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Complexity in water and carbon dioxide fluxes following rain pulses in an African savanna

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Abstract The idea that many processes in arid and semi-arid ecosystems are dormant until activated by a pulse of rainfall, and then decay from a maximum rate as the soil dries, is widely used as a conceptual and mathematical model, but has rarely been evaluated with data. This paper examines soil water, evapotranspiration (ET), and net ecosystem CO₂ exchange measured for 5 years at an eddy covariance tower sited in an *Acacia-Combretum* savanna near Skukuza in the Kruger National Park, South Africa. The analysis characterizes ecosystem flux responses to discrete rain events and evaluates the skill of increasingly complex “pulse models”. Rainfall pulses exert strong control over ecosystem-scale water and CO₂ fluxes at this

site, but the simplest pulse models do a poor job of characterizing the dynamics of the response. Successful models need to include the time lag between the wetting event and the process peak, which differ for evaporation, photosynthesis and respiration. Adding further complexity, the time lag depends on the prior duration and degree of water stress. ET response is well characterized by a linear function of potential ET and a logistic function of profile-total soil water content, with remaining seasonal variation correlating with vegetation phenological dynamics (leaf area). A 1- to 3-day lag to maximal ET following wetting is a source of hysteresis in the ET response to soil water. Respiration responds to wetting within days, while photosynthesis takes a week or longer to reach its peak if the rainfall was preceded by a long dry spell. Both processes exhibit nonlinear functional responses that vary seasonally. We conclude that a more mechanistic approach than simple pulse modeling is needed to represent daily ecosystem C processes in semiarid savannas.

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Introduction

About half of global lands experience rainfall in deficit of evaporative demand at timescales from weeks to years (e.g., Slaymaker and Spencer 1998). In these water-limited systems, pulses of rain excite ecosystem dynamics such as microbial decomposition, germination and growth of plants, predator outbreaks and community succession (Schwinning and Sala 2004), with intervening periods of relative inactivity. Ecosystem water use, productivity, and respiration all

respond to the episodic availability of water (Austin et al. 2004; Baldocchi et al. 2006; Huxman et al. 2004; Jenerette et al. 2008; Porporato et al. 2001; Rodriguez-Iturbe et al. 1999; Xu et al. 2004). This has led dryland ecologists to propose various conceptual and mathematical models to describe ecosystem functional responses to pulses of rainfall or soil water (Schwinning et al. 2004). The pulse-reserve paradigm of Noy-Meir (1973), recently modified by Reynolds et al. (2004), and threshold-delay model of Ogle and Reynolds (2004) elaborated by Collins et al. (2008), span the earliest and most recent conceptual models proposed to represent ecological pulse responses. These conceptual descriptions of general system behavior tend not to be tested with data. It therefore remains to be seen if the pulse modeling paradigm is useful in the prediction of ecosystem water and C fluxes.

The pulse paradigm has promoted a focus on the roles of thresholds and lags in ecosystem dynamics (Schwinning et al. 2004). For example, evapotranspiration (ET) and net ecosystem CO₂ exchange are both stimulated by rainfall pulses (Gutierrez and Whitford 1978; Huxman et al. 2004; Knapp et al. 2002; Knapp and Smith 2001; Webb et al. 1978; Williams and Albertson 2004), but the degree, duration and timing of stimulation may be highly variable. While rapid responses to even small wetting events can occur (Fravolini et al. 2005; Sala and Lauenroth 1982), in other cases water and C fluxes exhibit a delayed response of several days associated with upregulation (physiological recovery from the preceding dry period), and this may reduce the impact of small pulses or reduce sensitivity during certain times of year (Baldocchi et al. 2006; BassiriRad et al. 1999; Schwinning and Sala 2004; Schwinning et al. 2003). Such nonlinear behavior has typically been evaluated using only a few wetting events and would benefit from more extensive quantitative assessment.

If ecosystem responses to rainfall are strongly dependent on when in the year they occur (seasonality) or antecedent vegetation and soil conditions, the simplest versions of the pulse paradigm may not be adequate for predictive modeling. “Path dependency” (i.e., a sensitivity to history), typical of highly seasonal environments (e.g., Scholes and Walker 1993) or those undergoing functional or structural transition (e.g., Briggs et al. 2005), adds complication to the model. Part of the within-pulse and seasonal pattern of water and CO₂ fluxes can be clearly attributed to direct effects of time-variation in environmental conditions (Baldocchi et al. 2004; e.g., Falge et al. 2002; Hui et al. 2003; Reichstein et al. 2002). Additional variability can be introduced by transience in functional responses to environmental conditions (Hui et al. 2003). For example, seasonal variation in temperature dependence of ecosystem respiration is often partially explained by coincident soil water status (Reichstein et al. 2002; Tang and Baldocchi

2005; Tang et al. 2005; Xu and Baldocchi 2004) but even this interaction fails to explain the particularly large CO₂ releases sometimes observed after even small wetting events following prolonged dry periods (e.g., Jarvis et al. 2007; Jenerette et al. 2008; Xu and Baldocchi 2004). The work of Ogle and Reynolds (2002) illustrates another time-varying functional response with *Larrea*, whose success in the face of drought may be enhanced by seasonal acclimation of stomatal response to plant water status with growing season temperature. Such functional adjustments are a challenge to model using simplified pulse-response approaches. This leads us to investigate in this paper the degree of variation of water and CO₂ flux responses to soil water pulses in a semi-arid savanna, and how much of that variation is captured by models of increasing complexity.

We address the following hypotheses:

1. Soil water pulses stimulate ET, productivity, and respiration processes, with a general decline in activity during the ensuing dry-down (hypothesis 1).
2. The time lag between the increase in soil water and the peak of activity varies between these three (i.e., ET, productivity, and respiration) processes (hypothesis 2).
3. The magnitude of the peak, and lag time to peak, both increase with the intensity of ecosystem dryness prior to re-wetting (hypothesis 3). This stems from a general expectation of the need for upregulation of ecosystem physiological activity following dryness-induced dormancy, akin to the “Birch effect” discussed below.
4. As a consequence of the above factors, a time-invariant pulse-response model with a fixed characteristic shape misses modulation by seasonal phenology and antecedent wetness, and thus represents daily fluxes poorly (hypothesis 4).

To address these hypotheses we analyze time series of soil water, ET, and net ecosystem CO₂ exchange (partitioned into production and respiration) measured over 5 years in an *Acacia-Combretum* savanna in South Africa. Our analysis assesses the degree to which coincident weather and surface states control ecosystem flux responses to discrete rainfall events. It begins by documenting the average response of C and water fluxes to soil water pulses. Then, using a 5-month case study which contains three main pulse events, we show such responses to be time-variant and nonlinear. We quantify lags in the response of water and CO₂ fluxes to wetting, and then test the ability of alternate “pulse models” of increasing complexity to capture lagged ecosystem responses. The discussion explores minimum parameterization of ecosystem flux responses to soil water pulses, comments on the implications of our findings for the pulse paradigm, and outlines specific challenges that remain in representing complex, transient ecosystem responses to pulses.

Materials and methods

Site characteristics

The flux and state observations analyzed in this study were taken between April 2000 and August 2004 at a site 15 km south west of Skukuza, South Africa. The Skukuza site is 370 m a.s.l, receives 550 ± 160 mm of rainfall annually, with about 65 rainy days per year almost entirely between November and April. The year is divided into a hot, occasionally wet growing season and a warm, dry non-growing season (Fig. 1).

The shallow coarse sand to sandy loam soils (about 65% sand, 30% clay, and 5% silt) overlay granite, which outcrops in places (Biggs et al. 2003; Sankaran et al. 2004). The landscape is gently undulating, with broad-leaved savanna on the crests dominated by the small tree *Combretum apiculatum*, and fine-leaved savanna in the valleys dominated by *Acacia nigrescens* (Scholes et al. 1999). Within the 300×300 -m square centered on the tower, tree cover is about 28% and evenly mixed between *Combretum* and *Acacia*. Woody plant basal area is $7 \text{ m}^2 \text{ ha}^{-1}$ (Scholes et al. 1999). Tree canopies average 5–8 m high with

occasional trees (mostly *Sclerocarya birrea*) reaching 10 m. The grassy and herbaceous understory contains *Panicum maximum*, *Digitaria eriantha*, *Eragrostis rigidor*, and *Pogonarthria squarrosa* among others. The tree and herbaceous vegetation both root throughout the ~ 0.6 -m-deep soils.

Leaf area index (LAI; $\text{m}^2 \text{ leaf m}^{-2} \text{ ground}$) from 2000 to 2004 was obtained from MODIS LAI cutouts centered over the Skukuza site, made available through the Oak Ridge National Laboratory Distributed Active Archive Center and recalibrated ($\text{LAI}_{\text{field}} = 0.5 \text{ LAI}_{\text{MODIS}}$) against in situ observations made on multiple occasions with a Decagon Accupar ceptometer (Pullman, Wash.) at 49 systematically sampled locations within 150 m of the tower. Growing season LAI averaged about 1.1 (Fig. 1) during the period of flux tower observations reported here, but has reached as high as 2.0 for the more extended MODIS LAI record.

Measurements and data processing

A 22-m tower was instrumented at 16 m with a sonic anemometer (Gill Instruments Solent R3, Hampshire, England) measuring three-dimensional, orthogonal components of velocity (u, v, w ; m s^{-1}) as well as the “sonic” air temperature (T_a ; $^{\circ}\text{C}$), and a closed-path infrared gas analyzer (IRGA; LiCor 6262; LiCor, Lincoln, Neb.) measuring concentrations of water vapor (q ; $\text{mmol H}_2\text{O mol}^{-1}$ moist air), and CO_2 ($\mu\text{mol CO}_2 \text{ mol}^{-1}$ air). Manual IRGA calibrations were performed approximately monthly. Calibrations were done in the field using Level-5 (99.999% pure) N for CO_2 and H_2O zero (this was also the reference gas running continuously through the reference cell in the 6262). Spans were carried out using National Oceanographic and Atmospheric Administration (NOAA) secondary standard calibration gases calibrated to <0.2 p.p.m. for CO_2 and a LiCor dew point generator for H_2O . Analytical flux footprint estimation (Gash 1986; Hsieh et al. 2000) indicates that a source area within 130 m upwind of the tower typically contributes 90% of the measured flux and a source area within 1.3 km contributes 99% of the flux.

Post-processing of the raw high frequency (10 Hz) data for calculation of above-canopy turbulent fluxes of sensible heat (H ; W m^{-2}), water vapor (LE; W m^{-2}), and CO_2 (F_c ; $\text{g CO}_2 \text{ m}^{-2} \text{ time}^{-1}$) calculated for half-hour periods is consistent with methods advised in Lee et al. (2004), and involved standard spike filtering, planar rotation of velocities applied to monthly data for 60° sectors (Wilczak et al. 2001), as well as lag correction to CO_2 and q from analysis of monthly peaks in lagged cross-correlations of vertical velocity and scalars. Heat and mass fluxes were calculated with conventional equations (see e.g., Aubinet et al. 2000;

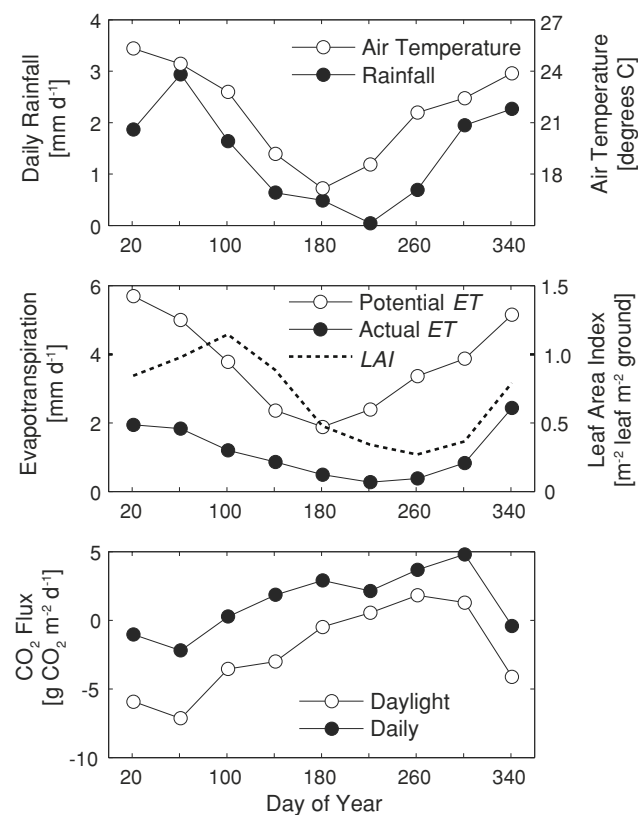


Fig. 1 Mean seasonality of environmental states and fluxes at the Skukuza site, averaged for observations within 40-day windows over years 2000–2004. LAI Leaf area index, ET evapotranspiration, d^{-1}

Moncrieff et al. 1997). All fluxes are reported as positive upward from the land to the atmosphere. Frequency response correction of some of the energy lost due to instrument separation, tube attenuation, and gas analyzer response for LE and F_c was performed with empirical cospectral adjustment to match the H cospectrum (Eugster and Senn 1995; Su et al. 2004).

Canopy storage flux was estimated from the half-hourly time derivative of a 16-m-column integral based on CO_2 concentrations measured with PP Systems (Amesbury, Mass.) CIRAS-SC infrared gas analyzers in two separate profiles 40 m on either side of the main tower, with air intake at heights of 0.75, 2.0, 3.5, and 5.25 m, plus the 16-m concentration on the main tower, and added to the above-canopy turbulent flux for data analysis. Average half-hourly incoming and outgoing longwave and short-wave radiation was measured with a Kipp and Zonen (Delft, The Netherlands) CNR1 radiometer mounted at 22 m, the balance of which provides net radiation (R_n ; W m^{-2}).

Average half-hourly volumetric soil water content (θ ; $\text{m}^3 \text{H}_2\text{O m}^{-3}$ soil) was estimated with 15-cm-long Campbell Scientific (Logan, Utah) frequency domain reflectometry probes (CS615) installed horizontally in four separate profiles, two in the *Acacia*-dominated [probes at soil depths (z , cm) of 3, 7, 16, 30, and 50 cm] and two in a *Combretum*-dominated area (probes at 5, 13, 29, and 61 cm). The probes have not been locally calibrated, and while manufacturer notes suggest absolute accuracy to within 2%, our estimates of soil water content are approximate, still providing a robust measure of the relative moisture dynamics. Half-hourly averaged soil heat flux (G , W m^{-2}) was obtained with HFT3 plates (Campbell Scientific) installed 5 cm below the ground both under and between tree canopies. Rainfall per half-hour was measured with a tipping bucket rain gage (TE525-L; Campbell Scientific) located on the tower top.

Above-canopy vapor pressure deficit was calculated as the difference between the saturation vapor pressure at T_a and near surface atmospheric pressure (P_a ; recorded at a nearby weather station), and the atmospheric water vapor pressure obtained from q and P_a . Total root zone soil water (S ; cm) was calculated as the sum of S_i , where

$$S_i = \begin{cases} \theta_1[(z_2 - z_1)/2 + z_1] & \text{for } i = 1 \\ \theta_i(z_{i+1} - z_{i-1})/2 & \text{for } 1 < i < N \\ \theta_N[65 - ((z_N - z_{N-1})/2 + z_{N-1})] & \text{for } i = N \end{cases} \quad (1)$$

and where N is the number of measurement depths. While we considered a root zone weighting of soil moisture for use in analyses of canopy ecophysiology, we proceeded with this bucket approach given that all the plant functional

types present in the tower's footprint root throughout the profile. Daily potential ET rate (PET; mm day^{-1}) is estimated with the Priestley and Taylor (1972) formulation

$$\text{PET} = \sum_{i=1}^{48} \left[\alpha(R_{ni} - G_i) \frac{\Delta}{\Delta + \gamma} \right] \frac{\tau}{L_v}, \quad (2)$$

where α ($= 1.26$) accounts for large-scale advection and entrainment, γ ($= 0.67 \text{ mb } ^\circ\text{C}^{-1}$) is the psychrometric constant, L_v ($= 2.45 \times 10^6 \text{ J kg}^{-1}$) is the latent heat of vaporization, Δ ($\text{mb } ^\circ\text{C}^{-1}$) is the slope of the saturation vapor pressure curve (Campbell and Norman 1998), and τ ($= 1,800$) is the number of seconds per half hour. Total daily ET (mm day^{-1}) is calculated from LE, L_v and τ . Energy balance closure, $(H + \text{LE})/(R_n - G)$, averages 74% for half-hourly data and $86 \pm 17\%$ for the daily time scale.

C fluxes are also represented as temporal sums over daily (24 h), daytime (12 h from 0800 to 2000 hours), and nighttime (8 h from 2200 to 0600 hours) of the day. Data were only included in the summation if friction velocity exceeded 0.1 m s^{-1} , a widely used threshold for valid eddy covariance measurements (Baldocchi 2003). In addition, a 15-day mean diurnal replacement as in Falge et al. (2001) was applied to fill missing values for daytime, nighttime and daily summations. Summations of gap-filled data were included in analyses only if fewer than 10% of the data had been filled by this procedure.

Analyses

The average temporal dynamics of fluxes responding to significant soil wetting events ($\geq +5 \text{ mm}$ soil water) are calculated for dry and wet season populations during the period April 2000 to July 2004. Here, observations were only included for a lag of one up to n days if a second soil wetting ($S \geq 5 \text{ mm}$) did not occur during the period. Neither the mean depth of a rainfall event nor the post-pulse accumulated rainfall differs between the dry and wet populations; the key difference is the gap between rainfall events. Functional control of fluxes by root-zone soil water was also examined with averages for data during the growing season. In both the temporal and functional analyses we investigate the presence of lags to peak response.

To more directly assess dynamics of the main C exchange processes we apply a simple approach to separating the net flux (F_c) into respiration and production components. Respiration is estimated by scaling mean nighttime CO_2 flux to a 24-h total, then subtracting this from total daily CO_2 flux to obtain an estimate of daily photosynthetic productivity. Temperature variations during the summer growing seasons at this site do not include extreme low or high temperatures that severely limit plant

or microbial physiology. Lacking clear relationships between nighttime CO₂ flux and air or soil temperature, it was not appropriate to include temperature as an independent variable in the estimation of daily respiration based on nighttime CO₂ flux despite its conventional appeal.

Time-dependency of water and C flux responses is examined with a case study from a 5-month period of 2003, illustrating lags and their association with time-varying environmental conditions. Then, to move toward predictive understanding of the observed lags and peaks, we evaluate two metrics of the recent history of water status in terms of their skill in predicting the lags of respiration and productivity. The first is simply an average of the x -day history of soil water content (S_x). The second is an index of water deficit days (WDD _{x}), defined as the cumulative sum of daily soil water deficits since the last time [T (days) with a max of x days] soil water dropped below a threshold (7 cm) level below which H₂O and CO₂ fluxes transition into a water-limited state at this site (evidenced in the results), and formally

$$\text{WDD}_x = \sum_{t=1}^T 7 - S_t, \quad (3)$$

where $t = 1$ to T days prior and T cannot exceed x days prior. The two metrics are negatively, linearly related below the threshold and unrelated above it. They are alternate means of representing a similar phenomenon. Only ten events contained the necessary data for inclusion in this analysis, which requires a rain event followed by rain-free conditions and gapless daily fluxes for at least as long as the 10-day lag period, and a pre-pulse record of at least as long as the relevant WDD history.

The final analyses involve a “model intercomparison”, evaluating data support from the full measurement record for empirical models of daily water and C processes that vary in complexity. We used the simplest possible representation of a pulse response—a “square wave” in which ET/PET, respiration, and productivity are assigned a constant high value where S is greater than 5 cm, and a low value if not—as a reference point, and then added progressive refinements. Rather than imposing a particular functional form to these more complicated models a priori, base models were first selected from regression fits of a wide range of linear and nonlinear models using the CurveFinder function of the program CurveExpert 1.3. From this analysis we found that linear and logistic models tended to provide the best functional descriptions without an excessive number of parameters. We then explored linear and logistic dependence of ET/PET, respiration, and productivity each on: (1) day of year as a purely seasonal model, (2) 0- to 30-day average rainfall, (3) 0- to 20-day

average S , and (4) 0- to 100-day WDD histories (Eq. 3). As a third step in model testing, we performed a linear regression of the residuals on LAI (linearly interpolated to a daily series). Full details of the model exercise can be found in the Electronic Supplementary Material.

Results

Pulse responses

Figure 2 shows the characteristic flux responses of ET, net ecosystem exchange, and respiration to rainfall pulses and associated soil wetting events ($\geq +0.5$ cm soil water). Soil water declines monotonically following wetting events, with an average decline of 40% between the peak and 30 days after wetting. ET and respiration (inferred from nighttime F_c) are both rapidly stimulated, with an initial increase to their maxima that lags 1–4 days after rainfall, followed by a general (though variable) decay. For ET, dry and wet season responses differ according to an analysis of covariance (ANCOVA) grouping by dry or wet season and testing covariation with time since wetting, which yielded a non-significant interaction (season \times time $P = 0.7497$) but significant dependence on both season ($P < 0.0001$, $df = 207$) and time ($P = 0.0004$, $df = 207$). The dry season pulse response of ET is lower and also slightly delayed because of the drier initial condition but reaches a similar peak to that achieved in the wet season. In contrast, the response of respiration to wetting did not differ between seasons (ANCOVA season \times time $P = 0.2644$, season $P = 0.351$, time $P < 0.0001$ with $df = 257$), though the daily net ecosystem exchange response did (ANCOVA season \times time $P = 0.0186$, season $P < 0.0001$, time $P = 0.004$, $df = 255$).

The rapid response of respiration to soil wetting dominates the daily total net C exchange (F_c) during the first 3 days after rainfall, suggesting that upregulation of productivity in response to the moisture pulse is delayed. This interpretation is supported by the continued net release of CO₂ for the dry season population, in contrast to the switch to net ecosystem C uptake (negative F_c) in the wet season, peaking on average about 9 days after wetting. A wide spread about the average for each functional response indicates that a single characteristic response irrespective of the degree of wetting, prevailing environment, or antecedent conditions provides a poor system description even when seasonally stratified. The fit is poorest for daily F_c .

An alternative to constructing the “characteristic” pulse trajectories shown in Fig. 2 is a functional response to soil moisture, independent of time, as shown in Fig. 3. While there is considerable variability around these average functional responses, the broad patterns are clear. ET, when

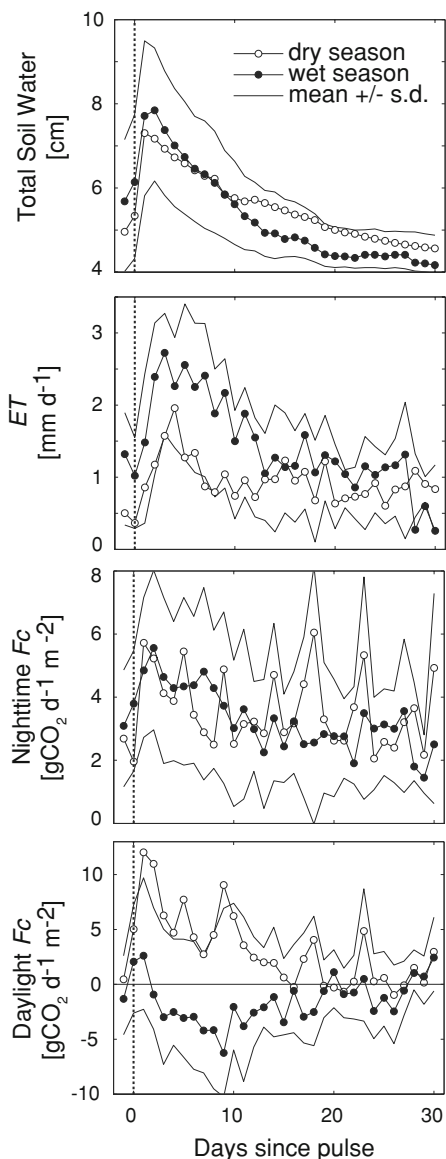


Fig. 2 Average (*bold line*) soil moisture, daily evapotranspiration, nighttime CO₂ flux, and daytime CO₂ flux following rainfall pulses averaged across 53 events of varying event size and preceding rain-free duration during the 2000–2004 observation period. Data are pooled into dry season (*open symbols*) and wet season (*closed symbols*). *Thin lines* represent ± 1 SE about the mean across dry and wet seasons combined for visual clarity

expressed relative to PET, is well predicted by a logistic function of total root zone water content (cm): $ET/PET = 0.59/[1 + 4,170 \exp(-1.78 S)]$, with a SE of regression = 0.11, coefficient of determination (R^2) = 0.70, and P -value < 0.001. Nighttime CO₂ flux (i.e., respiration) shows a remarkably similar positive relationship with total root zone water content {respiration ($\text{g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$) = $5.5/[1 + 269 \exp(-1.15 S)]$; $R^2 = 0.36$, $P < 0.001$ } These relatively simple log-linear

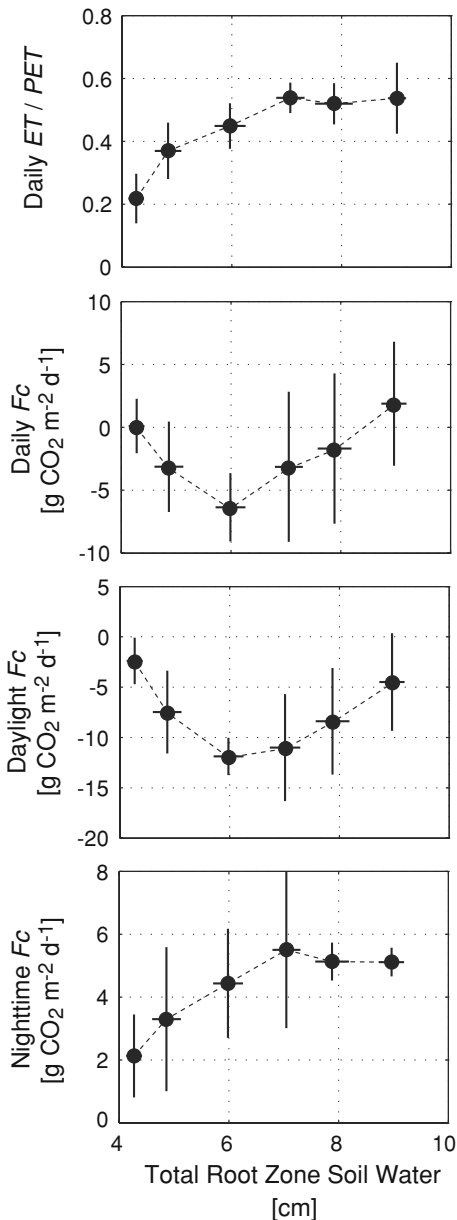


Fig. 3 Growing season (December–March, 2000–2004) average functional responses of CO₂ fluxes and ET to profile soil water content. One SD ranges shown with *solid vertical and horizontal lines*

functional responses to soil water content are consistent with the short lag times for these processes.

In contrast, responses of both daytime (12 h) and daily (24 h) net ecosystem exchange are more complex, since they include the longer lag inferred for photosynthetic upregulation. CO₂ exchange during daylight hours shows an apparent minimum (i.e., maximum uptake given that downward fluxes are negative) at intermediate rather than high soil water content, because the rapid decline in soil moisture in the days after wetting, coupled with a photosynthetic response lagged by up to a week, tends to obscure

the expected monotonic relation between soil moisture and net ecosystem exchange. Similarly, net 24-h CO_2 flux is apparently near zero at high soil water content, reaches a minimum at intermediate soil water content, and is near zero again when the soil is dry.

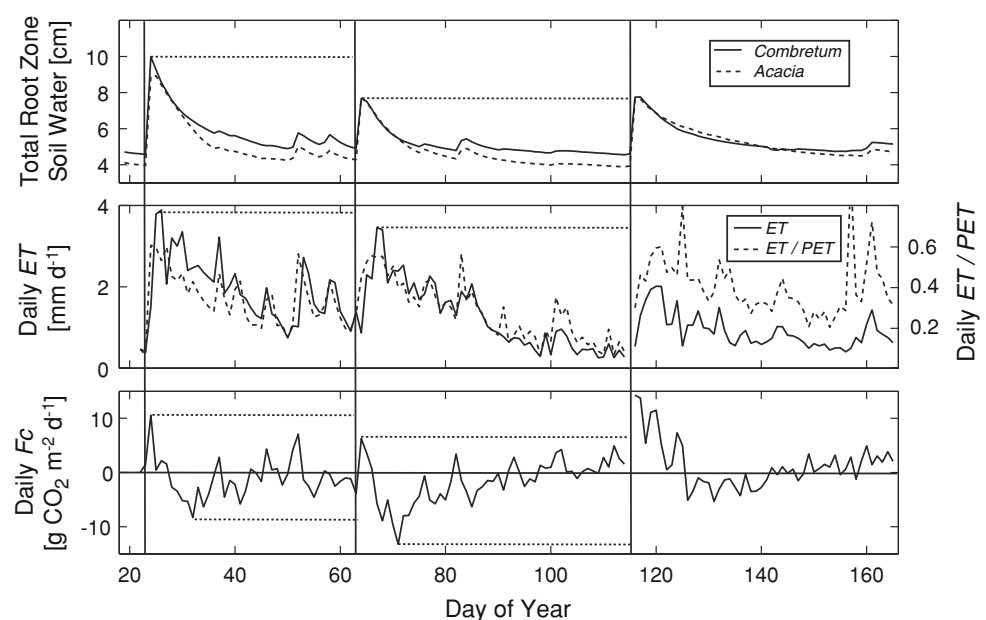
To examine the time dependency of these patterns, we turn to a case study from a 5-month period during 2003 (Fig. 4) extending from the peak of the wet season (February) through the early dry season (June). The LAI declined from about 0.7 to 0.4 during this period (linear regression, $P = 0.082$). The three largest daily rainfall pulses were 54, 36, and 37 mm (the third pulse spanning 2 days). Soil water content is seen to exert strong control on water and CO_2 fluxes, with ET increasing, and F_c initially rising to a positive peak, then switching to negative values peaking after about a week, then returning gradually to close to zero. However, comparison of flux responses between major wetting events shows that soil water is only one of a suite of environmental controls governing ET and F_c . Despite 1.3 times more water initially available in the first event [day-of-year (DOY) 23] relative to the second (DOY 63), peak ET was nearly identical. Furthermore, minimum F_c was about 2 times lower for the second event, with about $5 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ more CO_2 uptake for the DOY 63 event than the DOY 23 event after a lag of 8 days. Considering that net ecosystem CO_2 exchange is the difference between respiration and production, it could be inferred that respiration declines more rapidly for the event with lower soil water content (as in Fig. 3) or alternatively that production exhibits an acclimation to prior wetting, with a higher maximal productivity for an ecosystem already upregulated by recent wetting.

Comparing the second and third major wetting events (DOY 63 and 117), peak total root zone soil water is nearly equal (Fig. 4). However, soil water declines more rapidly in the second compared to the third wetting event, corresponding with a peak ET that is 1.7 times higher in the former. This is largely explained by the relatively low PET at the time of the third compared to second wetting event: note that the magnitude of ET/PET is similar in both cases (Fig. 4). However, this cannot explain the large difference in net C flux between the second and third events. Net C flux for each day after wetting is about $10 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ higher (more positive) for the third than second event. The difference is likely due to the respiration term remaining high but photosynthesis being reduced due to leaf senescence and abscission. Die-off of the herbaceous vegetation typically starts at the end of April in this region, while tree leaf fall begins during May if the soil dries out.

Respiration responds more rapidly to wetting than does productivity (Fig. 5), with a 1- to 3-day lag to the maximum respiration response and a 4- to 14-day lag to the maximum productivity response. Nonetheless, despite a relatively long lag to the peak productivity response, productivity begins to increase on the day immediately following soil water pulses (Fig. 5), rising slowly thereafter. In addition, small wetting events ($2\text{--}10 \text{ mm day}^{-1}$ of rain), despite leading to only slight increases in total root zone soil water, cause distinct increases in respiratory C flux but little or no response in productivity (Fig. 5, arrows).

Peaks and lags of ET/PET, productivity, and respiration responses to wetting are not related to the size of rain events triggering pulse responses ($P > 0.15$), and peaks are also unrelated to water stress history ($P > 0.25$). However,

Fig. 4 Time series of soil moisture pulses and associated daily (24 h) water and CO_2 flux responses spanning day-of-year 18–170 of 2003. Dotted lines provide a visual reference of the maximum responses for various processes contributing to ecosystem fluxes



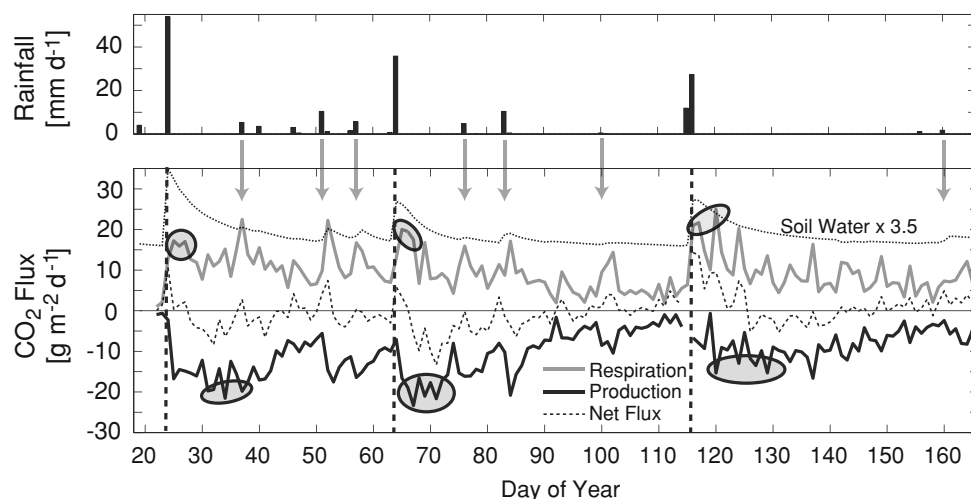
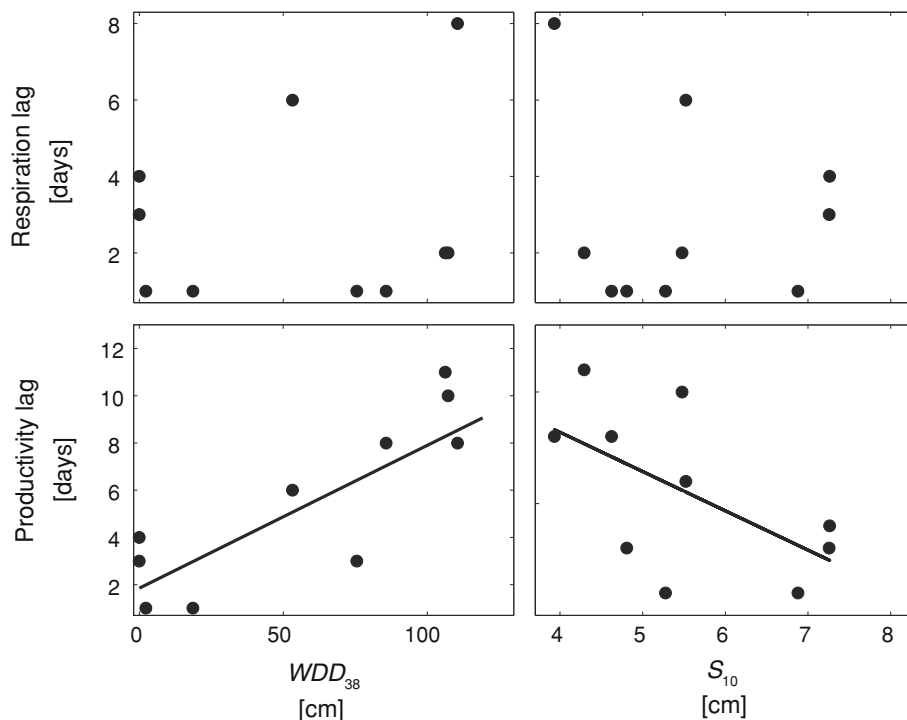


Fig. 5 Daily rainfall (*top panel*), respiration and production estimates (*bottom panel*) for a 5-month case study in 2003, where respiration is estimated from measured nighttime C flux and production is the difference of respiration and 24-h net C flux. Also shown is total root zone soil water (cm) measured in the *Acacia* savanna (increased by a

factor of 3.5 for clarity). *Dashed vertical lines* indicate major wetting events. *Dashed ellipses* highlight maximum production and respiration responses following wetting. *Arrows* highlight responses to smaller wetting events

Fig. 6 Lag to maximum respiration or productivity response versus the 38-day water deficit days index (WDD_{38}) and the 10-day average history of total root zone soil water (S_{10})



the lag time to peak productivity shows linear dependence on WDD_{38} ($R^2 = 0.72$, $P = 0.002$) and somewhat weaker dependence on S_{10} ($R^2 = 0.35$, $P = 0.073$) (Fig. 6). The subtle respiration lag is not predicted by water stress history ($P \geq 0.608$) (Fig. 6).

Model comparison

Figure 7 presents results of the model comparison, reporting statistics for the water stress index (S_x or WDD_x) that maximized model efficiency where appropriate.

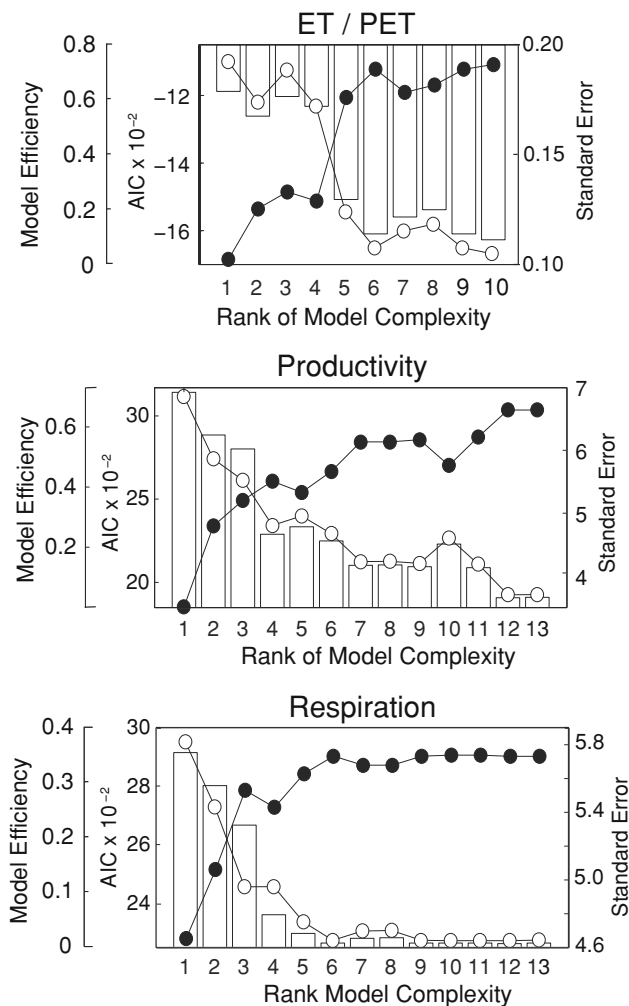


Fig. 7 Statistics of model fitting for ET/potential ET (PET), productivity, and respiration showing Akaike information criterion (*AIC*; bars), model efficiency or r^2 (closed circles), and SE of regression (open circles), where numbers on the x-axis correspond to the following models: linear regression with daily rainfall (1), linear regression with day of year (offset for water year) (2), square wave—constant values for a low soil moisture or high soil moisture class (3), 30-day moving average rainfall history (4), linear function of daily soil moisture (5), logistic function of daily soil moisture (6), linear function of x-day moving average soil moisture history (7), linear function of x-day moving average soil moisture history with linear function of LAI for residuals (8), logistic function of x-day moving average soil moisture history (9), logistic function of daily soil moisture with linear function of LAI for residuals (10), logistic function of x-day moving average soil moisture history with linear function of LAI for residuals (11), linear function of x-day history for WDD (12), linear function of x-day history for WDD with linear function of LAI for residuals (13). For other abbreviations see Figs. 1 and 6

Overall, the purely seasonal, square wave, and rainfall-based models performed poorly compared to models dependent on soil moisture, though prediction with rainfall alone did improve with increased time averaging from daily to a 30-day history.

For ET/PET, predictive skill is greatly improved from the square wave to a model that includes a linear dependence on soil water content (S), and was further modestly improved by a logistic dependence on S . AIC only weakly supported LAI as an additional predictor, accounting for longer term (8 days to several months) variations, explaining only an additional 2% of the variability in ET/PET. Remaining variation is partly due to the hysteresis resulting from the lag to maximal ET following wetting. However, a logistic function of soil water history (S_x) decreases the fit relative to simply using the soil water content on the day. Taken together, an equation of the form $ET = PET \times [\text{logistic } f(\text{soil water}) + \text{linear } f(\text{leaf area})]$ explains 72% of the variation in daily ET at the savanna site studied in this work.

Respiration is also better described by a logistic function of soil water than a square wave or linear model, but only 36% of the variance is explained and LAI adds little to no explanatory power. Models of productivity benefited most from added complexity. Including the effect of water stress history (the 15-day average soil moisture, or accumulated water stress days) generally improved the fit to productivity by capturing a short-term “memory” of ecosystem water status and the associated lag in productivity response. Residual dependence of productivity on LAI was poorly supported by information criteria and provides only a marginal increase to the coefficient of determination or reduction to SE of regression.

Discussion

Results confirm that rainfall events stimulate pulse responses of ET, respiration and productivity at the daily time scale in the savanna under study (hypothesis 1). Only a subtle lag to peak stimulation for ET and respiration, is contrasted by a significant lag to peak for photosynthesis, taking a week or longer to reach its peak and supporting hypothesis 2. Correspondingly, prior dryness was not a predictor of lags in ET or respiration responses; however, intensity and duration of pre-pulse dryness is a valuable predictor of lags in productivity, supporting hypothesis 3. It is still worth mentioning that a short, 1–3 day, lag to maximal ET following wetting is a mild source of hysteresis in the ET response to soil water even after controlling for PET variation.

The temporal dynamics of NEE reported here, with faster upregulation and ensuing decay for respiration compared to productivity, are consistent with those documented for irrigated grass communities of Arizona (Huxman et al. 2004), as well as a number of conceptual models (e.g., Schwinning et al. 2004). Rapid, punctuated increase in respiration following wetting as reported here is

common in water-limited systems (Jenerette et al. 2008; Xu and Baldocchi 2004). However, soil wetness accounts for only 36% of the total variation in respiration observed at the Kruger savanna. Again, pre-pulse dryness is not a significant predictor of respiration dynamics. Temperature dependence of respiration is unclear at the site though results from Kutsch et al. (2008) suggest that it may still account for some of the remaining variation. Perhaps more importantly, some measure of the availability of C substrate is a sensible candidate, possibly capturing a “Birch effect” (see Jarvis et al. 2007), meaning a burst of microbial decomposition and N mineralization excited by the rewetting of soils that have been dry for a long period. However, it is not possible to separate autotrophic and heterotrophic respiration from the ecosystem total fluxes alone and thus attribution of pulse respiration to a Birch effect cannot be evaluated here.

Results suggest that an integrated measure of plant water status such as stress history would improve model predictions of productivity. We note, however, that the peak magnitude does not depend on pre-pulse dryness. Thinking about mechanisms, it is not surprising that ecosystem physiological responses to wetting are delayed by prolonged dry spells, particularly in a water-limited system in which vegetation dehydrates and becomes dormant at monthly to seasonal time scales. One might then expect part of the variation in lag to peak productivity to be captured by LAI, so the general lack of residual dependence on LAI may seem surprising. However, this can be explained by the temporal correlation of LAI with S_x and WDD_x (the correlations were 0.79 and -0.79 for x equal to 20 days). Thus most of the effect of LAI is already expressed in the water stress index.

Implications for the pulse-reserve paradigm

The pulse-reserve paradigm, introduced by Noy-Meir (1973), modified by Reynolds et al. (2004), and reconceived as the threshold-delay model by Ogle and Reynolds (2004), purports to describe ecological dynamics based on a very simple principle: there is a characteristic pulse of activity following a wetting event. It is attractive because it reduces the system to a few simple inputs, such as initial resource condition and the time since a pulse. But this study demonstrates that in order to realistically capture the observed behavior of a pulsed system, pulses need detailed parameterization to adjust the generalized unit response function for weather, vegetation, and the recent history of the system (hypothesis 4), and likely for soils and climate. Such parameterizations may be site specific, and thus not suitable for extrapolation in general predictive models.

While the pulse-response approach lends itself to synthetic parameterization of system lags and thresholds such

as those documented here for the Skukuza site, our observations suggest that a reduced-form pulse-response model is probably not an appropriate choice for capturing the daily dynamics of net ecosystem CO_2 exchange (hypothesis 4). Models that represent the differentially lagged temporal responses of ET, respiration and productivity appear necessary. Thus, while the pulse-response paradigm has value for conceptualizing time-domain variation of ecosystem processes, the approach has few advantages for predicting how water and C dynamics relate to a changing environment.

Minimum parameterizations

Nonetheless, suggestions for minimum parameterizations emerge. For example, findings from the Skukuza tower site lend confidence to widely applied space-time models describing the co-evolution of ET and soil water dynamics (e.g., Rodriguez-Iturbe et al. 1999; Williams and Albertson 2005). In such minimum parameterizations, the core system behavior that needs to be carefully prescribed is the daily rate of ET as a function of soil water, with additional adjustment by vegetation fractional cover or leaf area. The daily canopy-scale ET of the heterogeneous savanna studied here is well-characterized by PET, total root zone soil water, and seasonal vegetation dynamics, consistent with Williams and Albertson (2005). While a sub-daily resolution may be important for some applications (i.e., land surface coupling to the atmospheric boundary layer) we find that 72% of the interstorm to seasonal dynamics are captured at a daily resolution.

Our findings also provide general support for the use of simple (“bucket”) soil water models, indicating that the added complexity of multi-layer models that parameterize wetting fronts, root distributions and soil water potential may not always be needed for describing daily to monthly time-scale behavior of the coupled ET and soil water dynamics. However, we note that sites with deeper soils might still require a soil water model and root distribution model with vertical detail, especially where there exists a vertical root niche separation between trees and grasses influencing their relative activity.

Previous work has explored the use of a constant canopy-scale water use efficiency to characterize daily net CO_2 flux as a function of ET during the growing season (Scanlon and Albertson 2004; Verhoef et al. 1996; Williams et al. 2004) motivated by functional coupling of leaf-scale water and CO_2 exchanges combined with similar sensitivity to soil water for productivity and respiration. In this study, the different time scales of the respiration and productivity responses to wetting call that idea into question. We note that the ratio of average monthly F_c to ET is surprisingly conservative during the growing season but different in

the dry season (not shown but can be loosely inferred from Fig. 1). While the application of seasonally varying parameters could improve fit, a more mechanistic approach would be preferred, possibly by representing temporal dynamics of likely drivers of ecosystem process peak rates, such as labile soil C, or lags, such as vegetation water stress history.

Some challenges

Space-time variation in the critical parameters that control how soil water status influences bare soil evaporation and transpiration is still limited by scarcity of detailed observational data. The few datasets that do exist tend to describe canopy-scale aggregate ET, field-scale ET from lysimetry, or leaf-scale transpiration on individual plants (Baldocchi et al. 2004; Black 1979; Dunin and Greenwood 1986; Federer 1979; Kurc and Small 2004; Mahfouf et al. 1996; Teuling et al. 2006; Williams and Albertson 2004). Aggregating or disaggregating these measures to the scale of functional units such as whole plants, plant functional types, or landscape patches continues to be a challenge, though stable isotopes (e.g., Ferretti et al. 2003; Williams et al. 2004; Yezpez et al. 2003) could be very helpful.

The biological mechanisms that cause lagged responses of respiration and productivity are still speculative. While recovery from a desiccated, water-stressed state is qualitatively understood and may even be parameterized experimentally, biochemical and biophysical models have not advanced to the level of refinement needed to characterize such up- or downregulation in a mechanistic way. Similarly, models that contain the detailed soil and plant biogeochemistry needed for characterizing C pool dynamics (e.g., Century, CASA, or Biome-BGC) are only beginning to be implemented at the daily time scale, and likely still miss the pulse-like responses that characterize water and C fluxes in intermittently wetted, semi-arid biomes.

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