of soil-water limitation to this model (Zhou+SWL). This pattern was found in both calibration schemes. The model variants including radiation performed substantially better. For
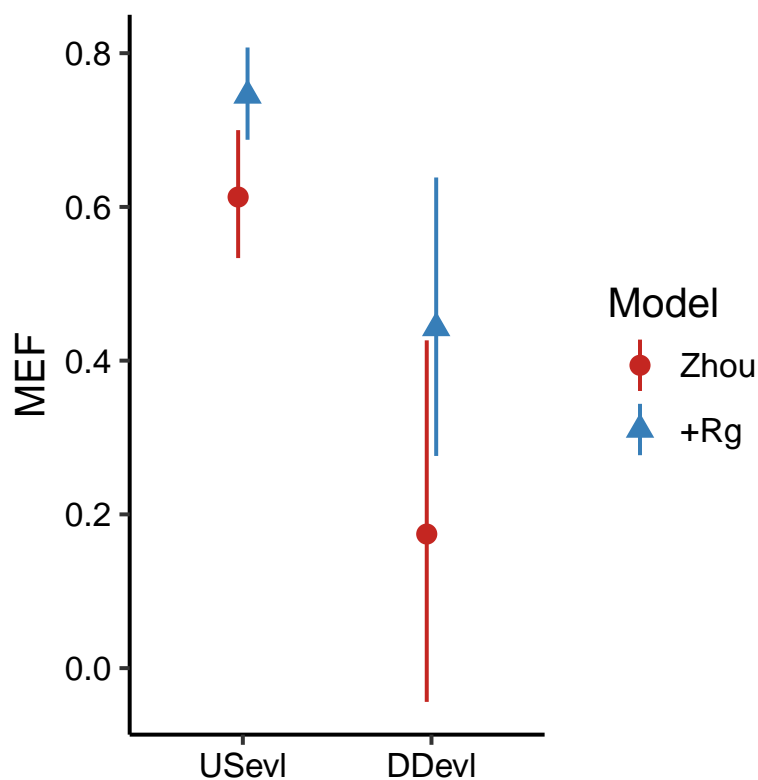
Figure 2. Model-efficiency of the Zhou and +Rg models when evaluated inside (DDevl) and outside (USevl, see *Methods / Experimental design*) water-limited dry-down events. The models were calibrated for all adequate site-observations (FLcal). The points indicate the mean MEF over all sites; the error-bars indicate the bootstrapped 95%-confidence-intervals of the mean across sites. Both models showed a significantly reduced performance when evaluated during dry-down events. Despite this, the +Rg model yielded superior performance even during these periods.

the +Rg variant, including the effect of soil-water limitation paid off with a substantially increased mean MEF. All models had relatively higher MEF when calibrated to the dry-down events rather than the full set of adequate observations for each site. This indicates that neither of the models could provide an unbiased representation of all adequate observations. The relative ranking of the models was however identical for both calibration schemes. The results indicate that only the combination of radiation and soil-water limitation provided the best predictions of ET during dry-down events.

The coefficient k quantifies the rate of the exponential decay during the dry-downs. Small values indicated a slow decay of evapotranspiration with time. Motivated by the findings of the change in MEF, we contrasted the k values calculated from the observed ET with those of the ET that the models predicted (Fig. 5). The Zhou yielded more accurate decay rates k when the effect of soil-water limitation was explicitly accounted for. For both variants, k values were unbiased when compared to estimates derived from the observations. By contrast, the +Rg model underestimated k significantly, implying that the predicted
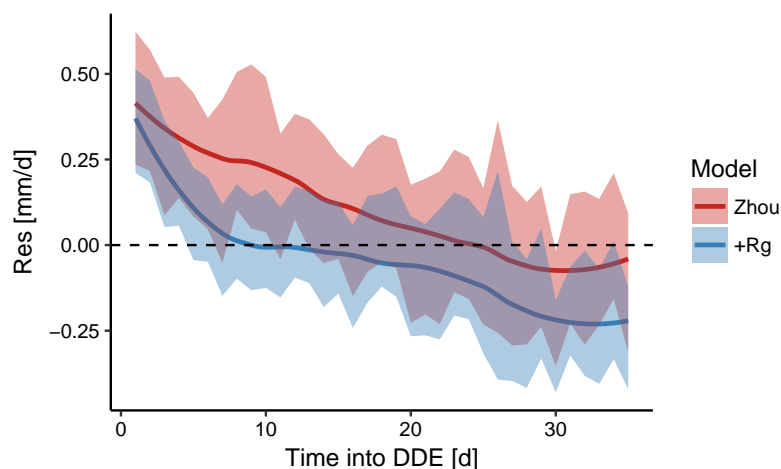
Figure 3. Mean model residuals across all dry-down events for the Zhou and +Rg model as a function of time during dry-down events. The shaded area reflects the 95%-confidence-intervals. Both models tended to underestimate ET near the beginning of the dry-down event while overestimating the flux with increasing length of the event. The former was more pronounced for the Zhou model, the latter more pronounced for the +Rg model.
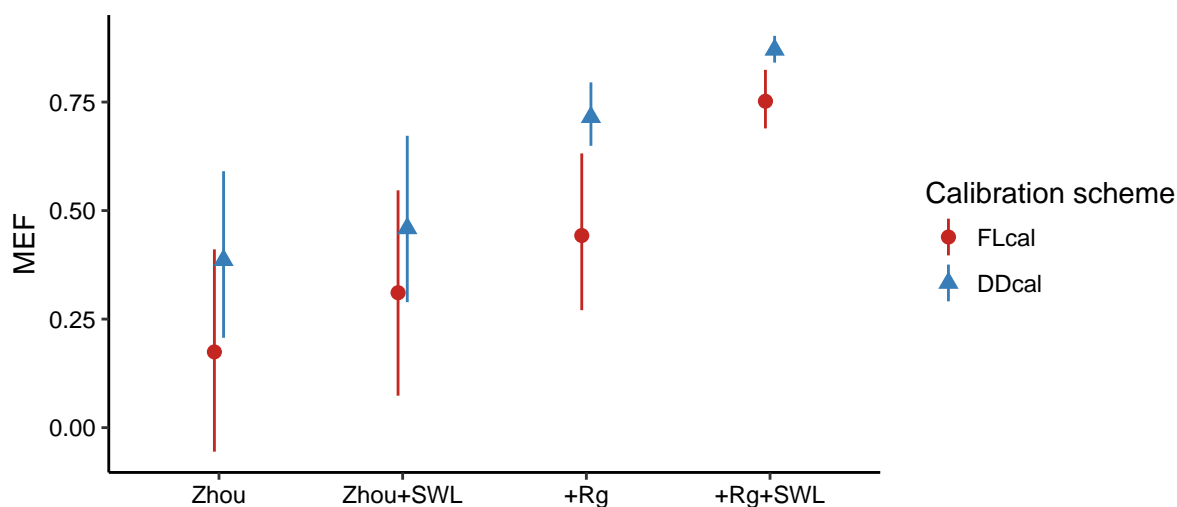

Figure 4. Model performance of the two original models and their amended variants which include an attenuation function reflecting soil-water availability. The models were evaluated during dry-down events, once after calibration to all adequate data records of the sites, and once after calibration only to dry-down events. Compared to the +Rg model, the Zhou model did not benefit significantly across sites from an addition of the attenuating function, even when calibrated specifically to dry-down events. By contrast, the +Rg model improved substantially, when the addition was made. This effect was true for both calibration schemes.

11

Figure 5. Observed plotted against predicted values of the decay-coefficient k (Eq. 10) for the four model variants in the full calibration (FLcal). Points represent individual dry-down events, for which a linear fit with confidence intervals is shown in red; the one-to-one line is dashed. For both the Zhou and the +Rg model, adding the attenuating effect of soil-water limitation (+SWL) improved the accuracy of derived k values. The +Rg model underestimated effective k values; this bias was mitigated with the addition of the +SWL term. Three outlying events for which k deviated exceedingly from the other events were removed.

Figure 6. The difference between observations and predictions (residuals) of the +Rg and +Rg+SWL variants as a function of S_{rem} evaluated for the two calibration schemes. The lines denote the mean response across all sites, derived with local polynomial regressions, while the shaded area denotes the uncertainty of the regressions. The residuals of the +Rg model showed a strong dependency on S_{rem} in both cases. The +Rg+SWL had unbiased residuals for intermediate to low S_{rem} conditions, however, smaller biases toward the beginning of the dry-down event were only mitigated when the model was calibrated exclusively to dry-down events (DDcal).

ET didn't decline fast enough while the dry-down events were continuing. However, once the effect of soil-water limitation was included in the +Rg+SWL was included, the k estimates were comparatively accurate and unbiased.

Further, we tested whether the residuals of the models during dry-down events still depended on our effective soil-water proxy S_{rem}. The remaining dependency differed notably for the two calibration schemes (Fig. 6). When the models were
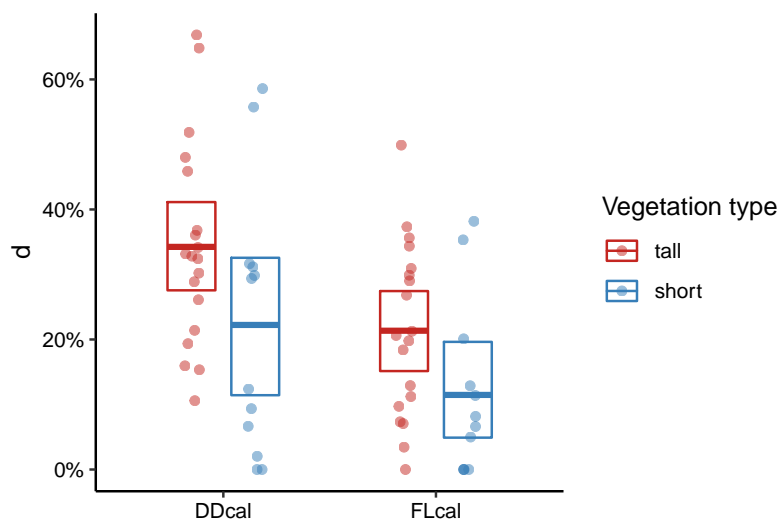
Figure 7. Fraction of relative ET reduction during dry-down events (d). The points represent the values for individual sites, the bold bar denotes the mean value of all sites, the box represents the bootstrapped 95%-confidence-interval. The relative attenuation d (Eq. 14) differed significantly between the two calibration schemes FLcal and DDcal. Notably, sites classified to have tall vegetation had significantly higher values of d. The mean of d was 20% across all sites for FLcal and 33% for DDcal. There was substantial between-site variability of d for both calibrations and vegetation types.

calibrated to the full data record of each site (FLcal), the +Rg model showed a strong relationship between the model residuals and S_{rem}. This dependency was decreased once the effect of soil-water limitation was included (+Rg+SWL). However, even for this variant, ET was systematically underestimated during the initial stages of the dry-down events if the model was calibrated to the observation outside and inside dry-down events (FLcal). By contrast, when the model were calibrated exclusively to

5   dry-down events, the +Rg+SWL did not exhibit systematic errors as a function of S_{rem}.

We further used the +Rg+SWL model variant to evaluate the relative reduction (d) of ET during dry-down events due to the introduced attenuation factor included in this model. This analysis was carried out for the two calibration schemes FLcal and DDcal, while stratifying the results along the vegetation type (Fig. 7). The magnitude of the relative attenuation depended significantly on the calibration scheme. The relative attenuation was higher (mean: 33%) when the models had been calibrated

10   to the dry-down events (DDcal) compared to when they had been calibrated to all site-observations in the FLcal scheme (mean: 20%). In both cases, sites with tall vegetation had significantly higher relative attenuation of ET compared to sites with short vegetation. However, for both calibrations and vegetation types, there was substantial variability between the different sites.

Boese et al. (2017) proposed a tentative attribution of transpiration to the stomatal conductance and radiation. Here, we analyzed how the fraction of radiation-attributed transpiration (ET_{frac}) changed as a function of the soil-water availability. The

15   daily ET_{frac} values for all included site varied widely along the observed S_{rem} (Fig. 8). Despite the strong variability between
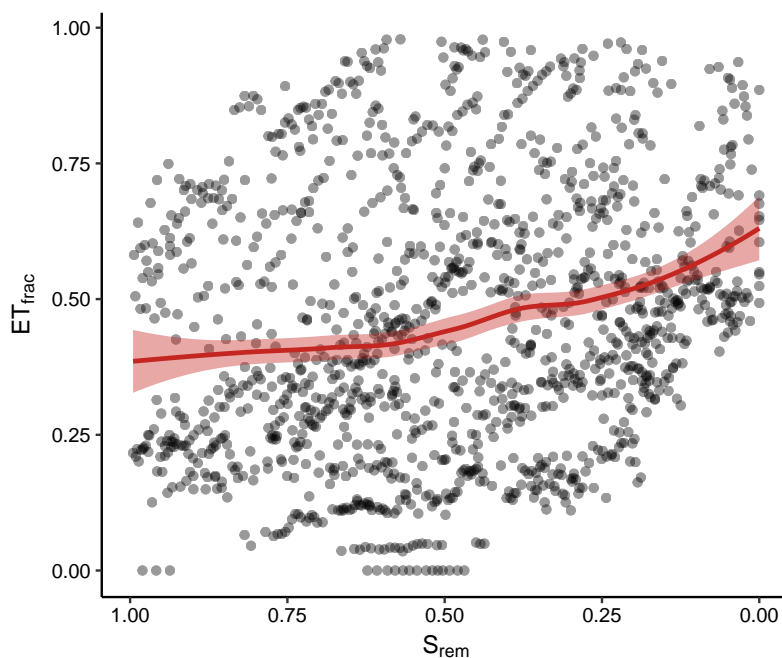
Figure 8. Fraction of radiation-associated evapotranspiration (ET_{frac}) as a function of S_{rem}. Points represent daily values for all dry-down events, the red line is the mean response for all events derived with local polynomial regression (shaded area reflects the uncertainty of the fit). This metric varied widely between sites and S_{rem} conditions. However, a significant trend with higher values for low S_{rem} conditions was visible.

the sites, the mean ET_{frac} showed a significant association with S_{rem}; ET_{frac} was significantly higher for observations with low S_{rem}.

The estimated decay-coefficient k reflects the rate of the exponential ET decline during the dry-down events. We found that k was significantly higher for dry-down events in sites with low vegetation, compared to high vegetation (Fig. 9), meaning that sites with low vegetation had faster decays of ET during periods of water limitation. However, there was substantial variability between the individual sites. Further, we noted a significant, negative correlation of k with the amplitude of the seasonal dryness across sites with tall vegetation, yet not those with short vegetation (Fig. 10).

4 Discussion

4.1 Findings

In this analysis, we showed empirically that water-use efficiency changes during progressive drought are associated with the interaction of radiation and soil-water availability. Merely including the effect of soil-water limitation in a water-use efficiency model without the radiation effect did not improve predictions substantially. This finding was consistent across the calibra-
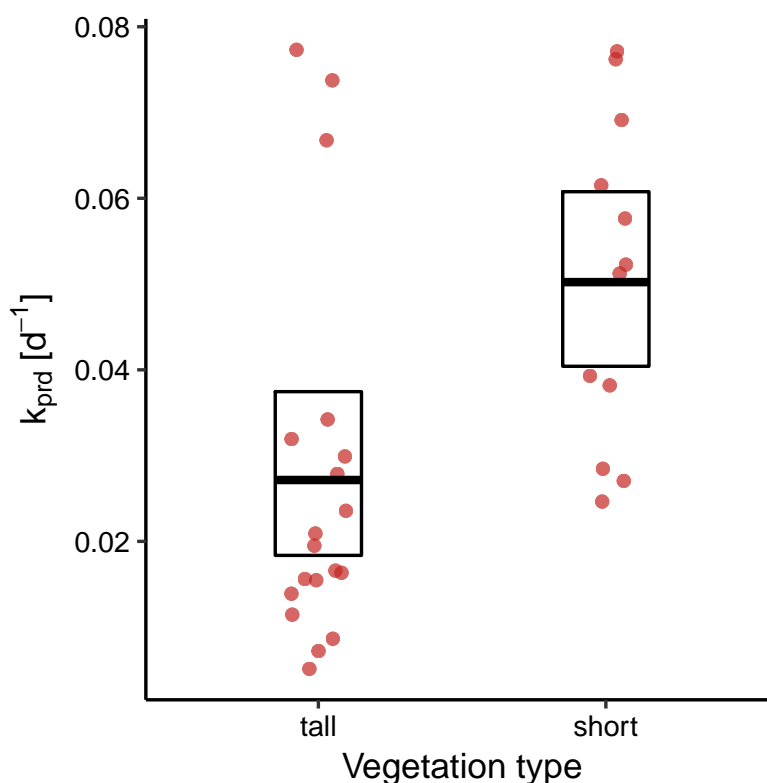
Figure 9. Between-site distributions of the predicted decay-rate k stratified along the vegetation type; the points represent individual sites, the bold line denotes the mean across sites, the box represents the bootstrapped 95%-confidence-interval. Notably, low vegetation sites had significantly higher values of k, indicating faster ET declines during dry-down events when compared to sites with high vegetation.

tion schemes used, as the Zhou+SWL variant showed no significantly higher average model-efficiency across sites for either calibration, when compared to the Zhou variant. By its added effect of soil-water limitation, the +SWL-variant can represent changes in uWUE that occur due to increasing water stress. Our results suggest that such changes were insuffcient to lead to significantly improved predictions of transpiration, adding to the finding of a study noting no increase in uWUE for a drought

5   event in evergreen needle-leaf forest (Gao et al., 2017). In contrast to the model without the radiation term, explicitly including soil-water limitation in the +Rg model lead to a significant and substantial improvement of the model performance. This further demonstrates that radiation is required as an important variable for predicting transpiration from GPP and VPD even during water-limited periods, extending the prior analysis that did not explicitly focus on water-limited periods (Boese et al., 2017).

     Importantly, established water-use efficiency models assume that the product $GPP \cdot \sqrt{VPD}$ can adequately predict tran-

10   spiration. Our analysis suggests an ecosystem scale soil-water availability effect on WUE that is statistically independent from VPD effects on the contraction of stomata. With magnitudes of 20–33% relative ET reduction, its effect was important to predict the rate of ET decline during dry-down events. The presence of the VPD-independent decline underlines the significance
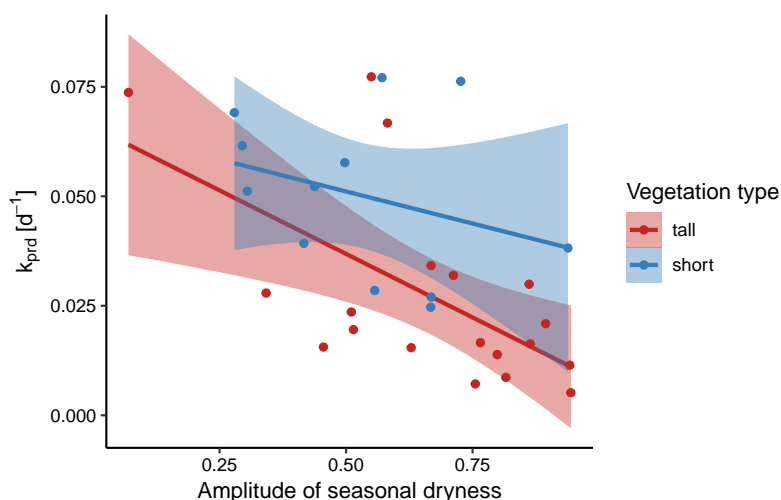
Figure 10. The decay-rate k correlated significantly with the mean amplitude of seasonal dryness across sites ($p < 0.001$, $R^2 = 0.33$). This correlation differed substantially between tall ($p = 0.007$, $R^2 = 0.36$) and short ($p = 0.33$, $R^2 = 0.1$) vegetation types.

of soil-water limitation for ecosystem water-use efficiency during drought. Importantly, the magnitudes of the observed atten-
uation was siginificantly higher in tall, compared to short vegetation types, indicating that the possibly hydraulic regulation of
transpiration during dry-down events is more prominent for these ecosystems.

Further, the rate of the exponential ET decline differed significantly between short and tall vegetation types, where short
5   vegetation had on average faster declines of ET, consistent with the observations by Teuling et al. (2006). The associated
vegetation types, e.g. grasslands and croplands, tend to be dominated by annual plants with shallower root networks (Jack-
son et al., 1996). These plants could favor fast, relatively unabated transpiration while competing for a quickly diminishing
resource. Conversely, tree species dominating the high vegetation sites have deeper root-networks and would be more circum-
spect in their water-use to avoid the risk of cavitation which would jeopardize their survival and seed production (McDowell
10 et al., 2008). Similar contrasts of the evapotranspiration response to drought between trees and grasses have been observed for
ecosystems were the two plant types co-occur (Baldocchi et al., 2004).

We also observed that the two calibration schemes had an important impact on model performance. For the calibration to
dry-down events, the model parameters were optimized to represent the time course of (evapo)transpiration during those events
and did not need to accommodate observations during times without water-limitation. However, the performance of the +Rg
15 and +Rg+SWL models differed significantly between the two calibration schemes, indicating that systematic problems persist.
Ideally, the best model should yield a full representation of the respective observations, without requiring specific calibrations
to account for a subset of the data (Yapo et al., 1996).

Furthermore, we detected a significant correlation between the decay-rate of ET during dry-down events and the mean
amplitude of seasonal dryness. Sites experiencing stronger amplitudes of seasonal dryness had lower decay-rates, while the
20 opposite was true for sites with low seasonal dryness variability. Our findings are consistent with the expectation that sites with

highly variability in the plant-available water during the growing season have developed adaptations that prevent excessive water stress (Schwinning and Ehleringer, 2001), further replicating Teuling et al. (2006). One likely adaptation in seasonally dry biomes are deeper root networks that allow for sufficient water supply and can potentially tap ground water (Kleidon and Heimann, 1998; Fan et al., 2017). By contrast, ecosystems with low variability of plant-available water have little such

5   adaptations, which are costly from a plant-economical perspective.

The presented results further imply that at ecosystem scale radiation-associated transpiration (Boese et al., 2017) remains an important process for water-use efficiency models during dry-down events. In fact, we found that the relative share of radiation-associated transpiration increased significantly over the course of dry-down events. Stomatal conductance was responsible for the majority of ET decline during dry-down events, as indicated by a marked decline of GPP during these periods. Toward

10   the later stages of a dry-down event, transpiration was therefore dominated by the part that was not reducible by stomatal regulation.

4.2   Uncertainties

Despite its demonstrated utility, the new soil-water proxy is also a source of uncertainty in this analysis. The S_{rem} variable is contingent on the assumption that the decay of ET during dry-down events can be approximated with an exponential function

15   to allow for easy integration. This corresponds to a simple water-balance model with one storage compartment, therefore neglecting both lateral and vertical flow components such as interactions with ground water. Since flux tower observations are largely confined to flat terrain, lateral water fluxes can be possibly neglected here. Potential interactions with ground water may play a role for some sites which would bias the S_{rem} values low. Deviations of observed ET decline from a truly exponential decay are likely not critical because it would only affect the normalized S_{rem} to some extent but not its general temporal

20   dynamics. Due to its character as an effective, ecosystem-scale variable, it integrates various factors affecting the availability of soil-water to plants. This includes biological factors, such as rooting patterns and root-water uptake dynamics, and physical factors, such as soil texture. Comparisons of the dry-down behavior for this variable would therefore need to account for soil properties by using measurements of grain-size distributions if ecological patterns are the focus of the respective analyses.

Overall, the results of this study are constrained by the sample size of adequate dry-down events in the FLUXNET data

25   base. Compared to studies that can utilize a large subset of observations, our analyses had to be restricted to events occurring infrequently and only at a small subset of sites in the data base. Despite the comparatively small sample size of dry-down events, the bootstrapped confidence intervals indicate that the patterns were robust for the available sample. Considerable potential lies in analyses of the between-site variability of parameters, which could be extended and be made more robust with more events from a larger set of ecosystems. Our analysis therefore highlights the need for more eddy-covariance measurement sites in

30   semiarid regions, which are particularly vulnerable to climate change and present a challenge for our current understanding of the interaction of the carbon and water cycle.

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4.3 Implications & outlook

We could demonstrate that a recursively derived proxy for soil-water limitation could be used to detect and mitigate systematic, structural deficiencies in commonly used semi-empirical water-use efficiency models at ecosystem scale. This variable neither requires soil-water observations that are consistent between multiple sampling locations nor questionable assumptions about

5   root-water uptake and is derived directly on the ecosystem-scale of interest. This is in contrast to in-situ measurements of soil-moisture which are subject to local heterogeneity and therefore require a potentially problematic upscaling from individual sample locations to the flux footprint of the eddy-covariance tower. More research is required to evaluate the utility of this variable for similar ecosystem-level studies. Its validity could be further tested by contrasting it with temporal profile measurements of soil-moisture, where the individual depths are weighted by the root density or other measures of root water uptake. By

10 its effective character, this proxy variable could see application for research on other ecological or biogeochemical questions that require measures of soil-water availability which are commensurable across different FLUXNET sites and between events.

The findings of this study indicate that previously developed ecosystem-level water-use efficiency models are biased during water-limitation if they lack the interacting effect of radiation and soil-water limitation. We thus provide evidence that soil-moisture stress has a notable effect on the coupling of carbon and water fluxes. The findings have consequences for semi-

15 empirical models that link GPP and ET on regional and global scales or when these models are used for the partitioning of latent heat fluxes into evaporation and transpiration. Partitioning estimates for these models could be systematically biased if the interacting effects of radiation and water-limitation are neglected. Our findings also suggest that attenuating effects of soil-water availability should be carefully examined in biosphere and land-surface models, because accurate predictions of ET decline during water-limitation are pivotal to understand stress-induced vegetation responses during long droughts. Further research

20 should address whether the observed attenuation effect is of physical or biological nature, which has important implications for understanding plant water-use strategies at ecosystem scale.

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