

Author's Response

The manuscript for our submitted paper *Carbon-Water Coupling Under Progressive Drought* has been revised in accordance to the feedback we received from the three reviewers.

The main points of criticism we addressed were:

1. The semi-empirical nature of this study, which requires site-specific, calibrated parameters and the resulting advantages and drawbacks;
2. The stratification of the sampled sites along vegetation types and how informative such an aggregated classification can be to clarify the importance of different processes;
3. Whether and how the proposed soil-water proxy variable *Srem* can represent antecedent water-stress conditions in the ecosystem;
4. The attribution of observed patterns in ecosystem-level fluxes to underlying processes and candidate explanations.

In addition, we have considered and integrated valuable feedback regarding the clarity and presupposed knowledge. We have added Figures depicting the dependence of water-use efficiency on the proposed soil-water proxy variable *Srem* and have further added plots showing the temporal behavior of observed vs. predicted ET in the supplement. The supplement now also contains an additional table documenting estimated parameters as well as site properties. The table listing the individual dry-down events has been amended with the regression parameters used in the detection the events. Figure 8 showing the dependency of model residuals to *Srem* has been omitted from the revised manuscript as we felt that it did not make a significant contribution to our argument.

We are happy that the updated manuscript could be improved thanks to the feedback we received from the three reviewers.

Amended and changed parts have been highlighted in green in the manuscript below.

Sven Boese on behalf of the authors

Replies to the Reviewers

Reply to Review 1

The original reply including additional figures can be found under:

<https://doi.org/10.5194/bg-2018-474-AC1>

We thank Martin deKauwe for his valuable feedback on the submitted manuscript. Below, we address general remarks and important specific remarks that required a response and describe how we incorporate these in the revised manuscript. In addition we carefully considered all specific comments related to spelling, clarity and references and integrated them into the revised manuscript where appropriate.

General remarks

- “In particular, I was hoping to learn about differences in dry- down as a function of vegetation types, hydro-climate, frequency of droughts, etc?”.

This point raises an important issue. We also considered a more granular analysis of underlying site-properties that could potentially explain the observed variability of obtained metrics. However, the limited sample size of this study did not allow for detailed stratifications of the data set.

Nevertheless, in the revised manuscript, we provide a better presentation of how the results can be disentangled according to climate and vegetation types. To account for the small sample size, we now aggregated multiple climate types (tropical, mediterranean, temperate-humid) and vegetation types (short with grasslands and crops, mixed with savannas and tall for forests). However, we agree that it would be ideal to ultimately link the observed patterns to the physical properties of the plants rather than ecosystem-scale proxy variables. This is an important point that is now stressed in the discussion.

- “We also explored [...] hydro-climatic properties of the sites’ and I don’t really see where they’ve done this?”

We agree that the previous wording failed to connect this statement to results presented later in the manuscript. Specifically, we referred to the mean seasonal WAI amplitude as indicator for regularly occurring water-limitation. We have clarified the manuscript accordingly.

- “Finally, I’m not clear why the authors only focus on ET? The paper frames the question around WUE and so they should also look at the evolution of GPP during a dry-down, shouldn’t they? They could easily argue that GPP isn’t directly observed and that is fine, but then I think changing the framing more clearly towards ET only, including removing ”carbon“ from the title, is warranted.”

We agree that the previous version of the manuscript failed to convey a central part of how our analysis was conceived. As also remarked by Reviewers 2 & 3, there is a discrepancy between the stated goal of examining carbon–water coupling via water-use efficiency models and the fact that most of the analysis take transpiration as the target variable. Here, we do not assume that the measured gross primary productivity exhibits any less observational and processing uncertainties. In brief, using $ET = f(GPP, x)$ instead of $WUE = f(x)$ is merely a reformulation that focusses on how different WUE models affect the flux magnitudes of ET rather than the ratio $WUE = GPP / ET$. In the latter approach, small GPP and even smaller ET values can lead to very high WUE values and can in a least-squares regression bias the analysis towards time periods that should not receive as much weight. We have thus added an appropriate paragraph to the introduction.

- “The authors propose the need for two additional corrections, one related to radiation and the other soil water availability. I’ve commented on this below, it feels unnecessary (mechanistically) and a form of an artificial correction, but I’m happy to be corrected on this and keen to read a more thorough justification.”

This comment engages a critical part of our analysis. For our level of analysis, we used a semi-empirical approach, the definition of which we also have explain more prominently in the revised manuscript. The approach is then primarily guided by empirical criteria such as goodness-of-fit measures, while aiming at effective model structures that can be related to physical processes at aggregated scales. In previous work, this approach was used by Boese et al. (2017) to identify a previously neglected driving effect of radiation on transpiration. As we also lay out in Fig. 1, the radiation-effect itself is beneficial to model performance both outside and inside dry-down events.

Yet its inclusion exacerbates systematic model errors (Fig. 2), which in turn require correction. The chosen approach is thus primarily motivated by empirical performance of the models. Yet while we succeeded in remediating the model performance during dry-down events, the link to responsible mechanisms does indeed remain tenuous. In the revised manuscript, we discuss this problem in more depth.

- “A number of studies [...] have highlighted the need for a non-stomatal correction to GPP (which indirectly affects ET) in order to correctly capture observed responses. This isn’t commented on here, but I note that the authors seem to be arguing the opposite, that is, there is a need for a more direct correction on ET but that GPP is fine.”

This is a valuable idea to discuss. In the previous version of the manuscript, we did not assume any non-stomatal limitations of GPP during water-limitation. It is nevertheless important to consider to which degree our analysis, if implicitly, addressed this point. The model Zhou+SWL predicts ET as a function of both GPP and soil-water limitation. In our conceptualization, the +SWL term serves as a corrective for non-stomatal limitations of ET. Yet it would also be possible to see the term as correcting for any difference in how soil-water limitation affects ET vs. GPP. Nevertheless, this is an important complication that deserves more attention in the discussion.

- “I really think it is important that the authors document all their fitted terms, e.g. the terms in the supplementary, otherwise this study isn’t reproducible.”

Agreed. We added the values of the optimized parameters as table in the supplement.

- “What role does LAI, or more specifically, leaf turnover play in the modelling done here? Is it possible that some events see leaf area adjustments which could impact on ET fluxes?”

We agree that changes of LAI have been neglected until now. Especially for dry-down events in vegetation adapted to humid conditions, decreasing LAI due to drought stress has been observed (Anderson et al. 2015). For our purpose, we would expect any negative change in LAI to both affect ET and

GPP negatively, as both fluxes depend on the effective surface area at which carbon uptake and water loss happen. It thus seems probable that changes in LAI would not manifest in changing WUE during drought.

SPECIFIC COMMENTS AND CRITICISM

Abstract

- “As written, I feel like it requires a fair amount of prior insight to follow [...]”

We edited the abstract to be more informative and easy to understand for readers unfamiliar with our approach.

Introduction

- Pg 1, line 20: it would be nice (but optional) to have a few physiological citations alongside the point about GPP decline with water limitations.

We have added appropriate citations at the respective location.

- Pg 2, line 18: the text about atmospheric and soil droughts co-occurring ... It reads as if there is an alternative? Surely, as far as the vegetation is concerned these two will always co-occur? If there is plenty of soil water, then even if there is a precipitation drought, it is not a drought for the vegetation. Am I missing something? I assume the point that is being made here is for the need to separate out the response to VPD vs the response to soil water. I think this could be more clearly articulated here.

This was indeed the point and we have clarified the text accordingly.

Methods

- Pg 3, line 24 onwards: this text isn't clear enough - “namely the quantity does not necessarily reflect the water-stress actually experienced by the plants” - what specifically do the authors mean? Do they mean because these data are usually of limited depth, so do not fully reflect the root-zone?

Thank you for pointing this out. Yes, partially because of differences between rooting-depth and the depth of soil-water measurements. But also because the soil-water contents at specific depths would need to be weighted with the root water uptake which can differ substantially based on root architecture and physiology (Schneider et al. 2010).

- Pg 4, Eqn 1: What about groundwater? This deserves some mention here, if only to highlight it in the assumptions made.

This is correct, we now state that we make the assumption that this does not include groundwater access.

- Pg 4, line 20: Again ... the text about the Boese study and radiation requires further explanation. I suggest it is done once and then it could be referred to as done here. I need to read this paper, but my initial reaction is to query the statement. Why is radiation an important driver of transpiration, independent of GPP? And why R_g and not net radiation? This feels like a form of double counting here (radiation via PAR is a driver of GPP and R_{net} is a driver of ET)? Clarifying this in the text would be worthwhile for the reader.

We agree that the manuscript assumed too much knowledge regarding the study of Boese et al. (2017). In that study, the authors identified that an additional radiation term was necessary to predict ET from GPP and VPD at the ecosystem-scale. Similar to the present study, this finding was thus an empirical one, justified by the performance of the models at multiple sites in cross-validation. Yet this finding can be connected to the theory of Jarvis and McNaughton (1986), in which one part of transpiration is driven by the gradient (imposed transpiration, in our case $GPP \cdot VPD^{0.5}$) and the other is driven by the radiative energy input (equilibrium transpiration, in our case $r^* R_g$). While preparing the analysis of the impact of radiation on WUE, we also considered R_{net} . As the model performance was slightly higher for R_g and as both variables are temporally very strongly correlated for each particular site, we used R_g in that study. However, this is merely one possible explanation discussed in the preceding publication for what is an empirical pattern. We acknowledge that this needs to be clarified for readers not familiar with that work.

- On a related point - what about evidence of the need for a non-stomatal limitation of photosynthesis during drought? How do the authors suggest

this factors into their analysis?

We addressed the closely related point regarding non-stomatal limitations of GPP above in the section “General Remarks”.

- Pg 5, Line 1 onwards: “Both models”?? I assume the authors mean eqn 3 and 4? It isn’t clear. I don’t follow this text - the soil water availability would also have an effect on ET, the reduction in stomatal conductance due to drought would lead to reduced ET. The text as written makes it appear that this only affects GPP. They then propose an empirical correction on transpiration for declining soil water. I fail to see why this is necessary? The ET quantity reflects the soil water availability? I find this quite worrisome, as above with the R_g , this feels like a double correction that isn’t warranted mechanistically.

We agree that the paragraph is unclear and can be misunderstood. In fact, we just wanted to state that while the models of eq. 3 & 4 (clarified in the revised version) do not contain an explicit variable for soil-water limitation, one can assume that any decrease of stomatal conductance would lead to reductions in GPP. As ET is here predicted from the variables on the right-hand side, any reduction of GPP induced by water-limitation would entail reductions in ET. The mentioned reductions introduced with the +SWL variants are necessary as Fig. 2 and especially Fig. 3 suggest that models with constant $uWUE$ and r parameters fail to predict ET accurately over the course of dry-down events. More mechanistically, the introduction of the s factor in eq. 6 could be seen as fulfilling a function similar to g_1 attenuation of stomatal conductance models in response to water-limitation.

- Pg 5, eqn 5: where is q given by site? It needs to be shown to the reader.

This has been added to the supplement together with the other fitted parameters.

- “Short” vs “Tall” feels a pretty vague distinction. I think the tall category would have considerable variability and it would be more interesting to consider the results in the context of the actual heights rather than this arbitrary binary classification. I am aware that it is difficult to obtain these kinds of site characteristics, so the authors do not need to do this; however, I think it would be more interesting if they could.

In the updated version of the manuscript, we added a third category, “mixed”, for savannah type ecosystems. This admittedly only partially resolves the problem that vegetation types are only crude proxies for the actual height of plants in ecosystems (which in turn can vary substantially for any given site). However, we also clarify that the stratification can reflect – through predominating growth forms – both differences in water-use strategies and rooting depths. Yet it has to be stated that these categories are at best imperfect proxies for variables that as of now are not at all or not consistently measured.

- Pg 8, Eqn 11: how does k vary between sites?

We apologize for the omission. For this analysis, we fixed k at 0.05 which is a reasonable expectation on a global scale (Teuling et al. 2006, also added the appropriate citation in the manuscript).

- How sensitive are the results from eqn 11 to the assumption of a WAI of 100 mm?

To address this point, we reran the analysis with three different values of WAI_max (as now referred to in the manuscript): 70, 100 and 130 mm. The corresponding plots with labels of the IGBP vegetation classes are attached below. The results suggest that there is indeed some sensitivity of our results, yet all levels show a significant correlation between k and the seasonal amplitude of dryness (higher correlation for lower WAI_max).

Results

- does figure 2 need to be a figure? It strikes me that it could as easily be a table? It might be then preferable to give an example of a time-series between each model evaluation?

We think that Fig. 2 is useful as it visually represents the fundamental motivation of the study: Namely that both the Zhou and +Rg models fail to predict accurately during periods of water-limitation. However, we agree that the importance of this discrepancy has not been properly addressed in the manuscript itself. We would prefer this as a figure, as the variability inside the groups (95% CI intervals) can not be easily rendered in text. We further concur that time-series can be helpful to understand the model errors. While Fig. 3 averages the time-series of multiple sites, we added instructive examples of individual sites in the supplement.

- Pg 10, line 10: This point about the ET not declining fast enough, would fit with the narrative I presented earlier of the need for a non-stomatal limitation on GPP, which would also reduce g_s and so ET. Of course this wouldn't work for this kind of empirical model. The correction (SWL) could be seen as effectively doing this, although I don't follow the justification for this approach.

This is an interesting point. In our model, the attenuating factor s could be seen as reflecting possible – process-agnostic – differences in the drought-sensitivity of GPP vs. ET. If, for example, GPP is additionally limited by non-stomatal factors during water-limitation, our model would be expected to underpredict ET (which is still mostly limited by stomatal conductance). If the +Rg+SWL model instead overestimates ET for longer events – while observed ET declines faster – it suggests that ET is more limited by non-stomatal factors when compared to GPP. It is however important to stress in the discussion that due to the empirical nature of the approach, observed patterns can only be tenuously be mapped back to particular processes.

- The interpretation of figure 8 seems a bit optimistic and at the very least should be justified (“significant association”) with statistics.

Agreed. We referred to the confidence interval of the local polynomial regression used for smoothing. However, the same statement can be better supported with a linear model, which we use in the updated version of the manuscript.

- Figure 9 ... the difference in k is presented in terms of the “height” of the vegetation, whereas in my eyes it could as easily be interpreted as related to rooting depth and/or leaf area. I'd suggest that height as an explanatory of the difference in dry-down doesn't really have a mechanistic interpretation. At the very least the authors should outline what they think it is a proxy for, or state more clearly how height impacts on the rate of dry-down? Are they hypothesising it is via differences in roughness length?

The tall/short distinction can indeed be seen as an approximate indicator for both water-use strategies and mean rooting depths (see longer response above). We did not consider the distinction to be mediated by differences in roughness length.

Discussion

- Pg 15, Line 10: “Our analysis suggests an ecosystem scale soil- water availability effect on WUE that is statistically independent from VPD effects on the contraction of stomata” - This is a big claim, where is this supported in the data, it would be really helpful to link this to the results. Furthermore, the authors need to unpick this further. If it is independent of the response of g_s to VPD, can they discuss the mechanisms they are invoking, presumably via the soil water. Why would it be invariant across ecosystems? This would argue against much of the emerging plant hydraulics literature, surely? Or have I simply misunderstood? I actually see they then link this to a hydraulic limitation related to height - which begs the need to be far more detailed in this analysis. In my eyes it is not sufficient to arbitrarily split the vegetation into small and tall and then to invoke a hydraulic explanation. The tall category could conceivably include a range of heights, do the authors know for certain it is largely made up of very tall trees? I am concerned this is pretty speculative to be honest.

This is a critical part of our discussion and we agree this needs to be discussed more carefully and linked better to the results. The statistical VPD-independence is connected to the observation that the Zhou-Model on its own cannot accurately predict the ET decline during dry-down events. This model integrates the mentioned effect of VPD on stomatal conductance (Zhou et al. 2015). As we demonstrate, this alone proves insufficient to explain ET decline during dry-down events (Fig. 2, 4). Yet even integrating the effect of soil-water limitation (Zhou+SWL) on $uWUE$ (which is inversely proportional to g_1) did not provide substantial benefits to model performance (Fig. 4). Instead the complete reduction of stomatal and non-stomatal ($r * R_g$) transpiration components (+ R_g +SWL) provided the highest performance of predicted ET. As the attenuating factor s is not exclusively reducing stomatal conductance in this model, it could be interpreted as sign of a process affecting both source of transpiration. A reduced stem hydraulic conductivity during water-limitation (Ladjal et al. 2005), could be responsible for this generalized decrease of transpiration. Nevertheless, our empirical approach at ecosystem-scale makes it difficult to pinpoint the mechanism responsible for the observed effects. In the discussion, we now make this clear and further highlight the importance of following up on the results with mechanistic studies in controlled settings.

Importantly, the reduction effect is certainly not invariant across ecosystems. As we show in Fig. 7, the effective reduction of ET varies notably between different ecosystems.

Additional References

Anderson, M. C., Zolin, C. A., Hain, C. R., Semmens, K., Yilmaz, M. T., & Gao, F. (2015). Comparison of satellite-derived LAI and precipitation anomalies over Brazil with a thermal infrared-based Evaporative Stress Index for 2003–2013. *Journal of Hydrology*, 526, 287–302.

Ladjal, M., Huc, R., & Ducrey, M. (2005). Drought effects on hydraulic conductivity and xylem vulnerability to embolism in diverse species and provenances of Mediterranean cedars. *Tree physiology*, 25(9), 1109–1117.

Schneider, C. L., Attinger, S., Delfs, J. O., & Hildebrandt, A. (2010). Implementing small scale processes at the soil-plant interface—the role of root architectures for calculating root water uptake profiles. *Hydrology and Earth System Sciences*, 14(2), 279–289.

Zhou, S., Yu, B., Huang, Y., & Wang, G. (2015). Daily underlying water use efficiency for AmeriFlux sites. *Journal of Geophysical Research: Biogeosciences*, 120(5), 887–902.

Reply to Review 2

The original reply including additional figures can be found under:

<https://doi.org/10.5194/bg-2018-474-AC2>

We thank Reviewer #2 for his valuable feedback on the submitted manuscript. Below, we address general remarks and important specific remarks that required a response and describe how we incorporate these in the revised manuscript. In addition we carefully considered all specific comments related to spelling, clarity and references and integrated them into the revised manuscript where appropriate.

General Remarks

- “This is partially recognized in the final Section 4.3 (P. 18 LL 7–8) but I have the feeling that some of the statement about the utility of this metric (e.g., P 18 LL 14–17) could be overoptimistic due to the local calibration and strong variability across sites.”

We agree that the discussion of our results requires a better differentiation between the diagnostic insights we could provide and its applications in future work. Due to the limitation of this metric (specifically the local calibration and its recursive, ET-dependent character), any future work should first try to link it with directly measurable variables. If representations of such variables reflecting soil-water content can be derived from mechanistic land surface models, this could provide an additional step to verify the presented patterns in ET–GPP coupling. We have changed the discussion accordingly.

- “[...] This scatter is probably due to observational uncertainties but also to behavior of the different ecosystems in response to specific dry-down events and to the definition of S_{rem} (see below). A few additional words on this problem could be added.”

The limited sample size of the study and vast variability in sampled climate, plant and ecosystem types does in fact pose a substantial challenge for obtaining generalizable understanding with a small sample of sites. We have added this to the section discussing limitations of our approach.

- “There is not a representation of how WUE (e.g., GPP/ET) varies with Srem based on observations.”

We concur that such a representation could be helpful to understand to what degree GPP–ET coupling holds during the periods of interest. We propose for this purpose to further not only show the covariation of Srem with WUE but also uWUE as proposed by Zhou et al. (2014 & 2015), which already accounts for the dependence of water-vapor diffusion and stomatal conductance on VPD.

- “However, the main issue I have with the definition of Srem is that it cannot keep track of any precedent effect of water availability or soil water stress in the system.”

This is an important point worth discussing more extensively in the manuscript. The Srem metric and its analysis is certainly limited to the approximately exponentially decaying ET of dry-down events. However, antecedent conditions can be reflected in this metric. Consider an ecosystem that experienced intermittent periods of water-limitation that did not qualify as dry-down events according to our definition. After a given last, weak precipitation event, we might see a longer period without any rain-fall in which ET starts following an exponential dry-down decay. Even though we identify only the latter part as dry-down event, plants in the ecosystem are already in drought stress at the beginning of the event. Yet this lower water availability would then also manifest in the reduced ET at the beginning of the event and subsequently a smaller integral of ET used to obtain Srem. Any normalization of the variable for the sites (p4 l10–11) will of course prevent a possible interpretation of q values between sites (as Srem_max can no longer be compared across sites).

We further verified the robustness of our results by using two additional calculations of Srem. In these, we used the lower and upper 95% confidence intervals of the parameters (ET_0 and k) used in the exponential model to obtain a higher and lower variant of Srem. The discrepancy of the two Srem calculations therefore incorporates uncertainties about how the exponential

fit could capture the ET decline despite unknown initial conditions and missing values in the time series. We attached this comparison as figure below. Nevertheless, antecedent conditions might well be responsible for deviations of the highly idealized behavior of the models we employed. As such, we haven't given this limitation more prominence in the discussion.

Specific comments

- “P 2. LL 7. As a matter of fact, stomatal closure is occurring always at higher potentials than critical cavitation levels for xylem (Martn-StPaul et al 2017).”

We have amended the sentence in question.

- “P. 2 LL 8. Increased leaf-temperature does not necessarily lead to a decrease in photo- synthesis; it depends on the actual temperature and temperature-sensitivity of a given species.”

We agree that this statement was too generalized. We have corrected this in the revised manuscript.

- “P. 2. LL 25. Why are you stating that ET and soil moisture are following a linear relation? Is this following the exponential decrease of ET with time? Then, very likely, the linearity is with some “proxy” values of soil moisture as S_{rem} and not with the actual soil moisture.”

For our analysis, we assumed that the rate of supply-limited ET depended linearly on the water available for root water uptake (Teuling et al. 2006) as in a one-storage water balance model. Thus: $ET \sim k * S_{rem}$. We agree that even this simplification only holds for the plant-available water and not for the total soil moisture. We have corrected the sentence accordingly!

- “P. 8 LL 10–17. For how many steps the WAI_t variable is computed? Since the beginning is from the arbitrary 100 mm in order to extract the mean seasonal cycle of WAI, you need several years.”

This is correct. We used 115 years from CRUNCEP reanalysis to obtain mean seasonal WAI amplitudes. Further, we reran the analysis with three different values of WAI_{max} (as now referred to in the manuscript): 70, 100 and 130

mm. The corresponding plots with labels of the IGBP vegetation classes are attached below. The results suggest that there is indeed some sensitivity of our results, yet all levels show a significant correlation between k and the seasonal amplitude of dryness (higher correlation for lower WAI_{max}).

- “P. 8. LL 19. Given how WAI is computed, memory effects refer only to seasonal effects, since WAI is averaged.”

We have clarified this in the description of the metric.

- “P. 9. LL 21. This is very much expected since they do not have any way of accounting for soil-water limitations.”

This is an important point. The two models indeed do not contain explicit variables reflecting the soil-water status of the ecosystems. Yet indirectly, observed reductions of GPP, even with a constant underlying water-use efficiency $uWUE$, could reflect plant responses to soil-water scarcity. Yet we agree that this wasn't phrased well enough and have amended the sentence accordingly.

- “P 13. LL 11–12. This result is a bit counterintuitive to me. At first glance, I would expect sites with short vegetation to have a higher ET attenuation than sites with taller vegetation, especially because sites with shorter vegetation have a faster decline of ET (P 14 LL 4–5). The two results seem in contradiction. How do you explain this? Is because ET in shorter vegetation is more coupled to GPP than to the decrease associated to soil water availability and this reflects in a lower value of d ?”

Thank you for noting this crucial point. We believe that the two observations do not have to be seen as standing in contradiction. As you mention, in low vegetation types (in our case dominated by grasslands), rapidly declining GPP seems to be largely sufficient to predict the also quickly diminishing ET. For tall vegetation types (dominated by trees), more gradual, possibly hydraulic limitations could lead to a shallower decline of ET, while a deeper root zone can sustain ET for comparatively longer periods.

- “P. 17. LL 30. I would tend to disagree with this statement. The results show eventually that we need more eddy-covariance measurements everywhere or other type of observations that could be used for similar purposes. Overall, semiarid regions are more resilient to decay of ET according to

Fig. 10.”

We concur that this statement does not follow from our results in its current form. What is primarily needed is more focus on regions prone to intermittent water-scarcity. For semi-arid regions, it is better to see the remaining scatter rather than than mere amplitudes as indication for more eddy-covariance measurements. We have clarified this in the discussion.

Additional References

Teuling, A. J., Seneviratne, S. I., Williams, C., & Troch, P. A. (2006). Observed timescales of evapotranspiration response to soil moisture. *Geophysical Research Letters*, 33(23).

Reply to Review 3

The original reply including additional figures can be found under:

<https://doi.org/10.5194/bg-2018-474-AC3>

We thank Referee #3 for his valuable feedback on the submitted manuscript. Below, we address general remarks and important specific remarks that required a response and describe how we incorporate these in the revised manuscript. In addition we carefully considered all specific comments related to spelling, clarity and references and integrated them into the revised manuscript where appropriate.

General Remarks

1. Mechanisms of Limitation

This is a critical point of our approach and we agree that the previous version of the manuscript communicated this insufficiently. In a previous study, Boese et al. (2017) first observed the existence of a GPP-independent association of transpiration to radiation. As in the present work, its semi-empirical approach targeted at a high model performance of predicted evapotranspiration, while associating the detected effects to plausible physical variables. In our manuscript, we aimed to expand this research to water-limited periods, in which the water supply is an additional factor controlling transpiration rates.

As we demonstrate, declining GPP due to stomatal contraction proves insufficient to explain ET decline during dry-down events (Fig. 2, 3, 4). Yet even integrating the effect of soil-water limitation (Zhou+SWL) on uWUE did not provide substantial benefits to model performance (Fig. 4). Instead the complete reduction of stomatal and non-stomatal ($r^* R_g$) transpiration components (+Rg+SWL) provided the highest performance of predicted ET. As the attenuating factor s is not exclusively reducing stomatal conductance in this model, it could be interpreted as sign of a process affecting both source of transpiration. A reduced stem hydraulic conductivity during water-limitation (Ladjal et al. 2005), could be responsible for this generalized decrease of transpiration. Nevertheless, our empirical approach at

ecosystem-scale makes it difficult to pinpoint the mechanism responsible for the observed effects. In the discussion, we now make this clear and further highlight the importance of following up on the results with mechanistic studies in controlled settings.

3. Stratification of Sites Along Vegetation Structures

In the updated version of the manuscript, we added a third category, “mixed”, for savannah type ecosystems. This admittedly only partially resolves the problem that vegetation types are only crude proxies for the actual height of plants in ecosystems (which in turn can vary substantially for any given site). However, we also clarify that the stratification can reflect – through predominating growth forms – both differences in water-use strategies and rooting depths. Yet it has to be stated in the manuscript that these categories are at best imperfect proxies for variables (e.g. average rooting depth or plant water-use strategies of woody vs. non-woody plants) that as of now are not at all or not consistently measured. Overall, the semi-empirical models we employed provide an effective description of how different ecosystem fluxes interact empirically. While the calibration to local properties impedes ad-hoc generalizations, the variability of parameters between sites can be interpreted as reflecting the variability of ecosystem functional properties (such as uWUE). For ecosystems containing various plant types with differing structural or physiological properties, the observed patterns are then aggregated signals for the whole system.

***Srem* and Antecedent Conditions**

The utilized *Srem* variable does indeed have important shortcomings. As we described, our motivation for its introduction was to serve as a proxy variable for extractable soil-water that does not rely on incomplete and inconsistently measured observations of soil-water content. However, due to its nature as calculated proxy metric, it suffers some notable limitations. As you mention, its reliance on an approximately exponentially decreasing ET omits preceding water-stress. However, antecedent conditions can be reflected in this metric. Consider an ecosystem that experienced intermittent periods of water-limitation that did not qualify as dry-down events according to our definition. After a given last, weak precipitation event, we might see a longer period without any rain-fall in which ET starts following an exponential dry-down decay. Even though we identify only the latter part as dry-down event, plants in the ecosystem are already in drought stress at the beginning of the event. Yet this lower water availability would then also manifest in the reduced ET at the beginning of that event and subsequently a smaller integral

of ET used to obtain Srem. Any normalization of the variable for the sites (p4 110–11) will of course prevent a possible interpretation of q values between sites (as Srem_max can no longer be compared across sites).

We further verified the robustness of our results by using two additional calculations of Srem. In these, we used the lower and upper 95% confidence intervals of the parameters (ET_0 and k) used in the exponential model to obtain a higher and lower variant of Srem. The discrepancy of the two Srem calculations therefore incorporates uncertainties about how the exponential fit could capture the ET decline despite unknown initial conditions and missing values in the time series. We attached this comparison as figure below. Nevertheless, antecedent conditions might well be responsible for deviations of the highly idealized behavior of the models we employed. As such, we haven't given this limitation more prominence in the discussion.

3.1 Reliance on Locally-Calibrated Statistical Models

The local optimization of parameter values is certainly a limitation if the insights are to be generalized or included in mechanistic models. The lack of firm process understanding on the scale of ecosystems does however make a semi-empirical approach a valuable approach to capitalize on the availability of eddy-covariance observations for whole ecosystems. In this approach, local parameter estimates are understood as ecosystem functional properties which regulate ecosystem responses to environmental conditions. Therefore, the empirical justification of model terms (such as the linear Rg-term and the +SWL term) and systematic patterns in their parameter estimates provide information about the interaction of variables on ecosystem scale.

Nevertheless, we agree that this decidedly non-mechanistic approach has shortcomings that more process-motivated investigations can address. For the purpose of the study, we see the detection of the soil-water limitation effect and its variability across sites as a good starting point for further work. To clarify which mechanisms might be responsible for the effect and how they drive differences between ecosystems, different observations such as leaf and xylem water potentials as well as volumetric soil-water content might be necessary. In the revised introduction and discussion, we provide a better explanation for the scope of our study and highlight how our findings could stimulate experiments under controlled conditions and factorial model experiments. We also omitted the separation into two different calibration schemes which unnecessarily distracts from the main outcomes of the analyses.

3.2 Water-Use Efficiency vs. ET in Equations

We agree that our choice of ET as metric to evaluate water-use efficiency models needs a better explanation. In brief, using $ET = f(GPP, x)$ instead of $WUE = f(x)$ is merely a reformulation that focusses on how different WUE models affect the flux magnitudes of ET rather than the ratio $WUE = GPP / ET$. In the latter approach, small GPP and even smaller ET values can lead to very high WUE values and can in a least-squares regression bias the analysis towards time periods that should not receive as much weight. We have thus added an appropriate paragraph to the introduction.

Specific Remarks

- “P3 L12: How did you define a precipitation event (> 0mm?)?”

We used a cut-off value of 0.2 mm/d to define precipitation events. We have added this criterion to the methods section.

- P3 L15: How did you handle observed vs. gap-filled data? If some of the dry-down periods were heavily gap-filled or missing, were these still analysed? If so, I would question what can be learnt from these sites as it seems unlikely the gap-filled data can accurately reflect fluxes during extreme conditions. Also how were the sites selected? On line L22 you mention 31 sites were used, but there are many more in the La Thuile release alone (of course not all with dry-downs). I’m surprised if there are only 47 dry-down events in the 200+ site records, but this is of course possible.

Thank you for highlighting this important point. In the selection and preprocessing of the data, we applied strict filtering that only uses high-quality data that is either observed directly or gap-filled with high confidence. If this filtering resulted in gaps during dry-down events, they were only filled by interpolated values from an exponential fit to allow the calculation of a continuous time series of Srem. In all model fitting and evaluation, days with low quality observations in one variable were omitted completely from the analyses. Nevertheless, the fact that dry-down events, when not occurring seasonally, represent extreme conditions where data quality becomes particularly important is now stated explicitly in the revised manuscript.

- “P4 L10: How many missing values did you allow for?”

We did not set a specific threshold value for missing values during dry-down events. Instead, we check whether an exponential model could explain at least 40% of the variability of ET during these events. Please also see our comment regarding the antecedent conditions above for how we ascertained that the uncertainties in parameter estimations originating from longer gaps did not affect our results qualitatively.

Additional References

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Carbon–Water Flux Coupling Under Progressive Drought

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Abstract.

Water-use efficiency (WUE), 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. Here, we used 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 WUE on ecosystem scale. We first compared two water-use efficiency models: The first was based on the concept of a constant underlying water-use efficiency; The second augmented the first with a previously detected direct influence of radiation on transpiration. Both models predicting WUE strictly from atmospheric covariates failed to reproduce observed ET dynamics for these periods, as they did not explicitly account for the effect of soil-water limitation. We demonstrate that an attenuating soil-water availability factor in junction with the additional radiation term was necessary to accurately predict ET flux magnitudes and dry-down lengths of these water-limited periods. In an analysis of the attenuation for all included FLUXNET sites, up to 50% of the observed decline in ET was due to the soil-water availability effect we identified in this study. We conclude by noting the rates of ET decline differ significantly between sites with different vegetation and climate 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 Mediterranean regions (Hoerling et al., 2012; Sheffield 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) **due to photolimitation of photosynthesis (Quick et al., 1992; Ort et al., 1994)**. 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.

5 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 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 close stomates**
10 **before embolism can occur (Martin-StPaul et al., 2017)**, accepting restricted carbon assimilation (Schulze, 1986) and elevated leaf-temperatures, **which has the potential to further limit photosynthesis for certain species** (Salvucci and Crafts-Brandner, 2004). This response is triggered also by the soil- and leaf-water potential, mediated 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
15 model formulations, as the exact magnitudes and interactions of relevant processes remain uncertain (De Kauwe et al., 2013; Verhoef and Egea, 2014).

At the leaf-scale, **empirical and optimality-based models** can accurately predict stomatal conductance and WUE under well-watered conditions **(Leuning, 1995;** 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-
20 watered conditions (Zhou et al., 2014, 2015). Embedded in this is the premise that the **underlying water-use efficiency (uWUE)** 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**
the effects of low VPD and low soil-water availability difficult (Knauer et al., 2015). A preceding study further demonstrated that an additional, independent radiation term improves predicting transpiration from GPP and VPD at ecosystem-level (Boese
25 et al., 2017). In this case, a transpiration component not associated to GPP and VPD could be identified, suggesting that radiation directly controls a share of equilibrium-transpiration (Jarvis and Mcnaughton, 1986). Yet the semi-empirical water-use efficiency models suggested by Zhou et al. (2015) and Boese et al. (2017) 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.
30 Dry-down events are periods of many consecutive dry days during which ET declines approximately exponentially with time reflecting an approximate linear relationship between the rate of ET and the remaining plant-available soil-moisture at each time step (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. To test the different models, we
35 evaluated them against day-time ET observations. This has the advantage that the absolute flux magnitudes of ET and GPP are

taken into account. 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 on an effective water-balance-based variable helps in improving predictions under progressive drought. Finally, we assess how the rates of declining ET during dry-down events differ between vegetation and climate types.

5 2 Methods

2.1 Data & preprocessing

Observation-based products of gross primary productivity (GPP) and evapotranspiration (ET) obtained with the eddy-covariance method 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, we used the global radiation (R_g), 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). We omitted periods not gap-filled with high-confidence, which is particularly important for periods such as dry-down events, as they may represent significant deviations from regular ecosystem behavior. For our analyses, we included data fulfilling a set of minimum conditions: $\text{GPP} > 0.1 \text{ gC d}^{-1} \text{ m}^{-2}$, $\text{ET} > 0.05 \text{ mm d}^{-1}$ and $\text{VPD} > 0.001 \text{ kPa}$. 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 ($P > 0.2 \text{ mm d}^{-1}$) 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, the observed evapotranspiration after three successively rain-free days can be expected to approximate transpiration.

2.2 Detection of Dry-Down Events

The identification and selection of dry-down events required special attention. To obtain data that could be confidently assumed to be affected by soil-water limitation, we employed a selection procedure consisting of the sequential application of multiple conditions:

1. Periods with at least 15 successive days without precipitation.
2. Both evapotranspiration (ET) and the evaporative fraction (EF, defined as ET/R_n) had a significant negative trend over the course of the precipitation-free period.
3. ET had to be controlled more by the diminishing supply of water rather than atmospheric demand.

The latter condition was implemented by combining two models that individually represented demand and supply limited ET. For the demand limitation, ET was predicted as a linear function of Rg

$$ET = a \cdot Rg + b, \quad (1)$$

where a and b are estimated regression parameters. For the supply limitation, ET was predicted as an exponential decrease with time:

$$ET = ET_0 \cdot e^{-k \cdot t}, \quad (2)$$

where ET_0 denotes a parameter for the initial rate of ET at the beginning of the exponential decrease and k denotes the rate of the decay. The variable t denotes the days since the beginning of the selected period.

The demand model was applied to the beginning of any period fulfilling conditions 1. and 2. until a time $t = t_\alpha$, while the supply model was applied to the rest of the period. To find the time step after which supply limitation dominated ET dynamics, we initially set $t_\alpha = 5$ to allow at least 5 observations to be fitted with the demand model and all subsequent ones with the supply model. The residuals of both models were concatenated and the root mean squared error (RMSE) was calculated. We then increased t_α by daily increments until the period fitted with the supply model contained only 5 observations. For each change of t_α the RMSE was noted.

The beginning of supply limitation could then be defined as the t_α for which the RMSE was smallest. As any further increase of t_α would result in a higher RMSE, this indicates that the ET following t_α was best approximated with the exponential decay function which in turn represents supply limitation.

Figure 1 exemplarily shows ET and RMSE for a period fulfilling conditions 1. and 2. The RMSE decreased until $t_\alpha = 12$ and increased gradually thereafter. This means that the ET past $t_\alpha = 12$ could be better predicted with the exponential decrease depending on time rather than the atmospheric demand.

To verify that the selected period did indeed show an approximately exponential decay of ET, we further required that ET had to fit an exponential function with $R^2 > 0.6$.

A list of the 47 identified dry-down events detected at the 31 respective sites can be found in the supplementary materials. This table also contains the parameters a , b and k used in the detection of the dry-down events (Equations 1 and 2).

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 availability of consistent estimates of soil-water data-sets. To gauge the total amount of plant-available soil-water, measurements would need to sample the complete soil profile in small increments. 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. Furthermore, the soil-water contents at specific depths would need to be weighted with the root water uptake which can differ substantially based on root architecture and physiology (Schneider et al., 2010).

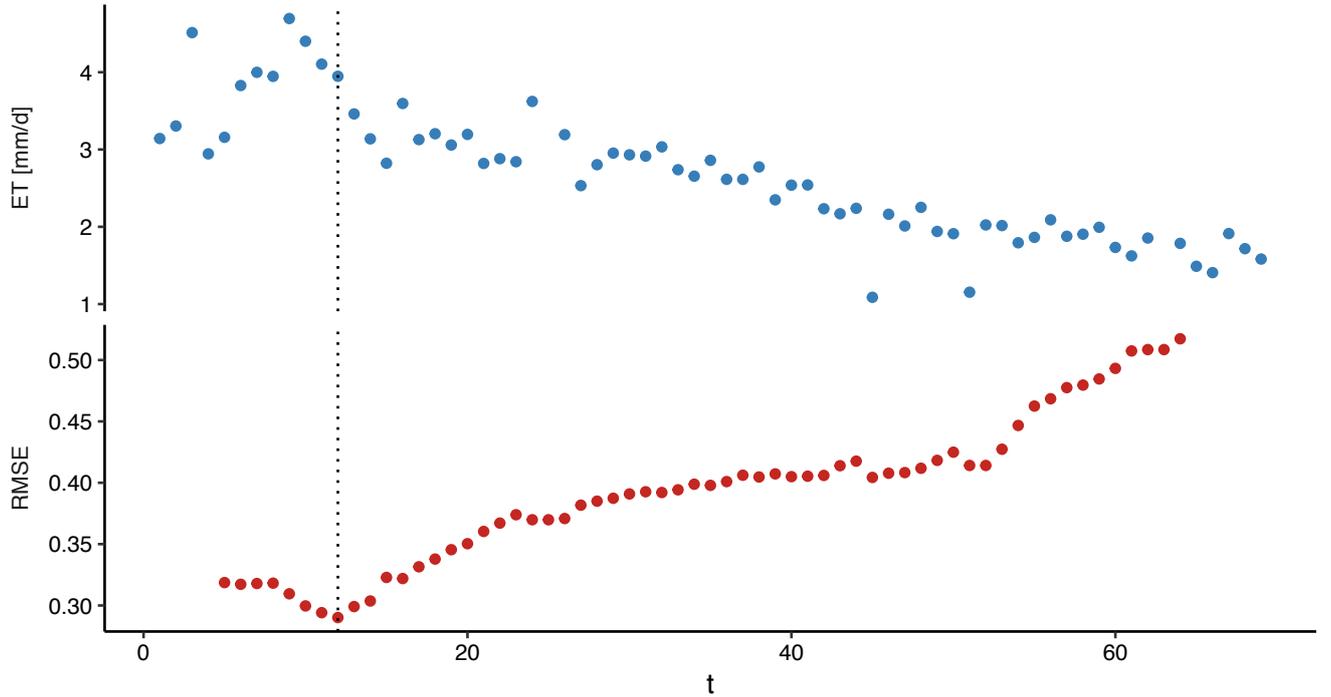


Figure 1. RMSE sequence used to identify supply limited ET at the FLUXNET site AU-Dry. The dotted line denotes the day with the smallest RMSE of the combined models, thus indicating the beginning of supply limited ET.

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 frequently used in ecosystem or land surface models. Conceptually, the magnitudes and rates of decline of ET under a high evaporative demand of the atmosphere can be seen as an integrated measure of the decreasing availability of the soil-water. This means that the proxy for soil-water availability can be inferred without using any sub-surface measurements, while reflecting the overall soil-water status of the ecosystem.

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

$$S_{\text{rem}0} = \int_{t=0}^{\infty} \text{ET}_t \quad (3)$$

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} :

$$S_{rem_{t+1}} = S_{rem_t} - ET_t \quad (4)$$

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_{rem_0} , 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 can only account for soil-water availability during periods with exponentially decreasing ET. Furthermore, we here assume that the influence of groundwater can be neglected if we observe decreasing ET during periods without precipitation.

In the calculation of S_{rem} , we normalize by the maximum calculated value. Thus, at least one value of S_{rem} for each site will be 1. It is important to note that this value must thus not signify unstressed conditions. In the absence of a knowing the true extent of the total soil-water storage, this limitation has to be accounted for by calibration of site-specific model parameters.

2.4 Models

A water-use efficiency (WUE) model can be formulated as:

$$WUE = \frac{GPP}{ET} = f(x_1, \dots, x_n), \quad (5)$$

where x_i can include different variables affecting WUE, such as the vapor-pressure deficit (VPD). Evaluating different models against the quotient of GPP/ET has the disadvantage that larger WUE values will be given disproportionate weight when fitting the model. However, these values can occur under conditions with very low GPP and ET, thus having little ecological significance.

To properly test the model with flux tower derived GPP and ET, while accounting for flux magnitudes, we first inverted the model to:

$$ET = \frac{GPP}{f(x_1, \dots, x_n)}, \quad (6)$$

For our analysis, we started with the WUE model proposed by Zhou et al. (2015):

$$ET_t = \frac{GPP_t \cdot VPD_t^{0.5}}{uWUE}, \quad (7)$$

where uWUE denotes the site-specific underlying water-use efficiency assumed to be constant in time. For increased clarity, variables are henceforth 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. While this model was derived

primarily as a response to systematic errors of the model by Zhou et al. (2015), a direct response of transpiration to radiation has been posited before (Jarvis and Mcnaughton, 1986). In this concept, one component of transpiration is driven by the gradient of the vapour-pressure deficit (imposed transpiration), while the other is driven by the radiative energy input (equilibrium transpiration). While water-use efficiency models based on stomatal conductance theory typically can account for the former part, they neglect the latter. Therefore, we formulated an amended version of the model by Zhou et al., further referred to as "Rad":

$$ET_t = \frac{GPP_t \cdot VPD_t^{0.5}}{uWUE} + r \cdot Rg_t, \quad (8)$$

where Rg denotes incoming solar radiation and r denotes a site-specific parameter controlling the radiation-associated equilibrium transpiration.

Both models outlined in Eqs. 7 and 8 do not explicitly account for the limiting effect of soil-water availability on transpiration. Indirectly, however, this effect is partly contained in one of the predictor variables, 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. **The GPP does thus contain information regarding the soil-water status during dry-down events. However, predicting ET from GPP assumes that soil-water limitation affects both GPP and ET equally, while studies suggest reductions of xylem conductivity during drought (Ladjal et al., 2005). Such a reduction would however not necessarily affect GPP in equal measure.** To model an explicit effect of the soil-water availability on transpiration, we used a stress scalar s adopted from Keenan et al. (2010):

$$s = \left(\frac{S_{remt}}{\max(S_{remt})} \right)^q, \quad (9)$$

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

$$ET_t = s \cdot \left(\frac{GPP_t \cdot VPD_t^{0.5}}{uWUE} \right) \quad (10)$$

for the Zhou+SWL model and as

$$ET_t = s \cdot \left(\frac{GPP_t \cdot VPD_t^{0.5}}{uWUE} + r \cdot Rg_t \right) \quad (11)$$

for the +Rg+SWL model.

2.5 Model calibration and evaluation

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 as the primary criterion to assess the accuracy of the predictions (Nash and Sutcliffe, 1970). It is defined as:

$$5 \quad \text{MEF} = 1 - \frac{\sum (Y_{\text{prd}} - Y_{\text{obs}})^2}{\sum (Y_{\text{obs}} - \bar{Y}_{\text{obs}})^2}, \quad (12)$$

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:

$$\text{MEF}_{\text{bounded}} = \begin{cases} \text{MEF} \geq 0 : \text{MEF} \\ \text{MEF} < 0 : e^{2 \cdot \text{MEF}} - 1 \end{cases} \quad (13)$$

10 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).

15 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

$$\text{ET}_t = \text{ET}_{t=0} \cdot e^{-k \cdot t} \quad (14)$$

The coefficient k denotes the slope of the exponential function. If this form is assumed to be the general form for dry-down events, then k reflects the rate at which ET decreases. A higher value of k would then indicate a faster rate at which
20 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. 2).

2.6 Experimental design

[Omitted calibration schemes]

The models outlined in Eqs. 7, 8, 10 and 11 were evaluated in two different **evaluation schemes**:

- 25 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**.
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**.

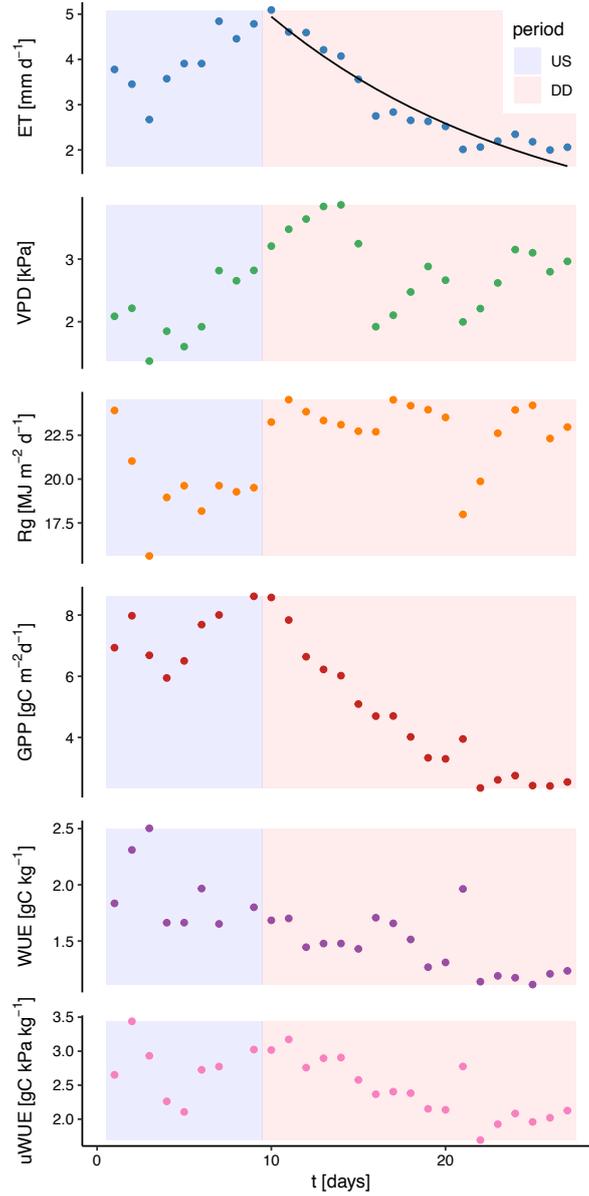


Figure 2. Temporal behavior of relevant ecosystem variables during an **unstressed** period (US) and a **dry-down** event (DD) at the FLUXNET site US-Arc. While ET and GPP show a distinct and exponential decay during the dry-down event, the variables reflecting the atmospheric demand (solar radiation, Rg and the vapor pressure deficit, VPD) remain high. The black line denotes an exponential fit to the decreasing ET.

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 variability of the predicted lengths of dry-down events between sites, we classified all sites according to their reported biome types into

three 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). Mixed included all sites with the vegetation types SAV (savanna), WSA (woody savanna), OSH (open shrubland) and CSH (closed shrubland). Due to the preponderance of forest ecosystems vegetation in the tall class, our distinction can elucidate the different ecosystems differ in their water-use strategies due to with shallower and deeper root networks (Jackson et al., 1996) and the risk of xylem embolisms (Ryan and Yoder, 1997; Koch et al., 2004). Despite the association that such a distinction allows, it has to be considered as an inexact proxy for the height distribution of plants in any given ecosystem. As that variable is not reported consistently across FLUXNET sites, the separation of ecosystems into the listed categories serves as a first, qualitative approximation and has to be interpreted with caution.

Furthermore, we also explored whether the lengths of included dry-down events depended on hydro-climatic properties of the sites:

Firstly, we used the documented Koeppen-Geiger climate classes for the different sites. Due to the limited sample size of this study, we aggregated the climate classes into four categories: Temperate/continental humid contained sites with Koeppen-Geiger classes Cfa, Cfb or Dfa. Mediterranean contained those with the classes Csa or Csb. Semi-arid / Arid contained those with classes BSk or BSh, while Savanna contained sites with class Aw.

Secondly, 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 $WAI = 100\text{mm}$ 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:

$$w_{out_t} = \min(PET_t, k \cdot WAI_{t-1}) , \quad (15)$$

where PET denotes the potential evapotranspiration, k denotes the maximum fraction of soil-water available for evapotranspiration without limitation of atmospheric demand. For this calculation, we set $k = 0.05$, which was found as a median value for different ecosystem types by Teuling et al. (2006). The water-availability index for each time step (WAI_t) was then calculated as:

$$WAI_t = \min(100, WAI_{t-1} - w_{out_t} + P_t) , \quad (16)$$

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 seasonal memory-effects and the co-limitation of supply and demand. After deriving mean-seasonal cycles of WAI at each site, we used the interquartile 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. 8 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

$$5 \quad ET_{\text{fract}} = \frac{r \cdot Rg_t}{\frac{GPP_t \cdot \sqrt{VPD_t}}{uWUE} + r \cdot Rg_t} \quad (17)$$

where ET_{fract} 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.

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

$$d = \frac{\sum(1-s)ET_{\text{rad}t}}{\sum ET_{\text{rad}t}} \quad (18)$$

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. 9).

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 site separately with all available and adequate observations, irrespective of the soil-water status. 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. 3). 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. 4). For the Zhou model, the absolute residuals were biggest at the beginning of the events. Based on the characteristic dynamic of the model

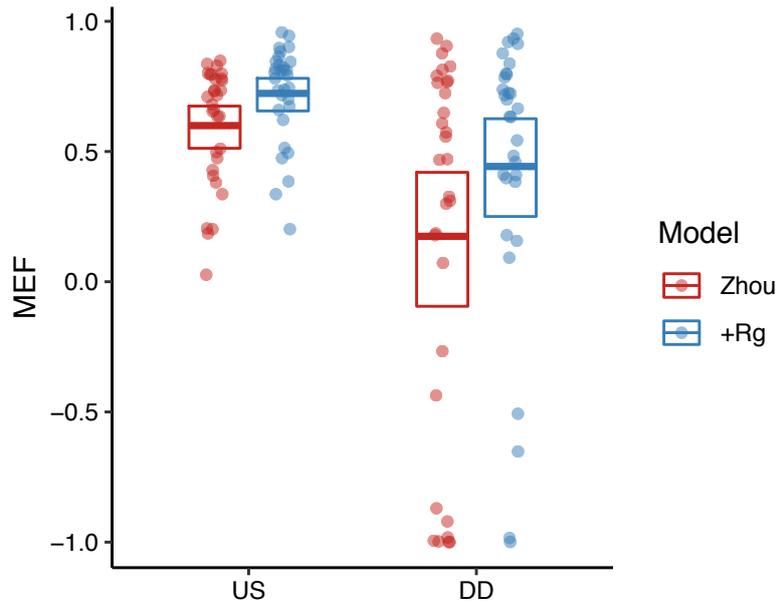


Figure 3. Model-efficiency of the Zhou and +Rg models when evaluated inside (DDev1) and outside (USev1, see [Methods / Experimental design](#)) water-limited dry-down events. The models were calibrated for all adequate site-observations. The points indicate MEF for individual sites. The bold lines denote the mean, while the boxes indicate the bootstrapped 95%-confidence-intervals of the mean.

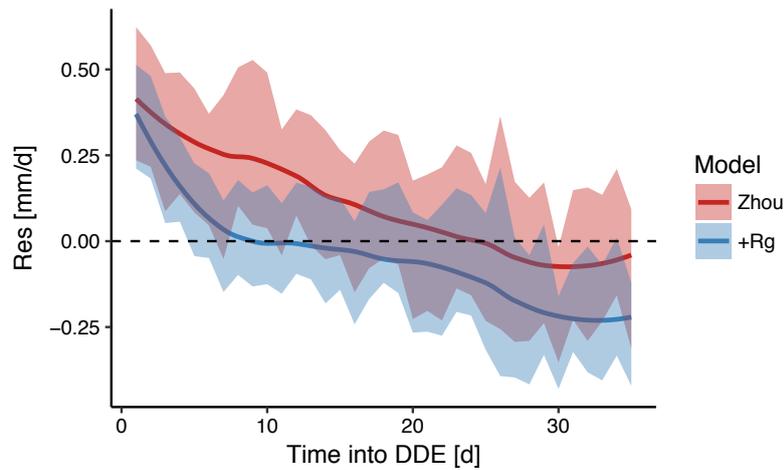


Figure 4. Mean model residuals across all dry-down events for the Zhou and +Rg model as a function of time during dry-down events. The shaded area reflects the 95%-confidence-intervals. Both models tended to underestimate ET near the beginning of the dry-down event while overestimating the flux with increasing length of the event. The former was more pronounced for the Zhou model, the latter more pronounced for the +Rg model.

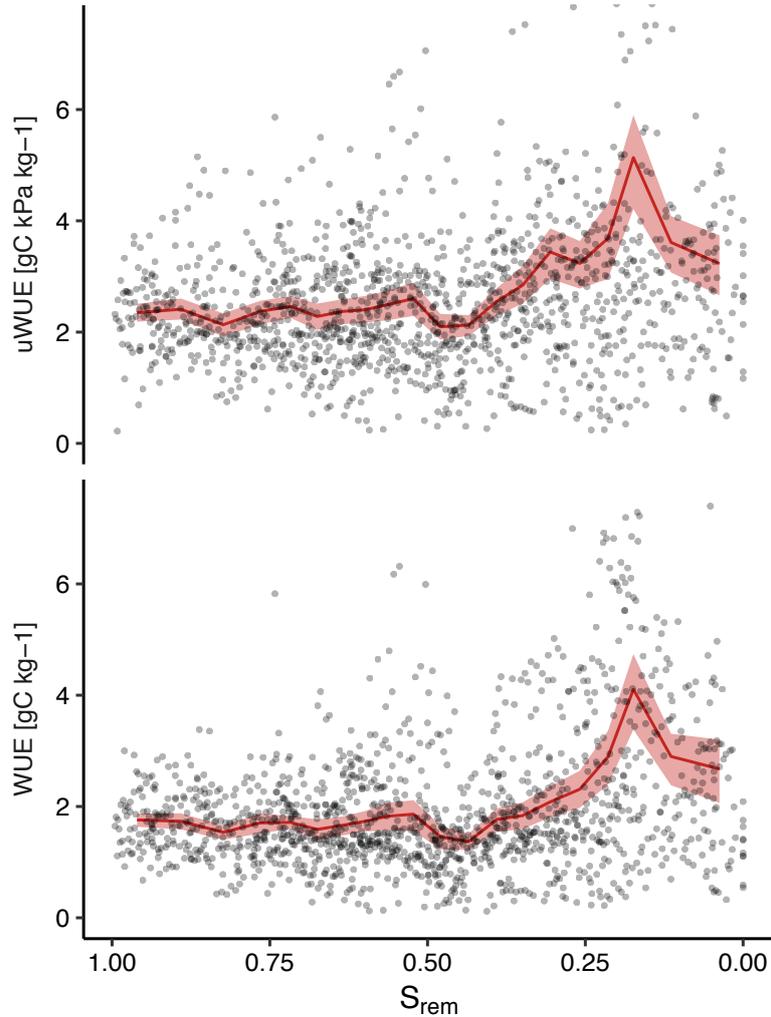


Figure 5. Response of the water-use efficiency (WUE) and the underlying water-use efficiency (uWUE) to the remaining soil-water (S_{rem}).

residuals we concluded that merely including the similarly declining GPP as predictor was insufficient to predict ET during these periods. 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.

- 5 As we noted, during dry-down events, GPP can show exponential declines similar to ET (Fig. 2). This raises the question why predicting ET using GPP introduces systematic model errors. We thus plotted both the water-use efficiency (WUE) and the underlying water-use efficiency (uWUE) against the S_{rem} variable reflecting the soil-water status of the ecosystem (Fig. 5). As we noted previously, all included models include the response of WUE to VPD and thus do not assume that WUE is constant over time. VPD can be expected to rise during dry-down events, as the moisture supply from the soil and biosphere

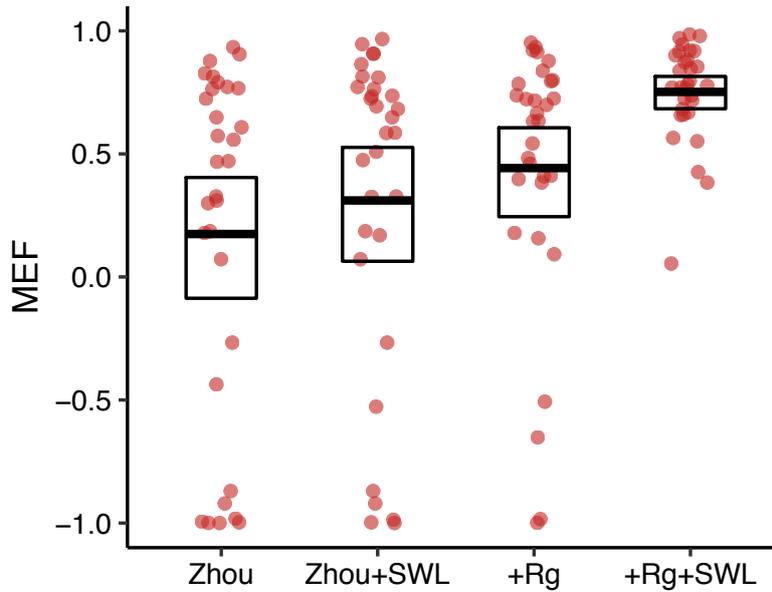


Figure 6. Model performance of the two original models and their amended variants which include an attenuation function reflecting soil-water availability. The models were evaluated during dry-down events. The dots denote individual sites. The bold line denotes the mean for all sites, while the box represents the 95% confidence intervals of the mean.

gradually diminishes. However, we observe an inverse tendency, in which WUE is, on average, higher when S_{rem} falls below 0.5. Thus, even when accounting for the effect of VPD, uWUE does not remain constant with regard to S_{rem} .

To address the decreased model performance during dry-down events, 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 (Fig. 6). The reference Zhou model shows the lowest mean MEF when averaged over sites. Notably, however, was that for the mean MEF across sites, no significant improvement resulted from adding the effect of soil-water limitation to this model (Zhou+SWL). The model variants including radiation performed substantially better. For the +Rg variant, including the effect of soil-water limitation paid off with a substantially increased mean MEF. 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. 7). 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 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.

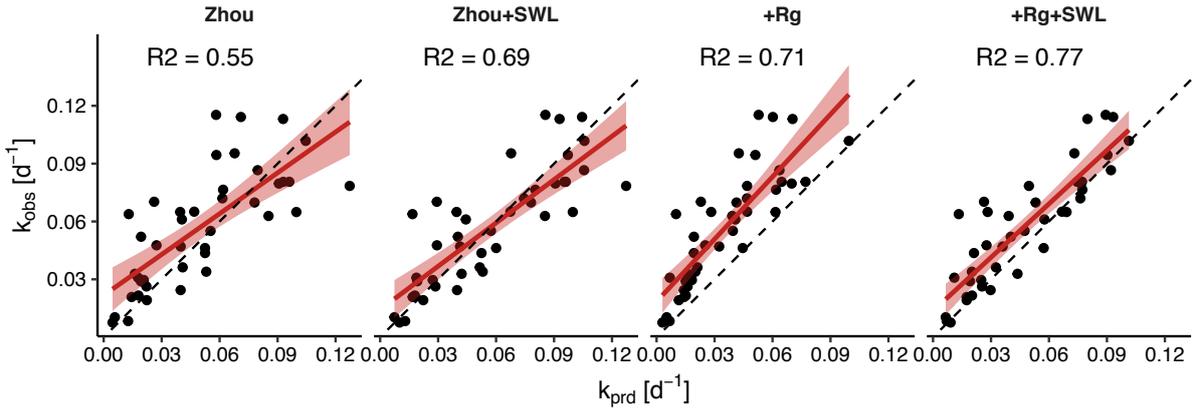


Figure 7. Observed plotted against predicted values of the decay-coefficient k (Eq. 14) for the four model variants. Points represent individual dry-down events, for which a linear fit with confidence intervals is shown in red; the one-to-one line is dashed. Three outlying events for which k deviated exceedingly from the other events were removed.

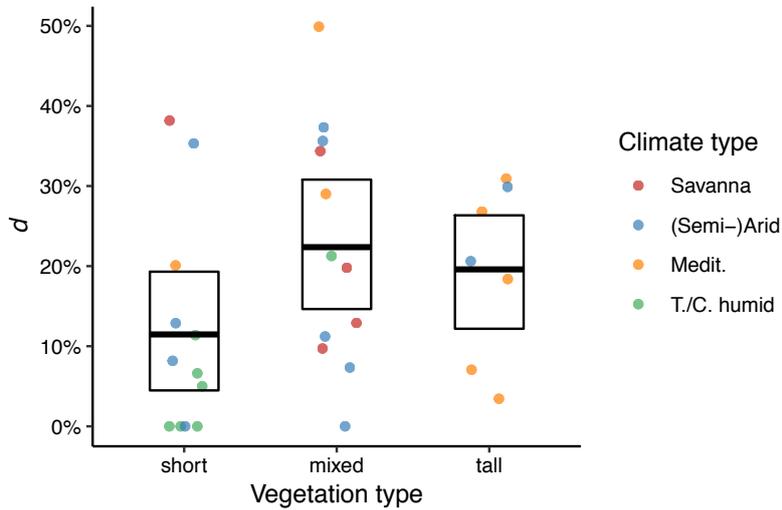


Figure 8. Fraction of relative ET reduction during dry-down events (d ; Eq. 18). The points represent the values for individual sites, the bold bar denotes the mean value of all sites, the box represents the bootstrapped 95%-confidence-interval.

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 stratifying the results along the vegetation and climate types (Fig. 8). Sites with tall and mixed vegetation had significantly higher relative attenuation of ET compared to sites with short vegetation. However, for both vegetation and climate types, there was substantial variability between the different sites.

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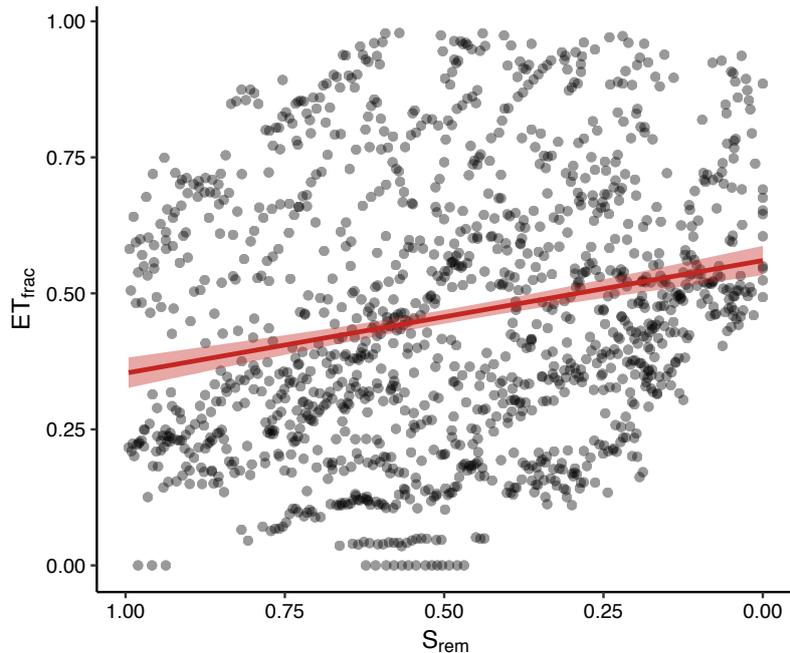


Figure 9. Fraction of radiation-associated evapotranspiration (ET_{frac}) as a function of S_{rem} . Points represent daily values for all dry-down events, the red line is the mean response for all events derived with a linear regression ($p < 0.001$).

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 daily ET_{frac} values for all included site varied widely along the observed S_{rem} (Fig. 9). Despite the substantial variability, the mean ET_{frac} showed a significant association with S_{rem} ; ET_{frac} was significantly higher for observations with low S_{rem} .

5 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 short vegetation, compared to tall vegetation (Fig. 10), meaning that sites with short vegetation had faster decays of ET during periods of water limitation. However, there was substantial variability within the vegetation types.

10 We also stratified 31 sites along hydro-climatic properties. In a first step, we used an aggregation of Koeppen-Geiger climate classes. We found that Savanna climates had the lowest rates of k indicating slowly declining ET. By contrast, sites with a Continental/temperate humid climate had the fastest declines, as evidenced by the higher values of k . Notably, sites with mediterranean climate tended to have lower k , except for one site with low vegetation. As Fig. 11 indicates, the Semi-arid / Arid and Mediterranean climate classes in particular contain a mixture of plant heights, which complicates inferences regarding the impact of climatic variability on k .

15 Further, we found a significant, negative correlation of k with the amplitude of the seasonal dryness ($p < 0.001$, $R^2 = 0.42$). When separating the three vegetation types, the correlation was significant for sites with mixed vegetation ($p = 0.007$), yet not

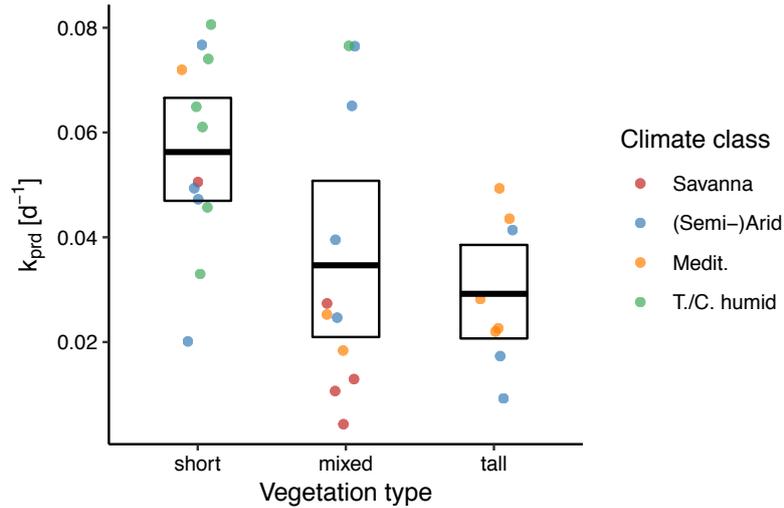


Figure 10. Between-site distributions of the predicted decay-rate k stratified along the aggregated vegetation and climate classes. The points represent individual sites, the bold line denotes the mean across sites, the box represents the bootstrapped 95%-confidence-interval.

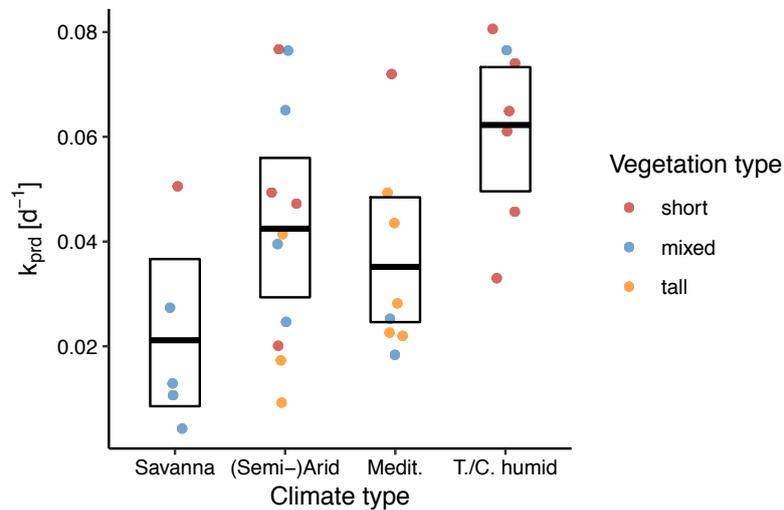


Figure 11. Between-site distributions of the predicted decay-rate k stratified along the aggregated climate and vegetation classes. The points represent individual sites, the bold line denotes the mean across sites, the box represents the bootstrapped 95%-confidence-interval.

those with short or tall vegetation ($p = 0.341$ and $p = 0.801$, respectively; Fig. 12). However, this analysis was severely limited by the sample size within the three vegetation types.

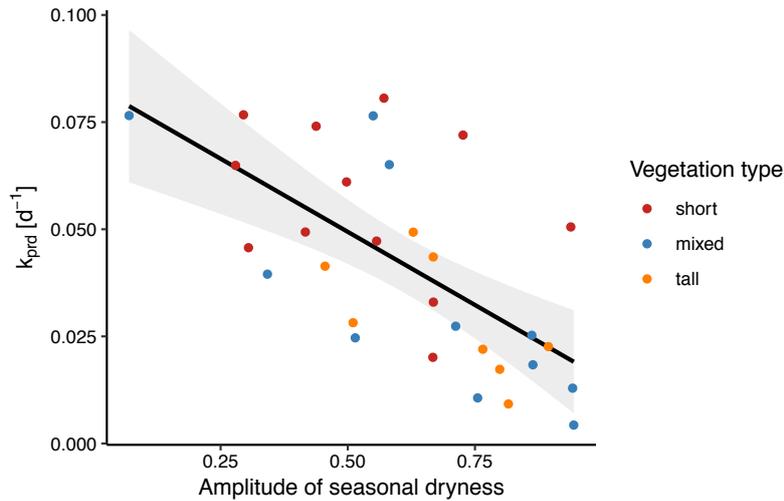


Figure 12. The decay-rate k correlated significantly with the mean amplitude of seasonal dryness across sites ($p < 0.001$, $R^2 = 0.42$). Among the vegetation types, this correlation was only significant for the mixed type ($p = 0.007$)

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. 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 insufficient to lead to significantly improved predictions of transpiration, adding to the finding of a study noting no increase in uWUE for a drought event in an 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 $\text{GPP} \cdot \sqrt{\text{VPD}}$ can adequately predict transpiration. 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 up to 50% of 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 of soil-water limitation for ecosystem water-use efficiency during drought. Importantly, the magnitudes of the observed attenuation was significantly 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. While the reduction of xylem conductivity in drought conditions has been studied (Ladjal et al., 2005) and is a candidate explanation for the observed attenuation, the ecosystem-scale of our analysis does not allow for a definitive association with physiological processes.

5 Our study posits the countervailing interaction of two additional factors controlling radiation: On the one hand, the positive effect of radiation and on the other hand, the negative effect of soil-water limitation. As we demonstrated in the assessments of model efficiency and the predicted dry-down rates, jointly accounting for both effects was justified on empirical grounds. Despite the effectiveness of the Rad+SWL model at ecosystem-scale, physiological studies under controlled conditions are needed to disentangle the interacting processes.

10 Further, the rate of the exponential ET decline differed significantly between short and mixed/tall vegetation types, where short 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 (Jackson et al., 1996). These plants could favor fast, relatively unabated transpiration while competing for a quickly diminishing resource. Conversely, tree species dominating the high and present in the mixed vegetation sites have deeper root-networks and would be more circumspect in their water-use to avoid the risk of cavitation which would jeopardize their survival and seed production (McDowell et al., 2008). Similar contrasts of the evapotranspiration response to drought between trees and grasses have been observed for ecosystems where the two plant types co-occur (Baldocchi et al., 2004).

20 Juxtaposing faster declines and lower attenuation in low vegetation types requires reconciling both seemingly contradictory observations. In the low vegetation type dominated by grasses, rapidly declining GPP seems to be largely sufficient to predict the also quickly diminishing ET. For the tall vegetation type that is dominated by trees, more gradual, possibly hydraulic limitations could lead to a shallower decline of ET. At the same time, a deeper root zone can sustain ET for comparatively longer periods, thus resulting in lower k values.

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

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

4.2 Uncertainties & limitations

In this study, we compared the capacity of different semi-empirical water-use efficiency models to predict ET during dry-down events. Previous studies have demonstrated the utility of this approach in identifying patterns and driving factors of ET on different time scales (Zhou et al., 2014, 2015; Boese et al., 2017; Nelson et al., 2018). In these models, the model structure is based on underlying physiological theories and can be amended based on observed model deficiencies. By contrast, the model parameters are calibrated to individual eddy-covariance sites as they are understood to represent constant ecosystem-functional properties (Reichstein et al., 2014). As we outlined in this study, we could evaluate different models and attribute differences in the performance to the inclusion of particular model terms. Because these terms can be linked to physical processes such as equilibrium transpiration (Jarvis and Mcnaughton, 1986) and limitations of hydraulic conductivity (Ladjal et al., 2005), differences between model performances signify the importance of these processes at ecosystem-scale. Nevertheless, the empirical nature and the site-specific calibration of the models can limit which inferences can be drawn from the results. Yet in our comparative approach, some models failed to provide sufficient goodness-of-fit to observed variables even when calibrated, thus allowing a consistent and informative comparison. The calibration to individual sites becomes limiting not for model selection, but rather when calibrated parameters have to be extrapolated while they could be influenced by multiple interlocking and incompletely understood processes. In light of both the observed patterns and the limitations of the employed methodology, experiments under controlled conditions of radiation and soil-water potential could thus shed light on how both variables interact with plant-specific properties to control water-use efficiency under drought.

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 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. However, ecosystems in which plants can access groundwater would also be less susceptible to declining ET during rain-free periods. 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 dynamics.

One inherent limitation of the S_{rem} metric is its dependency on periods with exponentially declining ET. Thus, the soil-water status of ecosystem preceding dry-down events cannot be directly accounted for. Indirectly, however, antecedent conditions are reflected in the metric. If the drier conditions preceded an identified dry-down event, the already depleted soil-water content would manifest in lower ET at the beginning of the event itself. This would thus also produce a lower integral in the calculation of $S_{\text{rem}0}$, which quantifies the total remaining soil-water for complete duration of the dry-down event. Nevertheless, despite normalizing the maximum S_{rem} for each site to 1, the time-step in question could already have depleted soil-water. While the site-specific calibration of the parameter q can compensate for these biases, they complicate interpretations of the parameter

across sites. Validating and possibly replacing the proxy variable with a quantity based on direct measurements should thus be a focus of future research.

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. In light of its possible limitations, any future work should first try to link S_{rem} with directly measured soil-water content. Where representations of soil-water content can be derived from mechanistic land surface models, this could provide an important validation of both the proxy variable itself and possible impacts on the presented findings.

Overall, the results of this study are constrained by the sample size of adequate dry-down events in the FLUXNET data 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. Yet when analyzing the variability of k between sites, we noted the considerable variability of values within climate and vegetation types. Superimposing both classifications indicates that variability in one classification can be partially attributed to the other. However, a full intersection of both classifications is currently impossible due to the sample size. Thus, the potential of analyses of the between-site variability of parameters could be extended and be made more robust with more events from a larger set of ecosystems. An increased availability of eddy-covariance sites would also aid disentangling a variety of confounding factors determining the rates of ET decline across sites. The drought-susceptible Continental/Temperate humid grasslands with their fast rates of ET decline and the (Semi-)Arid climate type with its large within-class variability of k could particularly benefit from an expansion of eddy-covariance sites.

In our analysis, we examined the different factors controlling transpiration rates during dry-down events. The gross-primary productivity (GPP) was thereby used as a predictor variable. In water-use efficiency models based on physiological theories, GPP contributes information about the degree of stomatal conductance. However, research has indicated that the reduction of GPP during periods of water-limitation cannot be entirely attributed to reduction of stomatal conductance alone, e.g. via reductions of mesophyll conductance (Keenan et al., 2009; Zhou et al., 2013). The model Zhou+SWL predicts ET as a function of both GPP and soil-water limitation. In our conceptualization, the +SWL term serves as a corrective for non-stomatal limitations of ET. However, it is also possible to conceive of the term as correcting for any difference in how soil-water limitation affects ET differently from GPP. As changes in mesophyll conductance will not affect transpiration rates (Barbour et al., 2010), while reduced xylem conductivity alone will not affect photosynthesis and thus GPP. Thus, a notable reduction in mesophyll conductance would likely manifest by counter-acting the reduced xylem conductivity and lead to a higher correspondance between GPP and ET than we observed.

To better understand the variability of rates of ET decline k between sites, we stratified our sample of included sites along aggregated vegetation and climate types. In the former case, we distinguished sites with short, mixed and tall vegetation. As the average rooting depth (Jackson et al., 1996) as well as the risk of xylem cavitation (Ryan and Yoder, 1997; Koch et al.,

2004) are associated to plant height, we employed this distinction to clarify whether variability of k could be associated to different plant water-use strategies. It is important to note that this approach is primarily the result of the absence of rooting depth observations for FLUXNET sites. However, any such aggregated classification will be limited in its predictive ability by the considerable variability of confounding factors between classes. The mere fact that both rooting depth and risk of cavitation are correlated to plant height has to caution against prematurely associating the observed variability to any one of these factors. Thus, our study should be seen as grounds for studies in which the effects of rooting depth and plant height can be disentangled and their respective influence on transpiration rates under drought can be quantified.

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 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 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. If the aforementioned limitations of S_{rem} can be overcome, this would have significant consequences for semi-empirical models that link GPP and ET on regional and global scales. Accounting for the observed biases is particularly relevant 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 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.

Data availability. For this study, we used observations of the FLUXNET initiative from sites with an open and fair use (La Thuile 2007 dataset) or Tier 1 (Berkeley 2015 dataset) data policy. The data sets are available at <http://fluxnet.fluxdata.org/data/download-data/>

Competing interests. The authors declare no competing interests.

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1 Time-Series of Evapotranspiration During Dry-Down Events

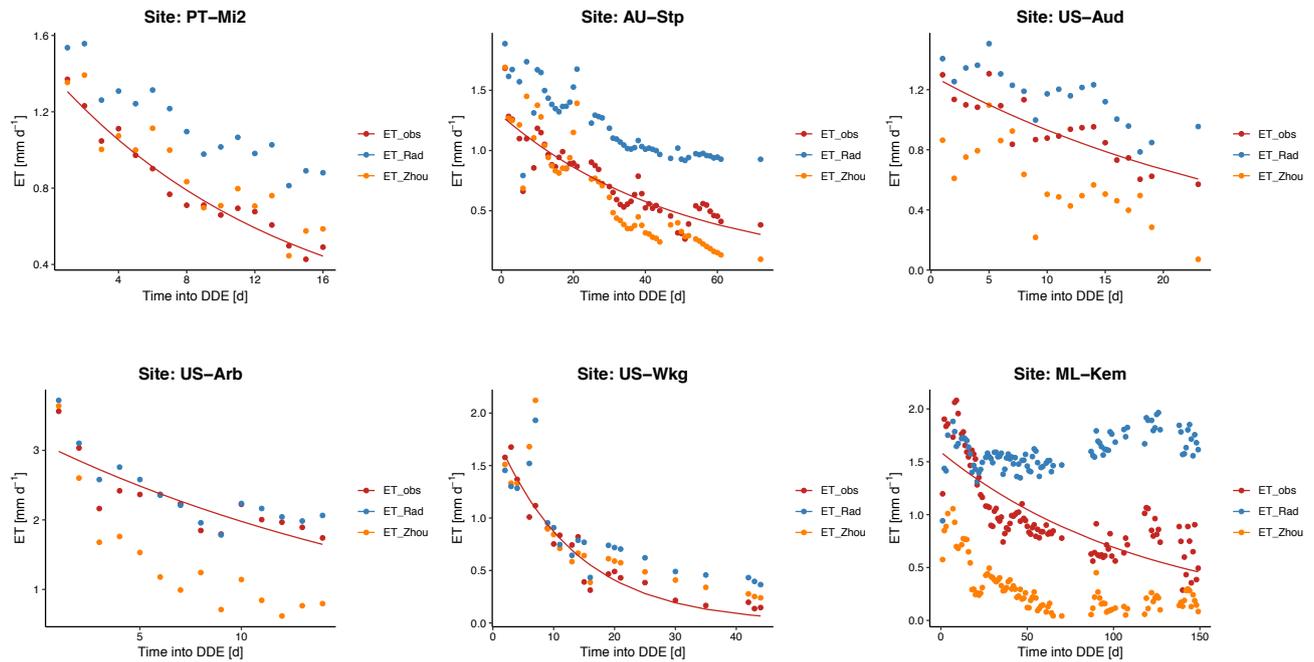


Figure 1. Observed evapotranspiration (ET) compared to predicted ET from the Zhou and Rad models for six different dry-down events and sites. The lines denote an exponential fit to the observed ET.

2 List of Sites and Estimated Parameters

3 List of Detected Dry-Down Events

Table 1. List of site **properties and estimated parameters.**

	Site	Vegetation type	Climate type	g	r	q	k	WAI _{amplitude}
1	AU-DaP	short	Savanna	0.203	0.073	0.572	0.051	0.938
2	AU-DaS	mixed	Savanna	0.153	0.067	0.471	0.013	0.942
3	AU-Dry	mixed	Savanna	0.373	0.005	0.163	0.011	0.755
4	AU-Gin	mixed	Medit.	0.254	0.012	1.082	0.025	0.862
5	AU-How	mixed	Savanna	0.324	0.032	0.922	0.004	0.944
6	AU-Stp	short	(Semi-)Arid	0.292	0.041	0.894	0.020	0.667
7	IT-Ro2	tall	Medit.	0.193	0.018	0.060	0.044	0.668
8	SD-Dem	mixed	Savanna	0.281	0.019	0.408	0.027	0.712
9	US-Blo	tall	Medit.	0.164	0.073	0.419	0.023	0.894
10	US-SRG	short	(Semi-)Arid	0.288	0.020	0.150	0.049	0.417
11	US-SRM	mixed	(Semi-)Arid	0.304	0.013	0.119	0.040	0.342
12	US-Ton	mixed	Medit.	0.253	0.029	0.507	0.018	0.864
13	US-Whs	tall	(Semi-)Arid	0.344	0.015	0.000	0.041	0.455
14	US-Wkg	short	(Semi-)Arid	0.312	0.010	0.097	0.077	0.295
15	BW-Ghg	mixed	(Semi-)Arid	0.302	0.058	0.631	0.076	0.550
16	BW-Ghm	mixed	(Semi-)Arid	0.247	0.063	0.726	0.065	0.582
17	BW-Ma1	mixed	(Semi-)Arid	0.291	0.015	0.101	0.025	0.515
18	DE-Meh	short	C/T humid	0.201	0.036	0.000	0.081	0.571
19	ES-ES1	tall	Medit.	0.219	0.044	0.056	0.049	0.629
20	IL-Yat	tall	(Semi-)Arid	0.244	0.011	0.312	0.009	0.816
21	IT-Amp	short	C/T humid	0.135	0.077	0.000	0.033	0.668
22	IT-LMa	short	C/T humid	0.269	0.034	0.328	0.061	0.498
23	ML-Kem	tall	(Semi-)Arid	0.114	0.045	0.394	0.017	0.799
24	PT-Esp	tall	Medit.	0.275	0.000	0.421	0.022	0.765
25	PT-Mi2	short	Medit.	0.306	0.012	0.455	0.072	0.727
26	US-Arb	short	C/T humid	0.198	0.059	0.000	0.046	0.305
27	US-Arc	short	C/T humid	0.257	0.056	0.141	0.065	0.279
28	US-Aud	short	(Semi-)Arid	0.184	0.027	0.000	0.047	0.557
29	US-Bo1	short	C/T humid	0.107	0.082	0.048	0.074	0.438
30	US-FR2	mixed	C/T humid	0.252	0.038	0.436	0.077	0.070
31	US-Fuf	tall	Medit.	0.415	0.014	0.362	0.028	0.510

Table 2. List of all detected dry-down events used in this study. The columns a , b and k contain the parameter values used in the detection of the events (see Section *Detection of Dry-Down Events*)

	Site	Start date	End date	a	b	k
1	AU-DaP	2009-4-8	2009-6-17	0.514	-8.683	0.048
2	AU-DaS	2011-4-28	2011-6-30	0.098	0.601	0.010
3	AU-Dry	2013-4-13	2013-6-9	0.133	0.859	0.014
4	AU-Dry	2014-5-23	2014-10-31	0.089	0.496	0.007
5	AU-Gin	2012-3-4	2012-3-28	0.005	1.328	0.024
6	AU-How	2014-6-7	2014-10-13	0.215	-1.003	0.004
7	AU-Stp	2012-5-24	2012-8-3	0.079	0.004	0.017
8	IT-Ro2	2011-8-8	2011-9-13	0.177	-1.027	0.024
9	IT-Ro2	2011-10-14	2011-12-19	0.107	0.206	0.025
10	SD-Dem	2007-10-6	2008-4-17	0.392	-6.922	0.025
11	US-Blo	2004-7-19	2004-9-18	0.125	0.349	0.021
12	US-SRG	2008-9-21	2008-10-9	0.076	0.555	0.062
13	US-SRG	2012-9-23	2012-11-7	0.133	-0.018	0.052
14	US-SRG	2014-3-16	2014-4-17	0.025	0.852	0.031
15	US-SRM	2008-9-21	2008-11-25	0.285	-4.308	0.044
16	US-SRM	2011-10-2	2011-11-4	0.069	0.457	0.027
17	US-Ton	2002-6-6	2002-10-22	0.059	0.637	0.019
18	US-Ton	2005-6-26	2005-9-22	0.224	-4.782	0.018
19	US-Ton	2006-5-27	2006-10-1	0.054	1.425	0.015
20	US-Whs	2014-10-26	2014-12-2	-0.058	2.577	0.042
21	US-Wkg	2004-10-3	2004-10-20	-0.019	1.551	0.077
22	US-Wkg	2011-9-22	2011-11-4	0.073	0.571	0.064
23	BW-Ghg	2003-3-16	2003-4-7	0.105	0.524	0.075
24	BW-Ghm	2003-3-15	2003-4-7	0.100	0.682	0.068
25	BW-Ma1	2000-6-12	2000-9-14	0.003	1.388	0.008
26	BW-Ma1	2000-12-31	2001-1-31	0.018	1.128	0.050
27	DE-Meh	2006-7-18	2006-7-29	0.115	0.312	0.090
28	ES-ES1	2003-7-2	2003-8-9	0.164	-1.229	0.010
29	ES-ES1	2004-8-9	2004-8-29	0.109	-0.511	0.071
30	ES-ES1	2005-12-5	2005-12-17	0.105	0.553	0.056
31	IL-Yat	2001-5-6	2001-11-12	0.001	1.153	0.009
32	IT-Amp	2003-7-18	2003-7-30	0.091	0.643	0.033
33	IT-LMa	2004-9-21	2004-10-3	0.138	-0.156	0.066
34	ML-Kem	2007-12-2	2008-4-28	0.193	-0.470	0.009
35	ML-Kem	2008-11-17	2008-12-29	0.027	2.033	0.027
36	PT-Esp	2003-7-23	2003-8-26	-0.024	2.829	0.024
37	PT-Mi2	2006-7-31	2006-8-15	0.074	-0.816	0.069
38	US-Arb	2006-7-20	2006-8-2	0.335	-4.265	0.033
39	US-Arc	2006-7-16	2006-8-2	0.189	0.850	0.063
40	US-Aud	2003-10-15	2003-11-7	0.115	-0.578	0.073
41	US-Aud	2004-4-21	2004-5-13	0.030	0.390	0.031
42	US-Bo1	1998-9-2	1998-9-11	0.183	0.056	0.030
43	US-Bo1	1999-9-3	1999-9-11	0.160	-0.113	0.095
44	US-Bo1	2000-8-30	2000-9-9	0.176	-0.012	0.109
45	US-Bo1	2005-9-2	2005-9-13	0.055	0.954	0.045
46	US-FR2	2005-9-17	2005-10-2	0.095	1.044	0.079
47	US-Fuf	2005-10-18	2006-1-17	0.003	0.434	0.033