

This discussion paper is/has been under review for the journal Biogeosciences (BG).
Please refer to the corresponding final paper in BG if available.

How do more extreme rainfall regimes affect ecosystem fluxes in seasonally water-limited Northern Hemisphere temperate shrublands and forests?

I. Ross¹, L. Misson^{1,†}, S. Rambal¹, A. Arneith^{2,3}, R. L. Scott⁴, A. Carrara⁵,
A. Cescatti⁶, and L. Genesis⁷

¹CEFE-CNRS, 1919 route de Mende, 34000 Montpellier, France

²Department of Earth and Ecosystem Sciences, Lund University, Sweden

³Karlsruhe Institute of Technology, Institute for Meteorology and Climate Research/Atmospheric Environmental Research, Garmisch-Partenkirchen, Germany

⁴USDA ARS, SW Watershed Research Center, Tucson, AZ 85719 USA

⁵Fundación CEAM, Paterna 46980, Spain

⁶European Commission, Joint Research Centre, Institute for Environment and Sustainability, Ispra, Italy

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



⁷Institute of Biometeorology (IBIMET), National Research Council (CNR), Via Caproni 8,
51045 Firenze, Italy

[†]deceased

Received: 1 September 2011 – Accepted: 20 September 2011

– Published: 29 September 2011

Correspondence to: I. Ross (ian@skybluetrades.net)

Published by Copernicus Publications on behalf of the European Geosciences Union.

BGD

8, 9813–9845, 2011

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Abstract

As a result of climate change, rainfall regimes became more extreme over the course of the 20th century, characterised by fewer and larger rainfall events. Such changes are expected to continue throughout the current century. The effect of changes in the temporal distribution of rainfall on ecosystem carbon fluxes is poorly understood, with most available information coming from experimental studies of grassland ecosystems. Here, continuous measurements of ecosystem carbon fluxes and precipitation from the worldwide FLUXNET network of eddy-covariance sites are exploited to investigate the effects of differences in rainfall distribution on the carbon balance of seasonally water-limited shrubland and forest sites. Once the strong dependence of ecosystem fluxes on total annual rainfall amount is accounted for, results show that sites with more extreme rainfall distributions have significantly lower gross productivity, slightly lower ecosystem respiration and consequently a smaller net ecosystem productivity.

1 Introduction

During the 20th century, intra-annual rainfall patterns shifted. Both precipitation intensity and the frequency of large rainfall events increased (Easterling et al., 2000; Trenberth, 2011). Studies have shown globally consistent (although spatially complex at large scales) increases in metrics of rainfall extremes (Tank and Konnen, 2003; Karl et al., 1996; Peterson et al., 2008; Alexander et al., 2006). Further anthropogenic climate change is expected to intensify this shift towards fewer, larger events (Trenberth et al., 2003). For the 21st century, general circulation models predict little change in total rainfall, but an increase in the frequency of heavy rainfall events (Tebaldi et al., 2006). Many regional climate change projections anticipate increased seasonality in precipitation (Manabe and Wetherald, 1987), with consistently drier summers over entire regions (e.g., southern and central Europe: Rowell and Jones, 2006).

BGD

8, 9813–9845, 2011

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



While the impacts of changes in rainfall amount on ecosystem productivity have received some attention (Wu et al., 2011), the ecological implications of greater intra-annual rainfall variability are less well understood (Jentsch et al., 2007), and results have so far been contradictory. There is evidence that increases in rainfall variability may exert as strong a control on future biogeochemical cycles as changes in total rainfall, atmospheric warming or increases in atmospheric carbon dioxide concentrations (Knapp et al., 2002; Weltzin et al., 2003). Knapp et al. (2002) used rainfall shelters in a mesic grassland to show that more extreme rainfall distributions, without concurrent changes in total rainfall quantity, increased plant species diversity but decreased soil carbon dioxide flux and above-ground net primary productivity (ANPP) in this ecosystem (see also Fay et al., 2000, 2002, 2003; Harper et al., 2005). In a semi-arid grassland, Heisler-White et al. (2008) found that increasing rainfall event size increased ANPP. In contrast, Miranda et al. (2009a) showed that changes in precipitation frequency had no effect on productivity, plant cover and diversity in a semi-arid annual plant community in the Mediterranean region. Fay et al. (2008) examined how variations in total rainfall amount, the interval between rainfall events, individual rainfall event size and interactions between these factors influenced leaf photosynthesis, ANPP and soil respiration in a perennial grassland, but the impacts of these factors resisted simple characterisation because of their complex interactions.

It is clear that the “repackaging” of rainfall and its “translation” into soil moisture available for exploitation by plants is strongly influenced by the temporal distribution of rainfall events (Heisler-White et al., 2008; Loik et al., 2004), but there is no clear consensus on the impact of different rainfall distributions on the productivity of different ecosystems. From an ecohydrological point of view, the optimal distribution of rainfall event size and frequency for a given biogeochemical process is expected to vary with total rainfall quantity, and to depend on the details of the processes of interception, runoff, drainage and evapotranspiration (Rodríguez-Iturbe et al., 2001; Porporato et al., 2001; Laio et al., 2001). The effects of intra-annual rainfall variability on these processes, including feedbacks on transpiration and soil water balance via altered stom-

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



5 atal conductance, will depend on soil water retention properties and ecosystem type as well as total annual rainfall amounts, making prediction and modelling difficult. At a more general level, Knapp et al. (2008) hypothesise that greater rainfall variability will increase soil water limitation in mesic systems but decrease stress in xeric systems, because increased soil water content variability will be unfavourable for normally unstressed mesic systems but favourable for predominantly stressed xeric systems.

10 Inconclusive observational evidence and theoretical complexity points to a need for studies to examine the influence of differences in rainfall event distribution on ecosystem productivity, across a range of ecosystems, soil types and climates. The effects of changes in rainfall variability are likely to differ between ecosystems because of variations in canopy structure, rooting depth and the ability of some dominant species to tolerate water stress (Porporato et al., 2001). In particular, the effects of changes in rainfall variability on net ecosystem productivity (NEP) will depend on the magnitude and timing of changes of gross primary productivity (GPP) and ecosystem respiration (RE). There is evidence that the response timescales of microbial soil respiration and plant photosynthesis to rain pulses can be quite different (Williams et al., 2009; Huxman et al., 2004b); the relative timing as well as magnitudes of these changes will most likely vary between ecosystems. (In this paper, we consider both RE and GPP to be positive, and use the term net ecosystem productivity, NEP, to refer to the difference
20 $NEP = GPP - RE$).

25 Almost all experimental field studies manipulating rainfall amount or distribution have been conducted on annual plant communities or perennial grasslands (Knapp et al., 2002; Miranda et al., 2009a), because of the difficulty of performing manipulation experiments on taller canopies (one exception: Volder et al., 2010). Despite the potential impact of changes in intra-annual rainfall patterns on shrublands and forests, data for these ecosystems is sparse. There are even few remote sensing studies that address this issue (Fang et al., 2005; Good and Caylor, 2011).

One approach to addressing these difficult questions is to exploit the continuous eddy covariance measurements of surface-atmosphere exchanges of carbon dioxide, water,

and energy now being made at hundreds of research sites globally (Baldocchi, 2008). Flux tower data allow direct quantification of NEP and its decomposition into GPP and RE (Reichstein et al., 2005) and make it possible to analyse relationships between ecosystem fluxes and rainfall characteristics across ecosystem types and sites in a robust way.

In this study, we use FLUXNET data to examine the relationship between intra-annual rainfall patterns and ecosystem fluxes in seasonally water-limited shrubland and forest ecosystems. We address four questions. (1) How does the distribution of rainfall event size influence ecosystem fluxes in shrublands and forests, independent of total rainfall amounts? (2) How does the influence of differences in rainfall distribution compare to the influence of differences in total rainfall amount? (3) Do drier and wetter shrublands and forests differ in sensitivity to these factors? (4) How do these patterns differ for GPP, RE and the resulting NEP?

2 Analysis and results

2.1 Site and data selection

In order to compare the effects of differences in the temporal distribution of rainfall on carbon fluxes of ecosystems in different states of water stress, we require reliable ecosystem flux and rainfall data from sites of varying ecosystem composition and climate types. We make use of the FLUXNET La Thuile dataset (<http://www.fluxdata.org>), which contains eddy covariance and meteorological measurements at 30-min temporal resolution from 966 site-years at 253 sites. NEP flux data are gap-filled and partitioned into GPP and RE using common standardised algorithms (Moffat et al., 2007; Papale et al., 2006; Reichstein et al., 2005). From the available sites, we identified ecosystems experiencing a climate with a dry season by selecting sites based on their Köppen climate classification (Kottek et al., 2006). We included sites in Northern Hemisphere temperate regions with arid/semi-arid (BSh, BSk), Mediterranean (Csa, Csb) and sub-

BGD

8, 9813–9845, 2011

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



tropical (Cfa) climate classifications. From those sites, we selected shrubland, woody savanna, deciduous broadleaf, evergreen and mixed forest sites that had not been recently disturbed or heavily managed. We then eliminated site-years that did not contain a sufficient proportion of high quality data: specifically, we retained only those site-years where at least 80% of the half-hourly data were either original or gap-filled with high confidence (as indicated by the quality flags provided in the La Thuile dataset). This site selection process yielded the 28 sites and 85 site-years displayed in Table 1.

2.2 Annual rainfall amounts

We first examine the effect of variations in total annual rainfall amount (mm y^{-1}) on annual ecosystem fluxes (GPP, RE, and NEP, $\text{gC m}^{-2} \text{y}^{-1}$). As expected, there is a strong relationship between total rainfall and both GPP and RE (Fig. 1a and b). We are interested in the impact of variations in the temporal distribution of rainfall, so need to control for the effect of overall variation in total rainfall. We do this by considering residuals of ecosystem fluxes with respect to a nonlinear model:

$$F(P) = F_{\max}[1 - \exp(-P/P_s)], \quad (1)$$

where F is ecosystem flux (either GPP or RE), P is total annual rainfall amount, and F_{\max} and P_s are regression constants fitted using a nonlinear least squares approach, representing respectively the maximum modelled flux and a precipitation scale governing the rate of increase of the flux with precipitation. For NEP, we consider residuals with respect to the difference of our models for GPP and RE, in keeping with the definition of NEP above. Because the rate of increase of GPP with total rainfall amount is greater than the rate of increase of RE, NEP also increases with total rainfall amount (Fig. 1c).

This modelling approach respects some essential features of the dependence of annual fluxes on rainfall amount, in particular the saturation of flux values at higher rainfall amounts and the fact that, when there is no rainfall, fluxes should be zero. For higher total rainfall amounts, we would expect to see a diminution in fluxes, but, since

BGD

8, 9813–9845, 2011

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



we confine our study to site-years with a maximum total annual rainfall of 1500 mm, we can neglect this effect.

To ensure that potential conflation of inter-site variability and inter-annual variability within sites is not an obstacle to the analysis presented below, Fig. 1 shows model fits both to data from individual site-years (solid curves) and to mean values across all available years for each site (dashed curves). Across the range of total annual rainfall amount considered, there is little difference between the two fitted models for GPP or RE. This implies that sensitivities of ecosystem fluxes to inter-site spatial and intra-site temporal variability in rainfall amount are comparable. We thus henceforth treat data values from individual site-years as independent samples of ecosystem flux and rainfall variability.

For further analysis, we arbitrarily divide our data into two groups of sites, a “dry” set with mean annual rainfall amount less than or equal to the median of mean annual rainfall across all 28 sites and a “wet” set with mean annual rainfall greater than the median (Table 2). Because most sites have multiple years of data, some site-years from sites in the “dry” group are in fact wetter than some site-years in the “wet” group, as can be seen in Fig. 1. Although the division into “dry” and “wet” groups of sites is essentially arbitrary, the precipitation cutoff of 725 mm provides a reasonable division between arid or semi-arid sites and sub-humid or humid sites.

2.3 Temporal structure of rainfall

We now examine the effect on ecosystem carbon fluxes of differences in the temporal distribution of rainfall throughout the year. In order to compensate for differences in overall annual rainfall amount, we consider residuals of ecosystem fluxes with respect to our nonlinear flux/rainfall model (1). We hypothesise that at least some proportion of these residuals can be explained by differences in the distribution of rainfall through the year, in particular the degree to which the precipitation regime is characterised by “extreme” rainfall, i.e. large rainfall events separated by long periods of dryness. Within each precipitation group defined in Table 2, residuals of ecosystem fluxes with

BGD

8, 9813–9845, 2011

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



respect to our nonlinear flux/total rainfall model were related to indices of intra-annual rainfall variability using linear regression. Rainfall indices were calculated from daily time series of rainfall amounts for each site-year, using a daily rainfall threshold of 5 mm to define days with rain.

5 We consider first regressions of ecosystem flux residuals onto precipitation intensity, i.e. mean rainfall amount for days with rain, in mm d^{-1} (Fig. 2a–c). Overall, negative correlations are observed between ecosystem flux residuals and precipitation intensity: for all sites together and for “dry” sites alone, regressions between ecosystem flux residuals and precipitation intensity are significant at the 5% level for GPP, RE and
10 NEP; for “wet” sites, the GPP and RE residual regressions are significant at this level, but not the NEP regression. This appears to indicate that, particularly for drier sites, after controlling for overall variations in annual rainfall amount, ecosystem fluxes are reduced at sites with more extreme rainfall regimes, in the sense that the same amount of overall rainfall is concentrated into fewer rain days. Further, the influence of variations in precipitation distribution is stronger for GPP than for RE, to the extent that NEP
15 (the difference of GPP and RE) is also significantly related to precipitation intensity at the 5% level.

We can compare these results for the relationship between flux residuals and precipitation intensity with similar results using other precipitation statistics. Figure 2d–f
20 presents relationships between flux residuals and $R95\%_{\text{tot}}$, the proportion of total annual rainfall amount due to days whose daily rainfall is greater than the 95th percentile of daily rainfall. This statistic is commonly defined in terms of the climatological distribution of daily rainfall, (e.g. Alexander et al., 2006), but since we do not have detailed climatology information for our sites, we instead define an $R95\%_{\text{tot}}$ statistic based on
25 each site-year’s distribution of daily rainfall. The resulting statistic carries much the same information as the standard $R95\%_{\text{tot}}$ statistic, in that larger values of the statistic indicate rainfall less evenly distributed throughout the year, with larger and more widely spaced rainfall events.

BGD

8, 9813–9845, 2011

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The R95%tot regressions displayed in Fig. 2d–f show similar behaviour to those in terms of precipitation intensity: for drier sites, there is a significant dependence of ecosystem flux residuals on the “extremeness” of the precipitation regime. Sites with more extreme rainfall, in terms of the proportion of total annual rainfall accounted for by larger daily rainfall events, have both smaller GPP and smaller RE. The relative strengths of the GPP and RE residual dependence on R95%tot are such that there is a significant linear regression between NEP residuals and R95%tot.

Next we examine the relative effect size of differences in intra-annual rainfall variability compared to differences in total annual rainfall amount, by calculating linear regressions between ecosystem fluxes (or ecosystem flux residuals, as appropriate) and predictor variables standardised by subtracting the mean of each variable and dividing by its standard deviation. The aim here is to provide an indication of the variability in ecosystem fluxes associated with typical variations in precipitation variables: regression slopes in this context can be thought of as the change in ecosystem flux values associated with a change of one standard deviation in the predictor variable. Results are shown in Table 3, both for each of our precipitation groups and for all sites together. The first part of the table shows regression slopes between ecosystem fluxes and standardised total annual rainfall amount. Although the nonlinear model (1) provides a better method for controlling for overall variations in annual rainfall amount, we present linear regression results in Table 3 to allow for comparison with the linear regressions between ecosystem flux residuals and measures of rainfall variability.

Among the regressions that are significant at the 5 % level (shown in bold in Table 3), the magnitudes of the standardised regression slopes for the precipitation variability indices (precipitation intensity and R95%tot) are of a comparable order to those for the total rainfall amount. For GPP, the effects of rainfall distribution are around 60–65 % the size of the effects of rainfall amount for all sites together, and around 90 % for dry sites alone. For RE the ratio is 60–70 %, and consequently the overall influences of the two factors on NEP are of similar size. This means that, for drier sites, as defined by annual total rainfall, variations in rainfall distribution can contribute as strongly to

variations in ecosystem carbon balance as do overall variations in rainfall amount. This result, although perhaps counterintuitive, is consistent with observations (Harper et al., 2005).

2.4 Biometeorological conditions

Rainfall distribution is strongly linked to other meteorological and hydrological variables. In particular, there are strong relationships with mean annual vapour pressure deficit (kPa), annual incoming solar radiation, R_G (kJ y^{-1}), and soil water status. In order to provide a homogeneous measure of soil water storage across sites, including those where soil water content was not directly measured, we characterise soil moisture status using the mean daily relative soil water deficit ($\overline{\text{WD}}$, %), defined as $\overline{\text{WD}} = \sum_{i=1}^{365} \text{WD}_i / 365$, where WD_i is the relative soil water deficit for day i of the year, $\text{WD}_i = 1 - (\theta_i - \theta_{\min}) / (\theta_{\max} - \theta_{\min})$; here θ_i is the mean daily soil water content (mm), and θ_{\min} and θ_{\max} are the annual minimum and maximum mean daily soil water content (mm), all taken from the upper layer of a simple bucket model driven by daily meteorological and radiation inputs (Reichstein et al., 2002).

Figure 3 shows mean biometeorological conditions for the two precipitation groups. Drier sites experience greater soil water deficit, atmospheric vapour pressure deficit and incoming radiation than wetter sites. For drier sites, these biometeorological variables were all significantly correlated with the R95%_{tot} statistic (Fig. 4). Mean daily relative soil water deficit, mean annual vapour pressure deficit and mean incoming radiation all increase in precipitation regimes characterised by fewer and larger rainfall events.

BGD

8, 9813–9845, 2011

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



3 Discussion

3.1 Rainfall variability and ecosystem fluxes

For the shrubland and forest sites considered here, rainfall regimes characterised by fewer and larger rainfall events, irrespective of total rainfall amount, have a negative impact on ecosystem fluxes, though primarily for drier sites (total annual rainfall ≤ 725 mm). By examining the variability of ecosystem fluxes associated with typical spatial and temporal variations in total rainfall amount and rainfall distribution indices, we found that variations in rainfall distribution have a comparable effect on ecosystem fluxes to variations in overall rainfall amount.

Our results for drier sites apparently contradict the conceptual model of Knapp et al. (2008). Their model implies that more extreme rainfall regimes are expected to have a negative impact on NEP in mesic ecosystems, but a positive impact in xeric ecosystems. They argue that soil water fluctuations are amplified by decreasing precipitation frequency and increasing precipitation intensity, and that these larger fluctuations in soil water content will cause mesic systems to spend more time in conditions of water stress and xeric systems less (Knapp et al., 2008, Figure 5). Previous observational studies have provided some evidence in support of this model in grassland ecosystems: Knapp et al. (2002) found that increasing precipitation interval decreased soil moisture and ANPP in a mesic grassland and Thomey et al. (2011) found results consistent with a slight modification of Knapp et al.'s model in an arid to semi-arid grassland, although Heisler-White et al. (2008) observed the opposite effect in a semi-arid grassland.

It is likely that the discrepancy between these grassland studies and our results are due to differences in the vegetation considered and consequent differences in soil-plant-water interactions. Grassland species are generally shallow-rooted and consequently sensitive to changes in water content in soil layers near the surface. In dry climates, grasses have a short growing season (generally triggered by intense rainfall) and are highly sensitive to short rain pulses. Trees and shrubs, in contrast, rely

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



more on year-round water availability. Knapp et al.'s model of soil water storage is a bucket model with a single shallow layer. For such a model, more extreme rainfall regimes in xeric ecosystems will necessarily lead to an increase in water content in the uppermost soil layer, reducing water stress for shallow-rooted plants. Plants with deeper roots may respond to infrequent heavy rainfall events rather differently and may not benefit from short-term changes in soil moisture in the upper soil layers in the way predicted by Knapp et al.'s model. In fact, the response of vegetation to rain events is likely to be highly dependent on plant life form, which is itself a function of climate and soil conditions (Sala and Lauenroth, 1985; Schenk and Jackson, 2002; Ogle and Reynolds, 2004; Viola et al., 2008). In dry climates, Porporato et al. (2001) found that there is an intermediate rainfall frequency at which drought stress is minimum, and that this optimal frequency depends on plant and soil properties (see also Rodríguez-Iturbe et al., 2001 and Laio et al., 2001). An increase or decrease in precipitation frequency from this optimum at constant total rainfall will increase drought stress.

The complexity of these relationships between plants, soil and water in arid and semi-arid ecosystems may result in different impacts on plant productivity due to changes in rainfall distribution, even for similar climate types or in the same region. A pair of studies in the Mediterranean region illustrate this phenomenon: Miranda et al. (2009a) found that experimental manipulations reducing rainfall frequency for three annual plant communities had no effect on productivity, while they found a negative effect on productivity for small shrubs in the same region (Miranda et al., 2009b).

As far as our results for shrubland and forest ecosystems are concerned, a recent remote sensing study associating fractional woody cover with precipitation across Africa is of interest: Good and Caylor (2011) found that more frequent, less intense rainfall consistently led to a higher fraction of woody cover for a given amount of total rainfall, for a range of total rainfall amounts, a result more consistent with our results than with the hypothesis of Knapp et al. (2008). Although Good and Caylor's study is concerned with vegetation in Africa rather than Northern Hemisphere temperate regions, it is striking how consistent is the relationship between woody fraction and precipitation

BGD

8, 9813–9845, 2011

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



distribution across the whole range of African climates.

Of the factors that we have not considered here, perhaps the most important is variation in soil texture and type between sites. The response of soil respiration to rainfall events is strongly dependent on soil type (Inglisma et al., 2009), and in many of the drier sites considered here, there may be additional geochemical carbon fluxes associated with the presence of calcareous substrates (Kowalski et al., 2008; Serrano-Ortiz et al., 2009).

3.2 Secondary factors

In general, we observe that more extreme rainfall regimes, characterised by less and larger rainfall events, are correlated with increases in soil water deficit (Fig. 4a), atmospheric vapour pressure deficit (Fig. 4b), and incoming solar radiation (Fig. 4c). The effects on atmospheric vapour pressure deficit and incoming radiation both arise because less frequent rainfall corresponds to longer drought periods.

It thus appears that for more extreme rainfall conditions, not only is soil water availability lower, but atmospheric water demand is greater. These hydrological factors are more limiting in drier climates, so we expect them to have a greater effect on ecosystem processes for drier sites than for wetter sites (Fig. 3a and b). Water limitation in drier climates also prevents plants from making effective use of the generally higher radiation levels seen in conditions of infrequent intermittent rainfall. At wetter sites, biological activity is more likely to be limited by other constraints such as soil nutrient or light availability (Huxman et al., 2004a). In addition, excess light producing photo-oxidative damage may contribute a supplementary stress factor for vegetation at drier sites (Martínez-Ferri et al., 2000).

Because of its direct and overriding influence on plant function, most ecohydrological studies have focused on the effect of rainfall variability on ecosystems via its control on soil water content (Eamus et al., 2006; Eagleson, 2002; Rodríguez-Iturbe and Porporato, 2004). However, atmospheric water demand and incoming solar radiation are potentially important secondary factors that should be also taken into account. Further

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



experimental and modelling studies will be needed to disentangle the effect of these different factors.

3.3 Differential ecosystem flux responses

At drier sites, our results show that the influence of variations in rainfall distribution is stronger for GPP than RE, leading to a decrease in NEP for more extreme rainfall regimes. Studies in a mesic grassland have previously observed a decrease in both leaf photosynthetic carbon gain and soil respiration as a result of more extreme rainfall patterns (Knapp et al., 2002; Fay et al., 2002; Harper et al., 2005), while Fay et al. (2008) reported increases in leaf-level photosynthesis and decreases in soil respiration due to increased rainfall event size for levels of total rainfall ranging from 400 to 1000 mm yr⁻¹. These studies did not provide information concerning the relative sensitivity of these individual processes to variations in rainfall pattern, so it is not possible to reconstruct the dependence of overall ecosystem carbon flux on precipitation frequency for these sites.

It is likely that the greater sensitivity of GPP compared to RE to changes in precipitation frequency is due to a combination of contributions from the factors described in Section 3.2, i.e. GPP is affected by concurrent increases in soil water stress, atmospheric vapour pressure deficit and excess radiation. RE is indirectly affected by these factors, through its dependence on GPP (Migliavacca et al., 2011), but is more directly responsive to changes in soil moisture. Moreover, increases in air temperature associated with decreased precipitation frequency may even provide a positive influence on RE, partially compensating for the decrease in RE due to decreased soil water content (Davidson et al., 1998). Other studies in arid and semi-arid ecosystems have observed differing responses of GPP and RE to rainfall pulse size (Huxman et al., 2004b; Potts et al., 2006; Arneth et al., 2006; Williams et al., 2009). The structure of respiration response has been attributed to the high sensitivity of soil microbes to rainfall events following drought conditions (Inglima et al., 2009; Misson et al., 2006; Xu et al., 2004; Lee et al., 2004; Jenerette et al., 2008), although the relationship between pulse size and

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



duration of active soil respiration seems to saturate at moderate event sizes (Huxman et al., 2004b; Sponseller, 2007), perhaps due to exhaustion of labile carbon sources. The response of vascular plant photosynthetic activity to rainfall events is generally of longer duration than the response of microbial respiration, with both the magnitude of the response (Ignace et al., 2007; Chen et al., 2009; Williams et al., 2009; Scott et al., 2006) and the duration of physiological activity (Huxman et al., 2004b; Williams et al., 2009) increasing following larger rainfall pulses.

The differential responsiveness of respiration and photosynthesis to discrete rainfall events seen in the studies reported above leads to variations in NEP with changes in precipitation intensity and distribution independent of total rainfall amount, moderated by other factors, such as temperature, light availability, initial soil water content or canopy conditions (Schwinning and Sala, 2004). Arneth et al. (2006) found remarkable plasticity in canopy photosynthetic parameters in response to intermittent dry periods during the rainy season in a semi-arid woodland. Ultimately, any decoupling between GPP and RE can only be temporary because, at larger temporal and spatial scales, respiration fluxes are controlled by substrate supply (Campbell et al., 2004; Janssens et al., 2001; Reichstein et al., 2003; Misson et al., 2007).

4 Conclusions

We have shown that more extreme rainfall regimes, characterised by fewer and larger rainfall events, can have a strong negative effect on both GPP and NEP of woody ecosystems in drier climates, independent of total rainfall amount. Future amplification of the hydrological cycle caused by global warming may thus pose a threat to the productivity and sustainability of shrubland and forest ecosystems in these climates. Increased rainfall variability will add a supplementary constraint to the more commonly known limitation imposed by an expected future decrease in total annual or seasonal rainfall in these regions (Gao and Giorgi, 2008; Giorgi and Lionello, 2008).

BGD

8, 9813–9845, 2011

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Here, we consider only annual quantities for a subset of climate conditions and ecosystem types. FLUXNET sites archive continuous time series data collected at a temporal resolution of 30 min, a level of detail that should permit more sophisticated analysis of the questions addressed here, including a comprehensive cross-site examination of the phasing of GPP, RE and NEP changes following rainfall pulses.

Acknowledgements. This article is based on an original idea and draft of Laurent Misson, who died in a mountaineering accident on 5 March 2010.

This work used eddy covariance data acquired by the FLUXNET community and in particular by the following networks: AmeriFlux (U.S. Department of Energy, Biological and Environmental Research, Terrestrial Carbon Program (DE-FG02-04ER63917 and DE-FG02-04ER63911)), AfriFlux, AsiaFlux, CarboAfrica, CarboEuropeIP, CarboItaly, CarboMont, ChinaFlux, Fluxnet-Canada (supported by CFCAS, NSERC, BIOCAP, Environment Canada, and NRCan), Green-Grass, KoFlux, LBA, NECC, OzFlux, TCOS-Siberia, USCCC. We acknowledge the financial support to the eddy covariance data harmonisation provided by CarboEuropeIP, FAO-GTOS-TCO, iLEAPS, Max Planck Institute for Biogeochemistry, National Science Foundation, University of Tuscia, Université Laval and Environment Canada and US Department of Energy and the database development and technical support from Berkeley Water Center, Lawrence Berkeley National Laboratory, Microsoft Research eScience, Oak Ridge National Laboratory, University of California – Berkeley, University of Virginia. All statistical analysis was performed using R version 2.13 (R Development Core Team, 2011).

References

- Alexander, L. V., Zhang, X., Peterson, T. C., Caesar, J., Gleason, B., Tank, A. M. G. K., Haylock, M., Collins, D., Trewin, B., Rahimzadeh, F., Tagipour, A., Kumar, K. R., Revadekar, J., Griffiths, G., Vincent, L., Stephenson, D. B., Burn, J., Aguilar, E., Brunet, M., Taylor, M., New, M., Zhai, P., Rusticucci, M., and Vázquez-Aguirre, J. L.: Global observed changes in daily climate extremes of temperature and precipitation, *J. Geophys. Res. Atmos.*, 111, 123–138, 2006. 9815, 9821
- Arneeth, A., Veenendaal, E. M., Best, C., Timmermans, W., Kolle, O., Montagnani, L., and Shibistova, O.: Water use strategies and ecosystem-atmosphere exchange of CO₂ in two

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



highly seasonal environments, *Biogeosciences*, 3, 421–437, 2006,

<http://www.biogeosciences.net/3/421/2006/>. 9827, 9828

Baldocchi, D.: Breathing of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems, *Aust. J. Bot.*, 56, 1–26, 2008. 9818

5 Campbell, J. L., Sun, O. J., and Law, B. E.: Supply-side controls on soil respiration among Oregon forests, *Glob. Change Biol.*, 10, 1857–1869, 2004. 9828

Casals, P., Gimeno, C., Carrara, A., Lopez-Sangil, L., and Sanz, M. J.: Soil CO₂ efflux and extractable organic carbon fractions under simulated precipitation events in a Mediterranean Dehesa, *Soil Biol. Biochem.*, 41, 1915–1922, 2009. 9839

10 Chen, S. P., Lin, G. H., Huang, J. H., and Jenerette, G. D.: Dependence of carbon sequestration on the differential responses of ecosystem photosynthesis and respiration to rain pulses in a semiarid steppe, *Glob. Change Biol.*, 15, 2450–2461, 2009. 9828

Chiesi, M., Maselli, F., Bindi, M., Fibbi, L., Cherubini, P., Arlotta, E., Tirone, G., Matteucci, G., and Seufert, G.: Modelling carbon budget of Mediterranean forests using ground and remote sensing measurements, *Agr. Forest Meteorol.*, 135, 22–34, 2005. 9839

15 Chiesi, M., Fibbi, L., Genesio, L., Gioli, B., Magno, R., Maselli, F., Moriondo, M., and Vaccari, F. P.: Integration of ground and satellite data to model Mediterranean forest processes, *Int. J. Appl. Earth Obs. Geoinform.*, 13, 504–515, 2011. 9839

Clark, K. L., Gholz, H. L., and Castro, M. S.: Carbon dynamics along a chronosequence of slash pine plantations in north Florida, *Ecol. Appl.*, 14, 1154–1171, 2004. 9839

20 Davidson, E. A., Belk, E., and Boone, R. D.: Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest, *Glob. Change Biol.*, 4, 217–227, 1998. 9827

Eagleson, P. S.: *Ecohydrology: Darwinian Expression of Vegetation Form and Function*, Cambridge University Press, UK, 2002. 9826

25 Eamus, D., Hatton, T., Cook, P., and Colvin, C.: *Ecohydrology: Vegetation Function, Water and Resource Management*, CSIRO Publishing, 2006. 9826

Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., and Mearns, L. O.: Climate extremes: Observations, modeling, and impacts, *Science*, 289, 2068–2074, 2000. 9815

30 Fang, J. Y., Piao, S. L., Zhou, L. M., He, J. S., Wei, F. Y., Myneni, R. B., Tucker, C. J., and Tan, K.: Precipitation patterns alter growth of temperate vegetation, *Geophys. Res. Lett.*, 32, 924–930, 2005. 9817

Rainfall extremes and ecosystem fluxes

I. Ross et al.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


- Fay, P. A., Carlisle, J. D., Knapp, A. K., Blair, J. M., and Collins, S. L.: Altering rainfall timing and quantity in a mesic grassland ecosystem: design and performance of rainfall manipulation shelters, *Ecosystems*, 3, 308–319, 2000. 9816
- 5 Fay, P. A., Carlisle, J. D., Danner, B. T., Lett, M. S., McCarron, J. K., Stewart, C., Knapp, A. K., Blair, J. M., and Collins, S. L.: Altered rainfall patterns, gas exchange, and growth in grasses and forbs, *Int. J. Plant Sci.*, 163, 549–557, 2002. 9816, 9827
- Fay, P. A., Carlisle, J. D., Knapp, A. K., Blair, J. M., and Collins, S. L.: Productivity responses to altered rainfall patterns in a C₄-dominated grassland, *Oecologia*, 137, 245–251, 2003. 9816
- 10 Fay, P. A., Kaufman, D. M., Nippert, J. B., Carlisle, J. D., and Harper, C. W.: Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change, *Glob. Change Biol.*, 14, 1600–1608, 2008. 9816, 9827
- Gao, X. J. and Giorgi, F.: Increased aridity in the Mediterranean region under greenhouse gas forcing estimated from high resolution simulations with a regional climate model, *Global Planet. Change*, 62, 195–209, 2008. 9828
- 15 Garbulska, M. F., Peñuelas, J., Papale, D., and Filella, I.: Remote estimation of carbon dioxide uptake by a Mediterranean forest, *Glob. Change Biol.*, 14, 2860–2867, 2008. 9839
- Giorgi, F. and Lionello, P.: Climate change projections for the Mediterranean region, *Global Planet. Change*, 63, 90–104, 2008. 9828
- 20 Goldstein, A. H., Hultman, N. E., Fracheboud, J. M., Bauer, M. R., Panek, J. A., Xu, M., Qi, Y., Guenther, A. B., and Baugh, W.: Effects of climate variability on the carbon dioxide, water, and sensible heat fluxes above a ponderosa pine plantation in the Sierra Nevada (CA), *Agr. Forest Meteorol.*, 101, 113–129, 2000. 9839
- Good, S. P. and Caylor, K. K.: Climatological determinants of woody cover in Africa, *Proc. Natl. Acad. Sci. USA*, 108, 4902–4907, 2011. 9817, 9825
- 25 Grünzweig, J. M., Lin, T., Rotenberg, E., Schwartz, A., and Yakir, D.: Carbon sequestration in arid-land forest, *Glob. Change Biol.*, 9, 791–799, 2003. 9839
- Gu, L. H., Meyers, T., Pallardy, S. G., Hanson, P. J., Yang, B., Heuer, M., Hosman, K. P., Riggs, J. S., Sluss, D., and Wullschlegel, S. D.: Direct and indirect effects of atmospheric conditions and soil moisture on surface energy partitioning revealed by a prolonged drought at a temperate forest site, *J. Geophys. Res. Atmos.*, 111, 791–802, 2006. 9839
- 30 Harper, C. W., Blair, J. M., Fay, P. A., Knapp, A. K., and Carlisle, J. D.: Increased rainfall variability and reduced rainfall amount decreases soil CO₂ flux in a grassland ecosystem, *Glob. Change Biol.*, 11, 322–334, 2005. 9816, 9823, 9827

- Heisler-White, J. L., Knapp, A. K., and Kelly, E. F.: Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland, *Oecologia*, 158, 129–140, 2008. 9816, 9824
- Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Loik, M. E., Smith, S. D., Tissue, D. T., Zak, J. C., Weltzin, J. F., Pockman, W. T., Sala, O. E., Haddad, B. M., Harte, J., Koch, G. W., Schwinning, S., Small, E. E., and Williams, D. G.: Convergence across biomes to a common rain-use efficiency, *Nature*, 429, 651–654, 2004a. 9826
- Huxman, T. E., Snyder, K. A., Tissue, D., Leffler, A. J., Ogle, K., Pockman, W. T., Sandquist, D. R., Potts, D. L., and Schwinning, S.: Precipitation pulses and carbon fluxes in semiarid and arid ecosystems, *Oecologia*, 141, 254–268, 2004b. 9817, 9827, 9828
- Ignace, D. D., Huxman, T. E., Weltzin, J. F., and Williams, D. G.: Leaf gas exchange and water status responses of a native and non-native grass to precipitation across contrasting soil surfaces in the Sonoran Desert, *Oecologia*, 152, 401–413, 2007. 9828
- Inglima, I., Alberti, G., Bertolini, T., Vaccari, F. P., Gioli, B., Miglietta, F., Cotrufo, M. F., and Peressotti, A.: Precipitation pulses enhance respiration of Mediterranean ecosystems: the balance between organic and inorganic components of increased soil CO₂ efflux, *Glob. Change Biol.*, 15, 1289–1301, 2009. 9826, 9827
- Janssens, I. A., Lankreijer, H., Matteucci, G., Kowalski, A. S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E. J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Gudmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N. O., Vesala, T., Granier, A., Schulze, E. D., Lindroth, A., Dolman, A. J., Jarvis, P. G., Ceulemans, R., and Valentini, R.: Productivity overshadows temperature in determining soil and ecosystem respiration across European forests, *Glob. Change Biol.*, 7, 269–278, 2001. 9828
- Jenerette, G. D., Scott, R. L., and Huxman, T. E.: Whole ecosystem metabolic pulses following precipitation events, *Funct. Ecol.*, 22, 924–930, 2008. 9827
- Jentsch, A., Kreyling, J., and Beierkuhnlein, C.: A new generation of climate-change experiments: events, not trends, *Front. Ecol. Environ.*, 5, 365–374, 2007. 9816
- Karl, T. R., Knight, R. W., Easterling, D. R., and Quayle, R. G.: Indices of climate change for the United States, *B. Am. Meteorol. Soc.*, 77, 279–292, 1996. 9815
- Knapp, A. K., Fay, P. A., Blair, J. M., Collins, S. L., Smith, M. D., Carlisle, J. D., Harper, C. W., Danner, B. T., Lett, M. S., and McCarron, J. K.: Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland, *Science*, 298, 2202–2205, 2002. 9816, 9817, 9824,

BGD

8, 9813–9845, 2011

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



9827

Knapp, A. K., Beier, C., Briske, D. D., Classen, A. T., Luo, Y., Reichstein, M., Smith, M. D., Smith, S. D., Bell, J. E., Fay, P. A., Heisler, J. L., Leavitt, S. W., Sherry, R., Smith, B., and Weng, E.: Consequences of more extreme precipitation regimes for terrestrial ecosystems, *Bioscience*, 58, 811–821, 2008. 9817, 9824, 9825

Kottek, M., Grieser, J., Beck, C., Rudolf, B., and Rubel, F.: World map of the Köppen-Geiger climate classification updated, *Meteorol. Z.*, 15, 259–263, 2006. 9818, 9839

Kowalski, A. S., Serrano-Ortiz, P., Janssens, I. A., Sánchez-Moraic, S., Cuezva, S., Domingo, F., Were, A., and Alados-Arboledas, L.: Can flux tower research neglect geochemical CO₂ exchange?, *Agr. Forest Meteorol.*, 148, 1045–1054, doi:10.1016/j.agrformet.2008.02.004, 2008. 9826

Laio, F., Porporato, A., Ridolfi, L., and Rodríguez-Iturbe, I.: Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress. II. Probabilistic soil moisture dynamics, *Adv. Water Resour.*, 24, 707–723, 2001. 9816, 9825

Law, B. E., Baldocchi, D. D., and Anthoni, P. M.: Below-canopy and soil CO₂ fluxes in a ponderosa pine forest, *Agr. Forest Meteorol.*, 94, 171–188, 1999. 9839

Law, B. E., Thornton, P. E., Irvine, J., Anthoni, P. M., and Tuyl, S. V.: Carbon storage and fluxes in ponderosa pine forests at different developmental stages, *Glob. Change Biol.*, 7, 755–777, 2001. 9839

Lee, X., Wu, H. J., Sigler, J., Oishi, C., and Siccama, T.: Rapid and transient response of soil respiration to rain, *Glob. Change Biol.*, 10, 1017–1026, 2004. 9827

Lipson, D. A., Wilson, R. F., and Oechel, W. C.: Effects of elevated atmospheric CO₂ on soil microbial biomass, activity, and diversity in a chaparral ecosystem, *Appl. Environ. Microb.*, 71, 8573–8580, 2005. 9839

Loik, M. E., Breshears, D. D., Lauenroth, W. K., and Belnap, J.: A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA, *Oecologia*, 141, 269–281, 2004. 9816

Ma, S. Y., Baldocchi, D. D., Xu, L. K., and Hehn, T.: Inter-annual variability in carbon dioxide exchange of an oak/grass savanna and open grassland in California, *Agr. Forest Meteorol.*, 147, 157–171, 2007. 9839

Manabe, S. and Wetherald, R. T.: Large-scale changes of soil wetness induced by an increase in atmospheric carbon dioxide, *J. Atmos. Sci.*, 44, 1211–1235, 1987. 9815

Martínez-Ferri, E., Balaguer, L., Valladares, F., Chico, J. M., and Manrique, E.: Energy dissi-

BGD

8, 9813–9845, 2011

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Rainfall extremes and ecosystem fluxes

I. Ross et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

pation in drought-avoiding and drought-tolerant tree species at midday during the Mediterranean summer, *Tree Physiol.*, 20, 131–138, 2000. 9826

Migliavacca, M., Meroni, M., Manca, G., Matteucci, G., Montagnani, L., Grassi, G., Zenone, T., Teobaldelli, M., Goded, I., Colombo, R., and Seufert, G.: Seasonal and interannual patterns of carbon and water fluxes of a poplar plantation under peculiar eco-climatic conditions, *Agr. Forest Meteorol.*, 149, 1460–1476, 2009. 9839

Migliavacca, M., Reichstein, M., Richardson, A. D., Colombo, R., Sutton, M. A., Lasslop, G., Tomelleri, E., Wohlfahrt, G., Carvalhais, N., Cescatti, A., Mahecha, M. D., Montagnani, L., Papale, D., Zaehle, S., Arain, A., Arneeth, A., Black, T. A., Carrara, A., Dore, S., Gianelle, D., Helfter, C., Hollinger, D., Kutsch, W. L., Lafleur, P. M., Nouvellon, Y., Rebmann, C., da Rocha, H. R., Rodeghiero, M., Rouspard, O., Sebastià, M. T., Seufert, G., Soussana, J. F., and van der Molen, M. K.: Semiempirical modeling of abiotic and biotic factors controlling ecosystem respiration across eddy covariance sites, *Glob. Change Biol.*, 17, 390–409, 2011. 9827

Miranda, J. D., Padilla, F. M., Lazaro, R., and Pugnaire, F. I.: Do changes in rainfall patterns affect semiarid annual plant communities?, *J. Veg. Sci.*, 20, 269–276, 2009a. 9816, 9817, 9825

Miranda, J. D., Padilla, F. M., and Pugnaire, F. I.: Response of a Mediterranean semiarid community to changing patterns of water supply, *Persp. Plant Ecol. Evol. Syst.*, 11, 255–266, 2009b. 9825

Misson, L., Gershenson, A., Tang, J. W., McKay, M., Cheng, W. X., and Goldstein, A.: Influences of canopy photosynthesis and summer rain pulses on root dynamics and soil respiration in a young ponderosa pine forest, *Tree Physiol.*, 26, 833–844, 2006. 9827

Misson, L., Baldocchi, D. D., Black, T. A., Blanken, P. D., Brunet, Y., Yuste, J. C., Dorsey, J. R., Falk, M., Granier, A., Irvine, M. R., Jarosz, N., Lamaud, E., Launiainen, S., Law, B. E., Longdoz, B., Loustau, D., Mckay, M., Paw, K. T., Vesala, T., Vickers, D., Wilson, K. B., and Goldstein, A. H.: Partitioning forest carbon fluxes with overstory and understory eddy-covariance measurements: a synthesis based on FLUXNET data, *Agr. Forest Meteorol.*, 144, 14–31, 2007. 9828

Moffat, A. M., Papale, D., Reichstein, M., Hollinger, D. Y., Richardson, A. D., Barr, A. G., Beckstein, C., Braswell, B. H., Churkina, G., Desai, A. R., Falge, E., Gove, J. H., Heimann, M., Hui, D. F., Jarvis, A. J., Kattge, J., Noormets, A., and Stauch, V. J.: Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes, *Agr. Forest Meteorol.*,

147, 209–232, 2007. 9818

Ogle, K. and Reynolds, J. F.: Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays, *Oecologia*, 141, 282–294, 2004. 9825

Papale, D., Reichstein, M., Aubinet, M., Canfora, E., Bernhofer, C., Kutsch, W., Longdoz, B., Rambal, S., Valentini, R., Vesala, T., and Yakir, D.: Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty estimation, *Biogeosciences*, 3, 571–583, 2006, <http://www.biogeosciences.net/3/571/2006/>. 9818

Pataki, D. E. and Oren, R.: Species differences in stomatal control of water loss at the canopy scale in a mature bottomland deciduous forest, *Adv. Water Resour.*, 26, 1267–1278, 2003. 9839

Pereira, J. S., Mateus, J. A., Aires, L. M., Pita, G., Pio, C., David, J. S., Andrade, V., Banza, J., David, T. S., Paço, T. A., and Rodrigues, A.: Net ecosystem carbon exchange in three contrasting Mediterranean ecosystems – the effect of drought, *Biogeosciences*, 4, 791–802, 2007, <http://www.biogeosciences.net/4/791/2007/>. 9839

Peterson, T. C., Zhang, X. B., Brunet-India, M., and Vázquez-Aguirre, J. L.: Changes in North American extremes derived from daily weather data, *J. Geophys. Res. Atmos.*, 113, 123–138, 2008. 9815

Porporato, A., Laio, F., Ridolfi, L., and Rodríguez-Iturbe, I.: Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress. III. Vegetation water stress, *Adv. Water Resour.*, 24, 725–744, 2001. 9816, 9817, 9825

Potts, D. L., Huxman, T. E., Cable, J. M., English, N. B., Ignace, D. D., Eilts, J. A., Mason, M. J., Weltzin, J. F., and Williams, D. G.: Antecedent moisture and seasonal precipitation influence the response of canopy-scale carbon and water exchange to rainfall pulses in a semi-arid grassland, *New Phytol.*, 170, 849–860, 2006. 9827

Powell, T. L., Bracho, R., Li, J. H., Dore, S., Hinkle, C. R., and Drake, B. G.: Environmental controls over net ecosystem carbon exchange of scrub oak in central Florida, *Agr. Forest Meteorol.*, 141, 19–34, 2006. 9839

R Development Core Team: R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org>, ISBN 3-900051-07-0, 2011. 9829

Rambal, S., Ourcival, J. M., Joffre, R., Mouillot, F., Nouvellon, Y., Reichstein, M., and Ro-

BGD

8, 9813–9845, 2011

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



chateau, A.: Drought controls over conductance and assimilation of a Mediterranean evergreen ecosystem: scaling from leaf to canopy, *Glob. Change Biol.*, 9, 1813–1824, 2003. 9839

Reichstein, M., Tenhunen, J. D., Rouspard, O., Ourcival, J. M., Rambal, S., Dore, S., and Valentini, R.: Ecosystem respiration in two Mediterranean evergreen Holm Oak forests: drought effects and decomposition dynamics, *Funct. Ecol.*, 16, 27–39, 2002. 9823

Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentini, R., Banza, J., Casals, P., Cheng, Y. F., Grünzweig, J. M., Irvine, J., Joffre, R., Law, B. E., Loustau, D., Miglietta, F., Oechel, W., Ourcival, J. M., Pereira, J. S., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M., Romanya, J., Rossi, F., Tedeschi, V., Tirone, G., Xu, M., and Yakir, D.: Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices, *Global Biogeochem. Cy.*, 17, 211–220, 2003. 9828, 9839

Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grünwald, T., Havránková, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J. M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., and Valentini, R.: On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm, *Glob. Change Biol.*, 11, 1424–1439, 2005. 9818

Rey, A., Pegoraro, E., Tedeschi, V., Parri, I. D., Jarvis, P. G., and Valentini, R.: Annual variation in soil respiration and its components in a coppice oak forest in Central Italy, *Glob. Change Biol.*, 8, 851–866, 2002. 9839

Rodríguez-Iturbe, I., Porporato, A., Laio, F., and Ridolfi, L.: Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress. I. Scope and general outline, *Adv. Water Resour.*, 24, 695–705, 2001. 9816, 9825

Rodríguez-Iturbe, I. and Porporato, A.: *Ecohydrology of Water-Controlled Ecosystems*, Cambridge University Press, 2004. 9826

Rowell, D. P. and Jones, R. G.: Causes and uncertainty of future summer drying over Europe, *Clim. Dynam.*, 27, 281–299, 2006. 9815

Sala, O. E. and Lauenroth, W. K.: Root profiles and the ecological effect of light rainshowers in arid and semiarid regions, *Am. Midl. Nat.*, 114, 406–408, 1985. 9825

Schenk, H. J. and Jackson, R. B.: Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems, *J. Ecol.*, 90, 480–

BGD

8, 9813–9845, 2011

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Rainfall extremes and ecosystem fluxes

I. Ross et al.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[◀](#)
[▶](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


494, 2002. 9825

Schmid, H. P., Grimmond, C. S. B., Cropley, F., Offerle, B., and Su, H. B.: Measurements of CO₂ and energy fluxes over a mixed hardwood forest in the mid-western United States, *Agr. Forest Meteorol.*, 103, 357–374, 2000. 9839

5 Schwinning, S. and Sala, O. E.: Hierarchy of responses to resource pulses in arid and semi-arid ecosystems, *Oecologia*, 141, 211–220, 2004. 9828

Scott, R. L., Huxman, T. E., Cable, W. L., and Emmerich, W. E.: Partitioning of evapotranspiration and its relation to carbon dioxide exchange in a Chihuahuan Desert shrubland, *Hydrol. Process.*, 20, 3227–3243, 2006. 9828

10 Scott, R. L., Jenerette, G. D., Potts, D. L., and Huxman, T. E.: Effects of seasonal drought on net carbon dioxide exchange from a woody-plant-encroached semiarid grassland, *J. Geophys. Res. Biogeosci.*, 114, 504–515, 2009. 9839

Serrano-Ortiz, P., Domingo, F., Cazorla, A., Were, A., Cuezva, S., Villagarcia, L., Alados-Arboledas, L., and Kowalski, A. S.: Interannual CO₂ exchange of a sparse Mediterranean shrubland on a carbonaceous substrate, *J. Geophys. Res. Biogeosci.*, 114, G04015, doi:10.1029/2009JG000983, 2009. 9826

Sponseller, R. A.: Precipitation pulses and soil CO₂ flux in a Sonoran Desert ecosystem, *Glob. Change Biol.*, 13, 426–436, 2007. 9828

20 Tank, A. M. G. K. and Konnen, G. P.: Trends in indices of daily temperature and precipitation extremes in Europe, 1946–99, *J. Climate*, 16, 3665–3680, 2003. 9815

Tebaldi, C., Hayhoe, K., Arblaster, J. M., and Meehl, G. A.: Going to the extremes, *Climatic Change*, 79, 185–211, 2006. 9815

Tedeschi, V., Rey, A., Manca, G., Valentini, R., Jarvis, P. G., and Borghetti, M.: Soil respiration in a Mediterranean oak forest at different developmental stages after coppicing, *Glob. Change Biol.*, 12, 110–121, 2006. 9839

25 Thomey, M. L., Collins, S. L., Vargas, R., Johnson, J. E., Brown, R. F., Natvig, D. O., and Friggens, M. T.: Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland, *Glob. Change Biol.*, 17, 1505–1515, 2011. 9824

Trenberth, K. E.: Changes in precipitation with climate change, *Climate Res.*, 47, 123–138, 2011. 9815

30 Trenberth, K. E., Dai, A., Rasmussen, R. M., and Parsons, D. B.: The changing character of precipitation, *B. Am. Meteorol. Soc.*, 84, 1205–1217, 2003. 9815

Valentini, R., DeAngelis, P., Matteucci, G., Monaco, R., Dore, S., and Mugnozza, G. E. S.:

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Seasonal net carbon dioxide exchange of a beech forest with the atmosphere, *Glob. Change Biol.*, 2, 199–207, 1996. 9839

Vickers, D., Thomas, C., and Law, B. E.: Random and systematic CO₂ flux sampling errors for tower measurements over forests in the convective boundary layer, *Agr. Forest Meteorol.*, 149, 73–83, 2009. 9839

Viola, F., Daly, E., Vico, G., Cannarozzo, M., and Porporato, A.: Transient soil-moisture dynamics and climate change in Mediterranean ecosystems, *Water Resour. Res.*, 44, 469–480, 2008. 9825

Volder, A., Tjoelker, M. G., and Briske, D. D.: Contrasting physiological responsiveness of establishing trees and a C₄ grass to rainfall events, intensified summer drought, and warming in oak savanna, *Glob. Change Biol.*, 16, 3349–3362, 2010. 9817

Weltzin, J. F., Loik, M. E., Schwinning, S., Williams, D. G., Fay, P. A., Haddad, B. M., Harte, J., Huxman, T. E., Knapp, A. K., Lin, G. H., Pockman, W. T., Shaw, M. R., Small, E. E., Smith, M. D., Smith, S. D., Tissue, D. T., and Zak, J. C.: Assessing the response of terrestrial ecosystems to potential changes in precipitation, *Bioscience*, 53, 941–952, 2003. 9816

Williams, C. A., Hanan, N., Scholes, R. J., and Kutsch, W.: Complexity in water and carbon dioxide fluxes following rain pulses in an African savanna, *Oecologia*, 161, 469–480, 2009. 9817, 9827, 9828

Wu, Z. T., Dijkstra, P., Koch, G. W., Peñuelas, J., and Hungate, B. A.: Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation, *Glob. Change Biol.*, 17, 927–942, 2011. 9816

Xu, L. K., Baldocchi, D. D., and Tang, J. W.: How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature, *Global Biogeochem. Cy.*, 18, 1424–1439, 2004. 9827

Rainfall extremes and ecosystem fluxes

I. Ross et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Table 1. Study sites. Shown are FLUXNET site identifiers, site locations, years of data available, IGBP ecosystem classification (CSH: closed shrubland, DBF: deciduous broadleaf forest, EBF: evergreen broadleaf forest, ENF: evergreen needleleaf forest, MF: mixed forest, SAV: savanna, WSA: woody savanna), Köppen climate classification (Kottek et al. (2006)); BSh: hot semi-arid; BSk: cold semi-arid; Cfa: humid subtropical; Csa: hot-summer Mediterranean; Csb: warm-summer Mediterranean), site elevation (m), climatological annual rainfall (mm), climatological annual mean air temperature (T_a , °C) and site description reference.

Site	Lat., Lon.	Years	IGBP	Köppen	Elev	Prec	T_a	Ref.
ES-LMa	39.94° N, 5.77° W	2004–2006	SAV	Csa	260	691	16.2	Casals et al. (2009)
FR-Pue	43.74° N, 3.60° E	2001–2006	EBF	Csa	270	930	13.6	Rambal et al. (2003)
IL-Yat	31.35° N, 35.05° E	2002, 2006	ENF	BSh	650	266	18.5	Grünzweig et al. (2003)
IT-Col	41.85° N, 13.59° E	1998	DBF	Cfa	1550	1240	7.7	Valentini et al. (1996)
IT-Cpz	41.71° N, 12.38° E	1997, 2001–2004, 2006	EBF	Csa	68	811	14.8	Garbulsky et al. (2008)
IT-Lec	43.30° N, 11.27° E	2006	EBF	Cfa	314	396	15.4	Chiesi et al. (2011)
IT-Non	44.69° N, 11.09° E	2001, 2002	DBF	Cfa	25	916	13.9	Reichstein et al. (2003)
IT-PT1	45.20° N, 9.06° E	2003, 2004	DBF	Cfa	60	659	14.5	Migliavacca et al. (2009)
IT-Ro1	42.41° N, 11.93° E	2002–2006	DBF	Csa	235	852	15.6	Rey et al. (2002)
IT-Ro2	42.39° N, 11.92° E	2002–2004	DBF	Csa	224	862	14.8	Tedeschi et al. (2006)
IT-SRo	43.73° N, 10.28° E	2000, 2003, 2004, 2006	ENF	Csa	4	702	15.4	Chiesi et al. (2005)
PT-Esp	38.64° N, 8.60° W	2004, 2006	EBF	Csa	95	660	16.0	Pereira et al. (2007)
PT-Mi1	38.54° N, 8.00° W	2005	EBF	Csa	250	479	15.9	Pereira et al. (2007)
US-Blo	38.90° N, 120.63° W	2000–2004	ENF	Csa	1315	1379	12.3	Goldstein et al. (2000)
US-Dk3	35.98° N, 79.09° W	2002–2004	MF	Cfa	163	1060	14.7	Pataki and Oren (2003)
US-KS2	28.61° N, 80.67° W	2004–2006	CSH	Cfa	3	1931	22.3	Powell et al. (2006)
US-Me2	44.45° N, 121.56° W	2004, 2005	ENF	Csb	1253	368	6.8	Law et al. (1999)
US-Me3	44.32° N, 121.61° W	2004, 2005	ENF	Csb	1005	451	8.5	Vickers et al. (2009)
US-Me4	44.50° N, 121.62° W	1999, 2000	ENF	Csb	922	641	8.3	Law et al. (2001)
US-MMS	39.32° N, 86.41° W	1999, 2001–2005	DBF	Cfa	275	1054	12.3	Schmid et al. (2000)
US-MOz	38.74° N, 92.20° W	2005, 2006	DBF	Cfa	219	878	14.9	Gu et al. (2006)
US-SO2	33.37° N, 116.62° W	2004–2006	WSA	Csa	1394	530	13.8	Lipson et al. (2005)
US-SO3	33.38° N, 116.62° W	2005, 2006	WSA	Csa	1429	454	15.9	Lipson et al. (2005)
US-SO4	33.38° N, 116.64° W	2004–2006	CSH	Csa	1429	485	14.7	Lipson et al. (2005)
US-SP2	29.76° N, 82.24° W	2002, 2003	ENF	Cfa	50	1070	20.6	Clark et al. (2004)
US-SP3	29.75° N, 82.16° W	2001–2004	ENF	Cfa	50	992	19.8	Clark et al. (2004)
US-SRM	31.82° N, 110.87° W	2004–2006	WSA	BSk	1120	303	19.0	Scott et al. (2009)
US-Ton	38.43° N, 120.97° W	2002–2006	WSA	Csa	177	573	17.4	Ma et al. (2007)

BGD

8, 9813–9845, 2011

Rainfall extremes and ecosystem fluxes

I. Ross et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[I◀](#)[▶I](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)**Table 2.** Precipitation groups defined by median of mean total annual rainfall amount across all 28 sites.

Group	Dry	Wet
Number of sites	14	14
Number of site-years	33	52
Precip. range (mm)	≤725	>725
Mean precip. ± SD (mm)	494 ± 181	987 ± 230

Rainfall extremes and ecosystem fluxes

I. Ross et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[I◀](#)[▶I](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)**Table 3.** Slopes of linear regressions between ecosystem fluxes (for total annual rainfall) or ecosystem flux residuals (for precipitation intensity and R95%tot) and standardised precipitation variables, for all sites and for precipitation groups defined in Table 2. Regressions significant at the 5 % level are indicated in bold.

	Annual rainfall		
	All	Dry	Wet
GPP	273.55	308.67	-57.89
RE	185.53	231.08	-66.80
NEP	88.02	77.59	8.91
	Precipitation intensity		
	All	Dry	Wet
GPP	-165.52	-282.11	-188.62
RE	-109.32	-161.93	-144.65
NEP	-56.21	-120.18	-43.97
	R95%tot		
	All	Dry	Wet
GPP	-177.72	-271.80	-43.77
RE	-107.77	-154.17	-11.67
NEP	-69.96	-117.63	-32.10

Rainfall extremes and ecosystem fluxes

I. Ross et al.

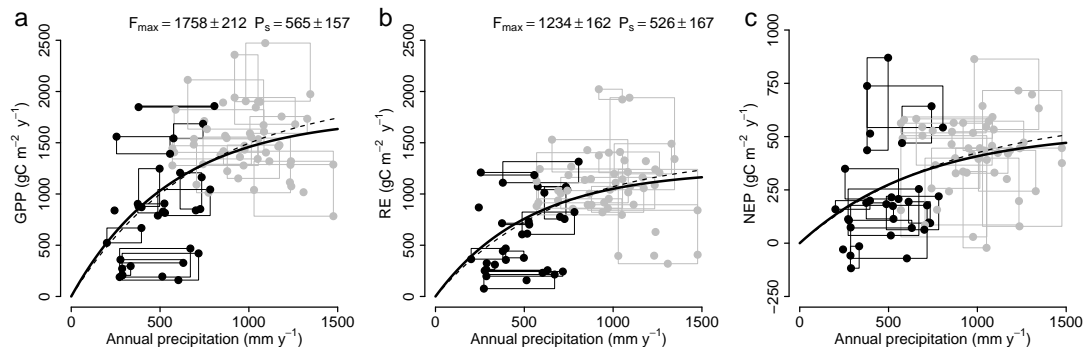


Fig. 1. Relationship between total annual rainfall and **(a)** GPP, **(b)** RE, and **(c)** NEP. Each point represents a single site-year (dry sites in black, wet in grey). Rectangles cover the range of interannual variability for each site. Curves show relationships of the form $F = F_{\max}[1 - \exp(-P/P_s)]$ determined using nonlinear least squares (for GPP and RE; for NEP, the curve shows the difference between the GPP and RE regressions) – the solid curves are fitted to individual site-years and the dashed curves to site mean values across all available site-years. Model parameters and standard errors for the site-year fits are shown at the top of the GPP and RE panels.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



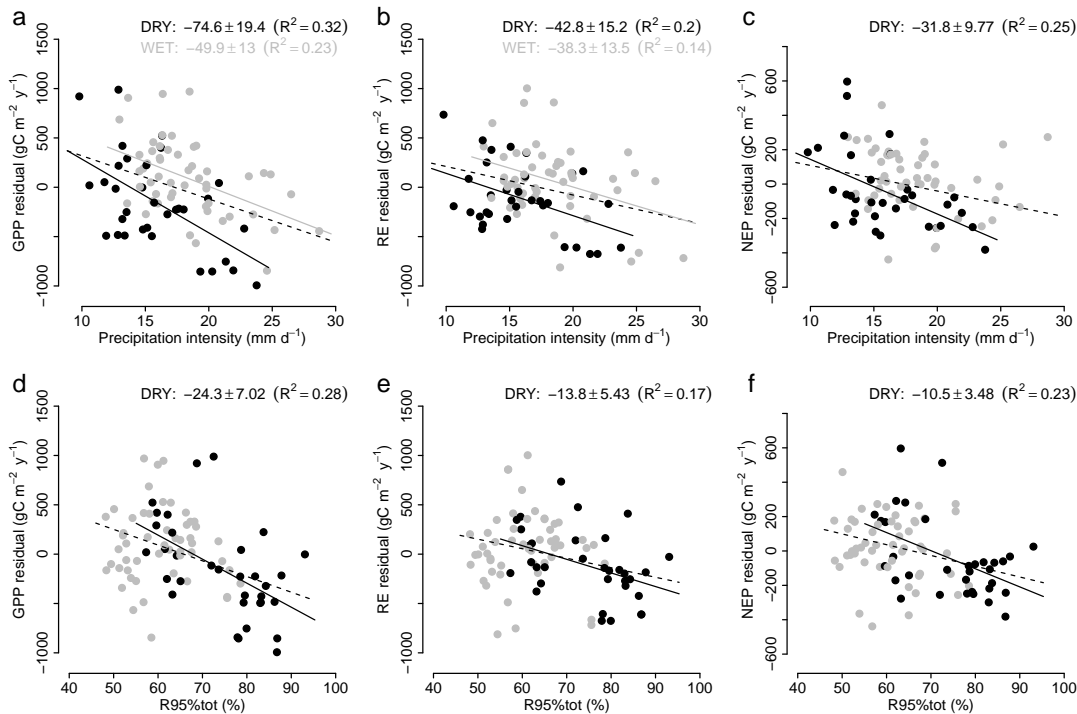


Fig. 2. Annual ecosystem flux residuals (GPP, RE and NEP) versus precipitation intensity (**a**, **b**, **c**) and R95%tot (**d**, **e**, **f**). Each point represents a single site-year (dry sites in black, wet in grey). Lines show linear regressions significantly different from zero at the 5 % level, solid lines for individual precipitation groups and dashed lines for the whole data set (for the solid lines, slopes, standard errors of slopes and R^2 values are shown at the top of each panel).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Rainfall extremes and ecosystem fluxes

I. Ross et al.

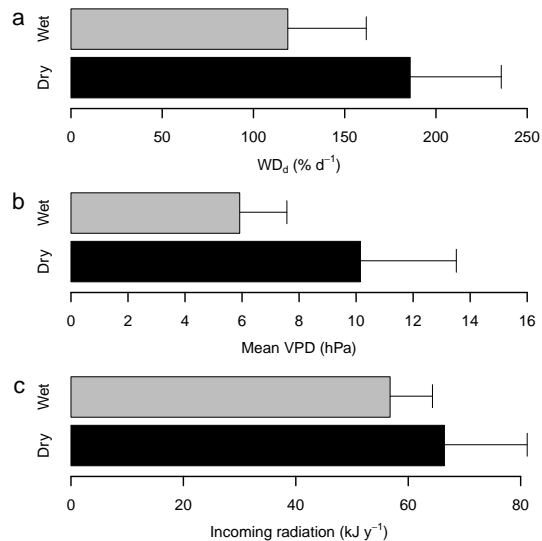


Fig. 3. Average biometeorological conditions for the different precipitation groups: **(a)** soil water deficit, **(b)** vapour pressure deficit, **(c)** incoming radiation (standard errors are shown).

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

Rainfall extremes and ecosystem fluxes

I. Ross et al.

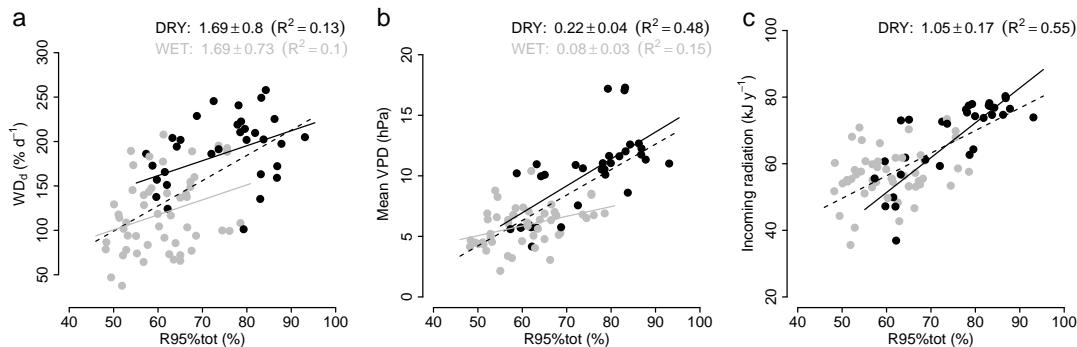


Fig. 4. Relationships between R95%tot and **(a)** mean soil water deficit, **(b)** mean annual vapour pressure deficit, **(c)** total incoming radiation. Details as for Fig. 2.

Discussion Paper | Discussion Paper | Discussion Paper | Discussion Paper | Discussion Paper

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

