Biogeosciences Discuss., 11, 853–899, 2014
www.biogeosciences-discuss.net/11/853/2014/
doi:10.5194/bgd-11-853-2014
© Author(s) 2014. CC Attribution 3.0 License.

Biogeosciences
Discussions
Open Access

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

Can current moisture responses predict soil CO_2 efflux under altered precipitation regimes? A synthesis of manipulation experiments

S. Vicca[1], M. Bahn[2], M. Estiarte[3,4], E. E. van Loon[5], R. Vargas[6], G. Alberti[7,8], P. Ambus[9], M. A. Arain[10], C. Beier[9,11], L. P. Bentley[12], W. Borken[13], N. Buchmann[14], S. L. Collins[15], G. de Dato[16], J. S. Dukes[17,18,19], C. Escolar[20], P. Fay[21], G. Guidolotti[16], P. J. Hanson[22], A. Kahmen[23], G. Kröel-Dulay[24], T. Ladreiter-Knauss[2], K. S. Larsen[9], E. Lellei-Kovacs[24], E. Lebrija-Trejos[25], F. T. Maestre[20], S. Marhan[26], M. Marshall[27], P. Meir[28,29], Y. Miao[30], J. Muhr[31], P. A. Niklaus[32], R. Ogaya[3,4], J. Peñuelas[3,4], C. Poll[26], L. E. Rustad[32], K. Savage[34], A. Schindlbacher[35], I. K. Schmidt[36], A. R. Smith[27,28,29,30,31,32,33,34,35,36,37], E. D. Sotta[38], V. Suseela[17,39], A. Tietema[5], N. van Gestel[40], O. van Straaten[41], S. Wan[30], U. Weber[42], and I. A. Janssens[1]

[1]Research Group of Plant and Vegetation Ecology, Department of Biology, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk, Belgium
[2]Institute of Ecology, University of Innsbruck, Sternwartestr. 15, 6020 Innsbruck, Austria

[3]CSIC, Global Ecology Unit, CREAF-CEAB-UAB, Cerdanyola del Vallés 08913, Catalonia, Spain
[4]CREAF, Cerdanyola del Vallés 08193, Catalonia, Spain
[5]Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, the Netherlands
[6]Department of Plant and Soil Sciences, Delaware Environmental Institute, University of Delaware, Newark, DE, USA
[7]University of Udine, via delle Scienze 206, Udine, Italy
[8]MOUNTFOR Project Centre, European Forest Institute, Via E. Mach 1, San Michele all'Adige (Trento), Italy
[9]Department of Chemical and Biochemical Engineering, Technical University of Denmark, 2800 Kgs. Lyngby, Denmark
[10]McMaster Center for Climate Change and School of Geography and Earth Sciences, McMaster University, Hamilton, Ontario, Canada
[11]NIVA – Norwegian Institute for Water Research, Gaustadalléen 21, 0349 Oslo
[12]Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA
[13]Soil Ecology, University Bayreuth, Dr.-Hans-Frisch-Str. 1–3, 95448 Bayreuth, Germany
[14]Department of Environmental Systems Science, ETH Zurich, Zurich, Switzerland
[15]Department of Biology, University of New Mexico, Albuquerque, NM, 87131, USA
[16]Department for Innovation in Biological, Agro-food and Forest systems, University of Tuscia, Viterbo, Italy
[17]Department of Forestry and Natural Resources, Purdue University, 715 West State Street, West Lafayette, IN 47907-2061, USA
[18]Department of Biology, University of Massachusetts, Boston, MA 02125, USA
[19]Department of Biological Sciences, Purdue University, West Lafayette, IN 47907, USA
[20]Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, C/Tulipán s/n, 28933 Móstoles, Spain
[21]USDA ARS Grassland Soil and Water Research Laboratory, Temple, TX, 76502, USA
[22]Oak Ridge National Laboratory, Oak Ridge, TN, 37831, USA
[23]Institute of Agricultural Sciences, ETH Zurich, 8092 Zurich, Switzerland
[24]MTA Centre for Ecological Research, 2–4, Alkotmany u., 2163-Vácrátót, Hungary

Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
◀| |▶
◀ ▶
Back | Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

[25]Department of Molecular Biology and Ecology of Plants, Tel Aviv University, Tel Aviv 69978, Israel
[26]Institute of Soil Science and Land Evaluation, Soil Biology, University of Hohenheim, Emil-Wolff-Str. 27, 70599 Stuttgart, Germany
[27]Centre for Ecology and Hydrology, Environment Centre Wales, Deiniol Road, Bangor, LL57 2UW, UK
[28]School of Geosciences, University of Edinburgh, Edinburgh, UK
[29]Research School of Biology, Australian National University, Canberra, Australia
[30]State Key Laboratory of Cotton Biology, College of Life Sciences, Henan University, Kaifeng, Henan 475004, China
[31]Max Planck Institute of Biogeochemistry, Department of Biogeochemical Processes, 07701 Jena, Germany
[32]Institute of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland
[33]USFS Northern Research Station, 271 Mast Road, Durham, NH 03824 USA
[34]The Woods Hole Research Center, 149 Woods Hole Rd, Falmouth, MA, 02540, USA
[35]Department of Forest Ecology, Federal Research and Training Centre for Forests, Natural Hazards and Landscape – BFW, A-1131 Vienna, Austria
[36]Department of Geosciences and Natural Resource Management, Copenhagen University, Denmark
[37]School of the Environment, Natural Resources, and Geography, Bangor University, Gwynedd, LL57 2UW, UK
[38]Embrapa Amapá Caixa Postal 10, CEP 68906-970, Macapá AP, Brazil
[39]School of Agricultural, Forest and Environmental Sciences, Clemson University, Clemson, SC 29634, USA
[40]Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA
[41]Buesgen Institute, Soil Science of Tropical and Subtropical Ecosystems, Georg-August-University of Goettingen, Buesgenweg 2, 37077, Goettingen, Germany
[42]Department of Biogeochemical Integration (BGI), Max-Planck-Institute for Biogeochemistry, Hans-Knöll-Str. 10, 07745 Jena, Germany

CC BY

Received: 26 September 2013 – Accepted: 26 December 2013 – Published: 14 January 2014

Correspondence to: S. Vicca (sara.vicca@uantwerpen.be)

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

cc BY

Abstract

As a key component of the carbon cycle, soil CO_2 efflux (SCE) is being increasingly studied to improve our mechanistic understanding of this important carbon flux. Predicting ecosystem responses to climate change often depends on extrapolation of current relationships between ecosystem processes and their climatic drivers to conditions not yet experienced by the ecosystem. This raises the question to what extent these relationships remain unaltered beyond the current climatic window for which observations are available to constrain the relationships. Here, we evaluate whether current responses of SCE to fluctuations in soil temperature and soil water content can be used to predict SCE under altered rainfall patterns. Of the 58 experiments for which we gathered SCE data, 20 were discarded because either too few data were available, or inconsistencies precluded their incorporation in the analyses. The 38 remaining experiments were used to test the hypothesis that a model parameterized with data from the control plots (using soil temperature and water content as predictor variables) could adequately predict SCE measured in the manipulated treatment. Only for seven of these 38 experiments, this hypothesis was rejected. Importantly, these were the experiments with the most reliable datasets, i.e., those providing high-frequency measurements of SCE. Accordingly, regression tree analysis demonstrated that measurement frequency was crucial; our hypothesis could be rejected only for experiments with measurement intervals of less than 11 days, and was not rejected for any of the 24 experiments with larger measurement intervals. This highlights the importance of high-frequency measurements when studying effects of altered precipitation on SCE, probably because infrequent measurement schemes have insufficient capacity to detect shifts in the climate-dependencies of SCE. We strongly recommend that future experiments focus more strongly on establishing response functions across a broader range of precipitation regimes and soil moisture conditions. Such experiments should make accurate measurements of water availability, they require high-frequency SCE measurements and they should consider both instantaneous responses and the po-

cc BY

tential legacy effects of climate extremes. This is important, because we demonstrated that at least for some ecosystems, current moisture responses cannot be extrapolated to predict SCE under altered rainfall.

1 Introduction

Soil respiration (SCE) is a crucial component of the terrestrial carbon cycle. Comprising about 100 $\mathrm{Pg\,C\,yr^{-1}}$ (Bond-Lamberty and Thomson, 2010b), it represents the largest terrestrial carbon flux to the atmosphere. Furthermore, because SCE includes both autotrophic and heterotrophic components, it reflects the performance of both plants and microbes. Soil respiration depends on available substrates and accordingly, differences in SCE across different ecosystems have been related to photosynthetic productivity (e.g., Janssens et al., 2001; Vargas et al., 2010; Högberg et al., 2001; Bahn et al., 2008), thereby emphasizing the interdependence of microbes and plants. The two key abiotic climate-related factors that influence SCE dynamics in terrestrial ecosystems are temperature and soil moisture (Raich and Schlesinger, 1992).

Raising temperature increases metabolic reaction rates, and hence microbial and plant respiration (Larcher, 2003). The temperature response of SCE can usually be expressed as an exponential curve, such as the frequently used Arrhenius function or Q_{10} function (Davidson and Janssens, 2006). The relationship of SCE with moisture is less straightforward than that with temperature. Briefly, at suboptimal soil moisture, osmotic stress and substrate diffusion limit microbial activity (Moyano et al., 2013; Schimel et al., 2007). In addition, root respiration typically declines when soil moisture decreases below optimal levels (Heinemeyer et al., 2012; Bryla et al., 2001; Burton et al., 1998; Thorne and Frank, 2009) due to reduced root growth and ion uptake, as well as by reduced maintenance costs following protein degradation, lower membrane potentials and increased root death (Huang et al., 2005; Eissenstat et al., 1999). At supra-optimum soil moisture levels, SCE decreases with increasing soil moisture, primarily because of reduced oxygen levels available to microbes (Moyano et al., 2013;

Jungkunst et al., 2008; Vicca et al., 2009) and plant roots (Mäkiranta et al., 2008). In summary, the short-term response of SCE to changes in soil moisture is not monotonic; SCE increases from low to intermediate soil moisture, reaches a plateau at optimum moisture, and decreases again at high soil moisture.

1.1 Responses of soil CO_2 efflux to precipitation manipulations

Given the strong non-monotonic response of SCE to soil moisture, changes in the hydrological cycle with climate change may have a large and non-linear impact on this carbon flux. Impacts of altered precipitation on ecosystem processes have been studied less extensively than those of warming and elevated atmospheric CO_2 concentrations (Jentsch et al., 2007), but multiple precipitation manipulation experiments have been conducted in several biomes in recent years (Beier et al., 2012). Wu et al. (2011) conducted a first meta-analysis of these experiments, reporting overall effects of altered rainfall on plant productivity and SCE. Because most of these experiments are conducted in ecosystems where water availability is at or below optimum levels, drought is generally reported to reduce SCE, whereas SCE usually increases in response to water addition (Wu et al., 2011). The non-monotonic relationship between SCE and soil moisture, however, suggests that the influence of altered rainfall patterns depends on the direction and magnitude of change in precipitation, but also on ecosystem characteristics such as climate (wet or dry region), soil type (defining water holding capacity), and timing of the rain or drought events (e.g., spring vs. summer) (Knapp et al., 2008). Soil type strongly affects responses to drought events (Kljun et al., 2006) by determining water holding capacity and thus water availability. However, the manipulation experiments conducted to date have rarely provided the necessary data (e.g., soil water potential) for estimation of available soil water to plants and microbes (Vicca et al., 2012a), which considerably hampers our ability to characterize global patterns of ecosystem responses to altered precipitation regimes.

CC BY

1.2 Extrapolation to different climate scenarios

Because model projections of future climate are highly sensitive to the assumed response of SCE to changes in its abiotic drivers (Friedlingstein et al., 2006; Wieder et al., 2013), a current challenge for ecologists is to test whether existing relationships between SCE and soil temperature (ST) and soil water content (SWC) can be extrapolated to predict future ecosystem-atmosphere feedbacks. Soil respiration has been measured in many observational studies, and data were recently collated into a global database (Bond-Lamberty and Thomson, 2010a). Such large datasets have great potential for improving our understanding of terrestrial carbon cycling and for improving Earth System Models. Nonetheless, it remains unclear to what extent current-climate observations are actually suitable for predicting future patterns of SCE, given that rainfall patterns are expected to change in the future. Extreme events such as severe heatwaves and droughts are expected to increase in intensity and periodicity particularly in the Mediterranean region, while for the northern latitudes more heavy rainfall events are projected (see e.g., Orlowsky and Seneviratne, 2012). Altered precipitation patterns, and extreme drought and rainfall events in particular, may cause structural changes in the ecosystem (for a detailed overview, see van der Molen et al., 2011). For example, changes in precipitation patterns can decrease microbial biomass and alter microbial community composition (Curiel Yuste et al., 2012; Tian et al., 2012; Sanaullah et al., 2011; Jentsch et al., 2011) as well as soil structure (Sowerby et al., 2008) and vegetation structure (e.g., root-to-shoot ratio) and composition (De Dato et al., 2008; Morecroft et al., 2004). Extreme drought events can also affect soil water availability and nutrient retention via increases in soil hydrophobicity (Bloor and Bardgett, 2012; Goebel et al., 2011; Muhr et al., 2010). Such structural changes can alter SCE in a way that may not be predictable from current-climate observations. Moreover, the relationships between SCE and temperature and soil moisture could change, or show large time lags in response to rewetting (Joos et al., 2010), rendering relationships based on

cc BY

current-climate observations invalid for predictions of SCE under altered precipitation regimes.

We use the most comprehensive dataset of ecosystem precipitation manipulation experiments currently available to explore if response functions for SCE established under ambient conditions are useful for explaining variation in SCE under altered precipitation regimes. Specifically, for each experiment, we tested the hypothesis (H1) that the relationship between SCE and temperature and volumetric soil water content (SWC) observed over time in the control plots can be extrapolated to predict SCE in plots exposed to a different precipitation regime. Testing this hypothesis is important because ecosystem models usually use functions dependent on both soil temperature and moisture to predict SCE under current and future climate scenarios. Rejection of H1 would suggest that the manipulation of precipitation altered the relationship of SCE with temperature and soil moisture. We then examined the vegetation types, climate zones, soil types and manipulation regimes for which H1 was and was not rejected. Finally, for the experiments where H1 was rejected, we tested whether rejection of our hypothesis was caused by SWC in manipulated treatments exceeding the range of SWC encountered in the control plots, or whether this rejection more likely resulted from structural changes within the ecosystem.

2 Methods

2.1 Data collection and analysis

We gathered information from single-factor field experiments in which precipitation was altered and where SCE as well as ST and SWC were measured in both control and treatment plots (further referred to as $SCE_{control}$ and $SCE_{treatment}$ etc.). Whenever available, we collected high frequency data (i.e., daily values; if hourly measurements were available, these were averaged to obtain daily values) of SCE, ST and SWC. In the majority of the experiments however, the measurement interval for SCE was larger

CC BY

than a day (see column 3, I, in Table C1). Detailed information for all manipulation experiments and the SCE data used in this study is given in Table A1. Timing of measurements and manipulation for all experiments are shown in Fig. S2 and Fig. S3. The individual responsible for data availability in each experiment, along with contact details is provided in Table S4. An overview of the average change in annual precipitation and the direction of the manipulation effect on SCE is presented in Fig. 1, for which differences in SCE between control and treatment were analyzed using repeated measures ANOVA, with measurement day as the within-subjects factor.

In order to test whether responses of SCE to fluctuations in ST and SWC observed in the control plots can be used to predict SCE under altered rainfall patterns, we followed the protocol presented in Fig. 2. We first tested which of four models best fitted $\mathrm{SCE}_{\mathrm{control}}$. For this and further analyses, experiments with no more than 10 data points were discarded. The four models (which have been used previously, see e.g., Curiel Yuste et al., 2003; Kopittke et al., 2013) were:

$$\log(\mathrm{SR}) = a + b\mathrm{ST} + c\mathrm{SWC} \tag{1}$$

$$\log(\mathrm{SR}) = a + b\mathrm{ST} + \log(c + d\,\mathrm{SWC}) \tag{2}$$

$$\log(\mathrm{SR}) = a + b\mathrm{ST} + \log(c + d\,\mathrm{SWC} + e\mathrm{SWC}^2) \tag{3}$$

$$\log(\mathrm{SR}) = a + b\mathrm{ST} + c\mathrm{SWC} + d\,\mathrm{SWC}^2 \tag{4}$$

These four models all reflect an exponential relationship between SCE and ST; the relationship between SCE and SWC is linear, quadratic, exponential linear and exponential quadratic for models 1, 2, 3 and 4, respectively. The first two models characterize soil moisture response as a monotonic function (increasing when d is positive), whereas models 3 and 4 allow non-monotonic responses. Model coefficients and goodness of fit parameters for all sites and models are presented in Supplement (SI).

Model selection was based on the second-order Akaike criterion (AICc). Across all sites, model 4 showed a significantly lower AICc than all other models (Wilcoxon sign rank test; $p < 0.05$). Therefore, we opted to use model 4 for all subsequent analyses.

However, residuals were not normally distributed for seven experiments, which were therefore discarded from the subsequent analyses (note that for these experiments the normal distribution criterion was usually not met for any of the other three models either).

We parameterized model 4 for each of the 45 remaining experiments using the control data, and used the resulting model coefficients specific to each site to test whether $SCE_{treatment}$ could be predicted. Subsequently, these results were used to test our hypothesis that the relation between SCE and fluctuations in ST and SWC as observed in the control plots can be extrapolated to predict $SCE_{treatment}$. We set forward two criteria indicative for goodness of extrapolation from control conditions to treatment conditions:

1. The difference between $SCE_{treatment}$ predicted by the control model (further termed "predicted $SCE_{treatment}$") and observed $SCE_{treatment}$ followed a normal distribution (Lilliefors test).
2. The RMSE for predicted $SCE_{treatment}$ was less than double the RMSE for predicted $SCE_{control}$. This second criterion is critical, because it indicates the goodness of fit to $SCE_{treatment}$, taking into account the performance of the control model. Because no generally accepted threshold for accurate data-model agreement exists, we opted for a stringent threshold where $RMSE_{treatment} < \cdot 2RMSE_{control}$, which in our case was exceeded in only few sites; Table C1). Visual inspection of the figures for predicted vs. measured values (Fig. S1), and of the residuals (Fig. S2) indicated that this criterion was justified for rejecting H1 (e.g., experiments Solling and Stubai).

When both conditions were fulfilled, the prediction of $SCE_{treatment}$ was considered reasonable and H1 was not rejected. It was rejected when at least one of both criteria was not met.

Rejection of H1 may have resulted from structural changes in the ecosystem, or may merely reflect erroneous extrapolation beyond the range of the conditions observed in the control. In order to test whether such erroneous extrapolation was responsible for rejection of H1, we performed the two tests for H1 also on a subset of the data, using only dates when $SWC_{treatment}$ was within the range of $SWC_{control}$ (further simply referred to as "common-SWC-subset"). Similar results for both the analysis for the entire dataset and for the common-SWC-subset indicate that our results are robust and potential rejection of H1 is unlikely due to extrapolation. Only for such robust sites, the subsequent CART-analyses and trend analyses were performed.

We used classification and regression tree (CART) analysis to investigate whether rejection of H1 was related to site or experimental characteristics. For this analysis, we included only those experiments for which the test for H1 with both the entire dataset and the common-SWC-subset yielded the same result. Predictor variables used in the CART-analysis were: vegetation type (grassland, forest, shrubland or agricultural land), hydrology (xeric, mesic or hydric – classification based on Köppen climate classification; see also Appendix A), percentage clay in the soil, mean annual precipitation (MAP), mean annual temperature (MAT), an aridity index (MAP/2MAT), treatment manipulation type (drought or irrigation experiment or altered precipitation pattern without a change in total precipitation), treatment manipulation duration (continuous manipulation, episodic manipulation or altered pattern during the entire experiment) and the percentage of measurement days for which $SWC_{treatment}$ was either above or below the natural boundaries of $SWC_{control}$ (i.e., an indication for potentially erroneous extrapolations beyond the range for which the model was parameterized). We further included as predictor variables the total number of SCE measurements (N), the median of the measurement interval (I; number of days) and N/I (which is low for sites with few and/or infrequent measurements; highest N/I is obtained for experiments with daily SCE measurements). As several experimental sites were represented by more than one experiment, we weighted the CART-analysis by the inverse of the number of experiments per site. For example, the Sevilleta-experiment consisted of two different irrigation experiments, and therefore, each experiment was weighted by 0.5 (Table C1).

To further analyze the possible cause for the failure of the control model to predict $SCE_{treatment}$, we examined the course of a predictability index over time, which was calculated for each measurement day as:

$$\mathrm{Pi} = |\text{predicted SR}_{\text{control}} - \text{observed SR}_{\text{control}}| - |\text{predicted SR}_{\text{treatment}} - \text{observedSR}_{\text{treatment}}| \quad (5)$$

where predicted $\text{SCE}_{\text{control}}$ and predicted $\text{SCE}_{\text{treatment}}$ are both calculated using model 4 (see above), and parameterized using the control data. Hence, Pi indicates the predictability of $\text{SCE}_{\text{treatment}}$, but taking into account the predictions of $\text{SCE}_{\text{control}}$ at the same moment in time. Values of Pi around zero indicate that the model parameterized for the control performs similarly for control and treatment, while negative values indicate that the prediction of the treatment is worse than that of the control (and vice versa for positive values). For the current analysis, we are particularly interested in the change of Pi over time. If Pi shows a trend towards increasingly negative values over time, then the predictability of $\text{SCE}_{\text{treatment}}$ becomes progressively worse. To test whether there was a significant trend in Pi (e.g. a decrease of Pi over time, or during part of the measurement period) we performed the runs test (non-parametric trend analysis), dichotomized around the median (Davis, 2002). This test checks the randomness of sequences. It creates "runs", defined as uninterrupted sequences of the same state (in this case either above or below the median), and then tests whether the number of runs is significantly different from what would be expected if they were randomly drawn from the same distribution. The runs test is thus not affected by the increased serial dependence of data with increasing measurement frequency, which is important because our study includes experiments with different measurement frequencies.

2.2 Test for artefacts related to SWC measurements

Given that measurements of SWC can be incorrect when, for example, the soil dries out and the contact between sensor and soil is interrupted, or when they do not reflect available water at all depths relevant for SCE, we needed to test the robustness of the results found for Pi. To this end, we used a simple bucket model (extracted from the

Rothamsted C cycling model; Coleman & Jenkinson, 1996) to simulate water availability in the main rooting zone independently of SWC measurements. Input parameters of this model are precipitation, potential evapotranspiration, % clay and main rooting zone. Potential evapotranspiration estimates were obtained via the Priestley-Taylor model, which is based on net incoming radiation (NIR), saturation vapour pressure and air temperature (Priestley and Taylor, 1972). Quantification of NIR was based on downward shortwave radiation, albedo and outgoing longwave radiation. Downward shortwave radiation was obtained via reanalysis of bias corrected data of WATCH (ERA40; see Weedon et al., 2011) and BC_ ERAinterim (ERA interim; see Piani et al., 2010). Albedo was derived from Modis MCD43C3.005, assuming a mean seasonal distribution. The outgoing longwave radiation was derived as a fraction of the daily temperature difference scaled by the fraction of actual vapour pressure and ratio of downward shortwave radiation and potential shortwave radiation.

The estimate of water availability obtained from the bucket model was then used to perform analyses analogous to those described above: coefficient estimates from a control model (in model 4, SWC was replaced by the water availability estimate from the bucket model, while ST did not alter) were used to predict $\mathrm{SCE}_{\mathrm{treatment}}$ at each measurement date. Subsequently, we tested H1 and estimated Pi, which was further analyzed for trends via the runs test. More details about this analysis based on the bucket model estimates of water availability are given in the Supporting Information.

All analyses were performed using Matlab software (2012b, The Mathworks Inc., Natick, MA).

3 Results

3.1 General response of soil CO_2 efflux to precipitation manipulation

Our dataset covers different climate regions and biomes (Fig. 1 and Table A1), but the temperate zone is clearly dominant. Few experiments were conducted in the tropics

cc BY

($n = 3$), and we found no precipitation manipulation experiments with SCE measurements for the boreal zone. Overall, decreased precipitation reduced SCE, whereas enhanced precipitation increased SCE (Fig. 1), although for six experiments, we found a significant response of SCE in the opposite direction. All but one of these are drought experiments (see Table B1).

3.2 Across-experiment variation in predictability of soil CO_2 efflux

We tested the goodness of the prediction of $SCE_{treatment}$ on the entire dataset for each site, as well as on the common-SWC-subset (i.e., excluding dates for which $SWC_{treatment}$ was outside the range of $SWC_{control}$). For 38 of the 45 experiments subjected to this analysis, both tests gave the same outcome and results can be considered robust (Table C1). These sites showed both over- and underestimations of $SCE_{treatment}$ (Fig. 3a and Table B1). Across all sites, using the common-SWC-subset instead of the entire dataset had a minor effect on the difference between predicted and observed $SCE_{treatment}$ (Fig. 3c and d), although for some sites, this reduction was substantial (Table B1).

For the 38 experiments for which both the entire dataset and the common-SWC-subset gave the same result, H1 was rejected in only seven, while we could not reject the hypothesis for the remaining 31 experiments (Table C1). Results for individual experiments were confirmed when SWC in model 4 was replaced by the bucket model results (although for several experiments this verification was not possible; see SI). The CART-analysis selected measurement frequency as the key predictor variable of whether or not H1 could be rejected. For experiments with median measurement intervals of SCE larger than 11 days, H1 was never rejected (Fig. 4), whereas H1 was rejected for seven of the 14 experiments with intervals ≤ 11 days, which included all five experiments with daily measurements (Table C1). The CART-analysis did not identify other predictive variables or thresholds.

cc BY

3.3 Within-experiment variability in predictability of soil CO_2 efflux

A trend analysis of the predictability of $SCE_{treatment}$(Pi) was made for the 38 experiments for which both the entire dataset and the common-SWC-subset gave the same result (i.e., those indicated as robust in Table C1). When Pi varies around zero, predictions of $SCE_{treatment}$ are comparable to predictions of $SCE_{control}$. Negative values indicate that the prediction of $SCE_{treatment}$ was less good than that of $SCE_{control}$ (and vice versa for positive values – but these were less abundant and always close to zero for all sites; Fig. S3). Significant trends in Pi indicate that the control model cannot reliably capture the variation in $SCE_{treatment}$. Significant trends in Pi reveal that model performance varied over time and thus suggest that the model parameterized for the control plots cannot reliably capture the variation in $SCE_{treatment}$. Whereas we detected a trend in Pi for only one of the 31 experiments for which H1 was not rejected (SulawesiForest; see Fig. S3 for a visual representation), we found a significant trend in the time course of Pi for five of the seven experiments for which H1 was rejected (Table C1). These five experiments were those with daily measurements of SCE. The time series of Pi for these five experiments is displayed in Fig. 5. For all other experiments, the course of Pi over time is shown in SI (Fig. S3). Here we briefly describe the patterns observed for the five experiments for which H1 was rejected and revealed a trend in Pi (i.e. the five experiments with daily measurements of SCE).

The Sevilleta-experiment, which consisted of two different irrigation treatments in a desert grassland (see Thomey et al., 2011 for details), showed little effect on Pi in the first year, while a marked decrease in Pi occurred in the second year, particularly for the treatment plots receiving the more intense rainfall events (Sevilleta_ Wet2; Fig. 5). Here, Pi values remained below zero over two months, even though SWC was very similar in control and treatment (Fig. 5). Such erroneous predictions of $SCE_{treatment}$ would, in the case of Sevilleta_ Wet2, lead to ca. 35 % underestimation of SCE over the entire measurement period (Table B1).

Likewise for Solling, despite that $\mathrm{SWC}_{\mathrm{treatment}}$ remained mostly within the range of $\mathrm{SWC}_{\mathrm{control}}$ (Fig. 5), Pi remained below zero during part of the experiment. Of particular interest is the decline of Pi upon rewetting, which occurred in both treatment years and reflects an increase of $\mathrm{SCE}_{\mathrm{treatment}}$ (see Fig. S2). Recovery of Pi took about four months in the second treatment year, but insufficient data were available to really test for the duration of recovery. Nonetheless, estimations of $\mathrm{SCE}_{\mathrm{treatment}}$ based on the control model would underestimate $\mathrm{SCE}_{\mathrm{treatment}}$ by 33 % over the entire experimental period (Table B1).

In contrast, in Stubai, the number of measurements was substantially reduced when selecting only the dates that $\mathrm{SWC}_{\mathrm{treatment}}$ was within the range of $\mathrm{SWC}_{\mathrm{control}}$ ($n = 103$, which is exactly 1/3 of the total number of data). Nonetheless, H1 was rejected also when only the common-SWC-subset of measurements was used (Table C1). Pi remained below zero even when $\mathrm{SWC}_{\mathrm{treatment}}$ had recovered after the manipulation had ended. Moreover, Pi remained negative just before the initiation of the manipulation in 2012 and across the three treatment years; this would result in an overestimation of SCE by 25 % when considering only the common-SWC-subset (Table B1).

At the TurkeyPoint site Pi started declining before the onset of the manipulation. This caused difficulty in distinguishing the effects of the manipulation from pre-treatment differences. Nonetheless, analysis of the residuals revealed that the difference between $\mathrm{SCE}_{\mathrm{control}}$ and $\mathrm{SCE}_{\mathrm{treatment}}$ shifted after the manipulation had ended (Fig. S2); whereas before and during the manipulation residuals for $\mathrm{SCE}_{\mathrm{treatment}}$ were consistently lower than residuals for $\mathrm{SCE}_{\mathrm{control}}$, the opposite was true for all measurement dates after the manipulation period. This suggests that the manipulation induced substantial changes in the ecosystem.

4 Discussion

4.1 General response of soil CO_2 efflux to precipitation manipulation

Precipitation manipulation experiments have been conducted mainly in the temperate zone, as shown in this study and in a general review by Beier et al. (2012). Particularly underrepresented in our study were the tropics and the boreal zone. Hence, it would be important to promote research in these regions for improving our global understanding of SCE responses to altered precipitation regimes. In agreement with Wu et al. (2011), decreased precipitation typically reduced SCE, whereas enhanced precipitation increased SCE (Fig. 1). However, some responses did not fit this pattern (Fig. 1). One reason that a reduction in rainfall could stimulate SCE is related to the non-monotonic response of SCE to moisture. This is especially likely for the one hydric experiment in our dataset, i.e. Clocaenog. This experiment showed a persistent increase in SCE following precipitation reduction (Sowerby et al., 2008), which is in line with the general observation of moisture responses of SCE in wetland ecosystems (Jungkunst and Fiedler, 2007).

4.2 Across-experiment variation in predictability of soil CO_2 efflux

The CART-analysis indicated that sampling frequency was an overriding factor determining whether or not H1 was rejected. The higher the measurement frequency, the more likely H1 was rejected, and in all five experiments where SCE was measured daily, $SCE_{treatment}$ could obviously not be predicted from $SCE_{control}$. Indeed, even when avoiding extrapolation beyond the range for which the model was parameterized, H1 was rejected for these experiments. Measurement frequency was crucial for detecting whether or not $SCE_{treatment}$ could be predicted from the ST-SWC relationship fitted to $SCE_{control}$. This result suggests that we may have missed important $SCE_{treatment}$ responses in experiments with larger measurement intervals. Infrequent measurement schemes have insufficient capacity to detect shifts in the climate-dependencies of SCE, which implies that type II errors (i.e., falsely accepting H1) for these experiments are probable. These results emphasize the need for high frequency SCE measurements to fully capture the response of SCE to changes in precipitation and other climatic variables such as temperature.

Nonetheless, of the 14 experiments with a measurement frequency < 11days (i.e., the threshold resulting from the CART-analysis), H1 could not be rejected for seven. These experiments represent in fact only four different sites (Duolun40, Duolun60, HarvardForest, Hohenheim_ LA, Hohenheim_ LF, RaMPs_ Dry and RaMPs_ DryAlt; see Table C1), and it is possible that for these sites, the criteria set for rejecting H1 were too stringent. Particularly for HarvardForest, the difference in RMSE was rather high (1.72; Table C1) and it is plausible that a more complete dataset (i.e., more frequent measures) would have given a different outcome (see also Fig. S3). On the other hand, experimental duration was rather short at the two experiments of the Mongolian Duolun grassland site, for which SCE was measured weekly, but only for about six months (Fig. S3), and for the experiments in Hohenheim, where SCE was measured for ca. 10 months, precluding firm conclusions. Alternatively, not rejecting H1 for some experiments that provided frequent measures of SCE may reflect real variability in the potential for predicting $\text{SCE}_{\text{treatment}}$ from relations found for the control. The RaMPs experiment illustrates that in some cases, predicting $\text{SCE}_{\text{treatment}}$ from $\text{SCE}_{\text{control}}$ may yield realistic results. This experiment covered four manipulation years, during which SCE was measured at ca. 5 day intervals during the growing season (Table C1). The fact that H1 could not be rejected and no trend was observed for both experiments of this site corresponds to the study by Fay et al. (2011). They reported that inter-annual rainfall variability was more determining for most ecosystem processes studied at the RaMPs site than the manipulations applied. Hence, the experimental manipulation seems not to have pushed the system beyond a threshold that would have yielded different responses of $\text{SCE}_{\text{treatment}}$. Whether this is related to the resilience of the ecosystem, or to the manipulation applied, remains to be tested.

4.3 Within-experiment variability in predictability of soil CO_2 efflux

We examined in more detail the predictability index of $SCE_{treatment}$ for experiments with daily SCE measurements. This detailed analysis allows detecting patterns and unravelling mechanisms that may remain unseen when studying only seasonal or annual totals (see e.g. the results for Solling below). High-frequency measurements of different ecosystem processes are becoming more abundant; besides SCE also for example photosynthesis or ecosystem respiration are can be measured at high frequency with automated cuvettes. Our approach provides a useful tool to test for variables measured at high frequency in manipulation experiments whether or not current models can be extrapolated to predict ecosystem processes under altered environmental conditions. In our study, this analysis revealed various patterns for the five experiments providing daily SCE measurements. These are discussed in the following paragraphs.

At the Sevilleta experiment, $SCE_{treatment}$ was equally well predicted as $SCE_{control}$ (no marked change in Pi) in the first year. In the second year and particularly for treatment plots receiving the most intense irrigation (Sevilleta_Wet2), Pi decreased strongly. The results from the Sevilleta site indicate that rainfall intensity is an important factor determining variation in SCE. Vargas et al. (2012) attributed the observed increase in SCE in irrigated plots to an enhancement of the autotrophic component of SCE. This example thus illustrates that if we are to understand the mechanisms driving moisture responses of SCE, measurements of the autotrophic and heterotrophic components of SCE are required. These data are not currently available for the experiments presented here.

For the Sevilleta experiment, Thomey et al. (2011) further indicated the importance of moisture in deep soil layers, which was replenished only when applying the most intense precipitation manipulation (e.g., one 20 mm rain event per month; Sevilleta_ Wet2 in the current study), but not as much by more frequent but less intense rain events (e.g., four 5 mm rain events per month; Sevilleta_ Wet1 in the current study). This finding emphasizes the need for precipitation experiments to measure SWC over the entire rooting zone, and not only top soil SWC (as is typically the case; see Vicca et al., 2012a for a discussion on this topic).

For the Solling site, Pi decreased markedly upon rewetting. The Pi decrease was due to suddenly higher observed $SCE_{treatment}$ than was predicted (see residuals in Fig. S2), which reflects a pulse of SCE often observed following soil rewetting after drought events, and known as the Birch effect (Birch, 1958). The Birch effect is thought to be caused by osmolyte disposal by microbes and rapid decomposition of cells that did not survive the drought or rewetting event (Schimel et al., 2007; Jarvis et al., 2007; Birch, 1958). When soil moisture decreases below optimum levels, microbes experience direct physiological stress and in order not to dehydrate they need to accumulate solutes (Schimel et al., 2007; Wood et al., 2001). Upon rewetting, microbes need to rapidly release their water-attracting osmolytes, before increasing osmotic pressure causes cell rupture (Schimel et al., 2007; Wood et al., 2001). Furthermore, when drying and wetting cycles become more pronounced, previously protected organic matter can be revealed through reduced aggregate stability (Borken and Matzner, 2009; Denef et al., 2001). In the case of Solling, the increase of SCE after rewetting more than compensated for reductions in SCE during the dry period (Table B1; see Borken et al., 1999 for details about SCE in the Solling experiment). Although such overcompensation for drought-related decreases of SCE after rewetting is not a universal phenomenon (Borken and Matzner, 2009), Birch effects are commonly observed in various ecosystems (Kim et al., 2012; Inglima et al., 2009; Jarvis et al., 2007), but are not usually accounted for by models. In order to improve our understanding of the Birch effect, and because it is supposed to be a primarily microbially-mediated phenomenon, we again stress that it is necessary to separate heterotrophic from autotrophic respiration in future SCE monitoring experiments.

At the Stubai grassland site, Pi decreased sharply over the course of several drought manipulations performed in consecutive years. Pi broadly followed the course of the $SWC_{treatment}$, but was mostly outside the range of $SWC_{control}$. In contrast to Solling, Pi returned rapidly to high values after rewetting, despite a noticeable Birch effect (Fig.

cc BY

S2), and appeared to be mostly determined by SWC. Nonetheless, when excluding the dates when $SWC_{control}$ was outside the range of $SWC_{treatment}$, H1 was still rejected (Table C1) and Pi remained below zero after the precipitation manipulation, (especially after the 2012 manipulation; Fig. 5), resulting in a substantial overestimation (25 %) of $SCE_{treatment}$ when using the common-SWC-subset (Table B1). This indicates that SCE did not fully recover after the drought, which could be related to structural changes in soil chemical properties, soil physical properties, microbial communities, and/or vegetation.

For the TurkeyPoint experiment, Pi was low during and after the manipulation treatment. This pattern corresponds to aboveground observations made at the site where the rainfall exclusion was conducted during spring, when tree growth is greatest in this region (Hanson and Weltzin, 2000). Tree growth was strongly influenced by the precipitation exclusion and did not fully recover after the drought period. Moreover, tree growth terminated earlier in the drought plots as compared to the control plots (MacKay et al., 2012). Strikingly, treatment-induced changes to tree growth dynamics positively influenced SCE, as residuals in autumn were higher for the treatment than for the control (Fig. S2). Possible mechanisms to explain this lag effect could be the Birch effect as described above, or the decomposition of roots that died during drought induced senescence. Moreover, plants can allocate large but variable fractions of their photosynthates belowground (Vicca et al., 2012b), with potentially rapid and strong effects on the autotrophic component of SCE (Högberg et al., 2001; Bahn et al., 2008; Kuzyakov and Gavrichkova, 2010). However, because autotrophic and heterotrophic respiration were not separated at TurkeyPoint experiment, we cannot fully explore the exact mechanisms underlying this particular response of SCE.

5 Concluding remarks

A current challenge for ecologists and biogeochemists is to establish whether relationships between abiotic factors and ecosystem processes can be extrapolated over time to predict ecosystem-atmosphere feedbacks (Evans and Wallenstein, 2012; Reichstein et al., 2013). Our analysis demonstrated the limits to applying current soil moisture responses for predicting soil CO_2 efflux under altered precipitation regimes; all experiments with daily SCE measurements revealed that SCE under altered precipitation regimes cannot be predicted from what is expected from current-climate observations, and the erroneous predictions were not related to extrapolation beyond the range for which the model was parameterized. Although necessary data to unravel the mechanisms behind the observed trends are generally lacking, there are clear indications that structural changes (in soil and/or vegetation) following the manipulation of water inputs can make current moisture responses of SCE inadequate for predicting SCE in future, when precipitation patterns alter.

In order to obtain realistic estimates of SCE under altered precipitation patterns, we need more experiments establishing response functions across a broader range of precipitation regimes and soil moisture conditions. Such experiments should make accurate measurements of water availability, they require high-frequency SCE measurements and they should consider both instantaneous responses and the potential legacy effects of climate extremes. Future studies should make an effort to obtain high-frequency measurements which – as we demonstrated – are essential for capturing dynamic responses during drying and after rewetting, and for quantifying their implications for the carbon cycle in a more extreme climate.

Author contributions

SV conceived the manuscript, and performed the analyses and writing. MB, ME and IAJ substantially contributed to the discussions prior to the writing. EEVL focussed specifically on the statistical analyses. All co-authors contributed with data and/or intellectual input during the writing process.

cc BY

Appendix A

General information for the experimental sites was generally obtained from the site investigators, except for the climate classification and the hydrology. For each site, we extracted the climate class from the Köppen classification (Hijmans et al., 2005) using latitude and longitude. This classification was further used to determine the hydrology. Sites classified as arid or semi-arid according to Köppen classification, i.e., those with a first letter "B", as well as those classified as "Dry-summer subtropical or Mediterranean climates" (i.e., Csa and Csb). Sites classified as tropical rainforest (Af), as humid subtropical (Cfa), as maritime temperate (Cfb), or as continental with wet summer (Dfa, Dfb, Dwb, Dfc). For all but two sites – Kiskunsag and Clocaenog – the resulting climate corresponded to the experience of the investigators. Kiskunsag is a shrubland on sandy soil, at the transition between deciduous forest and steppe and previously classified as xeric (Lellei-Kovacs et al., 2011); Clocaenog is a wetland with peaty soil in Wales, UK. Because the Köppen classification was clearly not indicative of the hydrology in these sites, we adjusted the hydrology to xeric and hydric for Kiskunsag and Clocaenog, respectively.

Appendix B

For each experiment, we fitted a model 4 to the data of the control plots using either the entire dataset, or to a subset of the data, including only the days where $\mathrm{SWC}_{\mathrm{treatment}}$ is within the range of SWC observed in the control (= common-SWC-subset). Subsequently, we tested the hypothesis that the response of soil CO2 efflux (SCE) to temperature and soil water content observed in the control can be extrapolated to predict

CC BY

SCE in the treatment for both the entire dataset and the common-SWC-subset via two tests (h1 and h2; see Methods for details). Results of both tests are presented for both datasets in Table C1.

Supplementary material related to this article is available online at http://www.biogeosciences-discuss.net/11/853/2014/ bgd-11-853-2014-supplement.zip.

Acknowledgements. This work emerged from the Carbo-Extreme project, funded by the European Community's 7th framework programme under grant agreement (FP7-ENV-2008-1-226701). We also acknowledge support of the ESF-network CLIMMANI and of the EU-funded INCREASE FP7-INFRASTRUCTURE-2008-1 (Grant Agreement no. 227628) project for data exchange. SV is a postdoctoral research associate of the Fund for Scientific Research – Flanders. MB and TLK acknowledge funding of the studies at Stubai from C-Extreme, the Austrian Science Fund (FWF) project P22214-B17 and the ERA-Net Circle Mountain project CAMELEON. NB acknowledges funding from the EU project Carbo-Extreme (Grant Agreement no. 226701) as well as from the BIOLOG project (BMBF) and NCCR Climate. JSD acknowledges support for the Boston-Area Climate Experiment from the US NSF and by the US Department of Energy's Office of Science (BER), through the Northeastern Regional Center of the National Institute for Climatic Change Research. Research at Sevilleta was supported by NSF LTER and DoE NICCR. P. Fay acknowledges funding from NSF, USDA, and the Konza LTER program. USDA is an equal opportunity provider and employer. FTM and CE were supported by the European Research Council under the European Community's Seventh Framework Programme (FP7/2007-2013/ERC Grant agreement 242658), and by the British Ecological Society (Studentship 231/1975), respectively. Financial support for the Big Bend project came from a USGS Global Climate Change Small Watershed Project grant to John Zak and a National Park Service grant to John Zak and David Tissue. LPB was funded by the United States Environmental Protection Agency (EPA) under the Greater Research Opportunities (GRO) Graduate Program. ELK acknowledges support from research grant of EU FW5 VULCAN project and NKFP-3B/0008/2002 grant from the Hungarian Government. The research of ME and JP was supported by the Spanish government grants CGL2010-17172, and Consolider Ingenio MONTES (CSD2008-00040), and by the Catalan government grant SGR2009-458. The Brandbjerg experiment (*Climaite*) was funded by the Villum Foundation.

References

Bahn, M., Rodeghiero, M., Anderson-Dunn, M., Dore, S., Gimeno, C., Drosler, M., Williams, M., Ammann, C., Berninger, F., Flechard, C., Jones, S., Balzarolo, M., Kumar, S., Newesely, C., Priwitzer, T., Raschi, A., Siegwolf, R., Susiluoto, S., Tenhunen, J., Wohlfahrt, G., and Cernusca, A.: Soil respiration in European grasslands in relation to climate and assimilate supply, Ecosystems, 11, 1352–1367, 2008.

Beier, C., Emmett, B., Gundersen, P., Tietema, A., Penuelas, J., Estiarte, M., Gordon, C., Gorissen, A., Llorens, L., Roda, F., and Williams, D.: Novel approaches to study climate change effects on terrestrial ecosystems in the field: drought and passive nighttime warming, Ecosystems, 7, 583–597, 2004.

Beier, C., Beierkuhnlein, C., Wohlgemuth, T., Penuelas, J., Emmett, B., Koerner, C., de Boeck, H., Christensen, J. H., Leuzinger, S., Janssens, I. A., and Hansen, K.: Precipitation manipulation experiments – challenges and recommendations for the future, Ecol. Lett., 15, 899–911, 2012.

Birch, H. F.: The effect of soil drying on humus decomposition and nitrogen availability, Plant Soil, 10, 9–31, 1958.

Bloor, J. M. G. and Bardgett, R. D.: Stability of above-ground and below-ground processes to extreme drought in model grassland ecosystems: interactions with plant species diversity and soil nitrogen availability, Perspect. Plant Ecol., 14, 193–204, 2012.

Bond-Lamberty, B. and Thomson, A.: A global database of soil respiration data, Biogeosciences, 7, 1915–1926, doi:10.5194/bg-7-1915-2010, 2010a.

Bond-Lamberty, B. and Thomson, A.: Temperature-associated increases in the global soil respiration record, Nature, 464, 579-U132, 2010b.

Borken, W., Xu, Y. J., Brumme, R., and Lamersdorf, N.: A climate change scenario for carbon dioxide and dissolved organic carbon fluxes from a temperate forest soil: drought and rewetting effects, Soil Sci. Soc. Am. J., 63, 1848–1855, 1999.

Borken, W., Savage, K., Davidson, E. A., and Trumbore, S. E.: Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil, Global Change Biol., 12, 177–193, 2006.

Borken, W. and Matzner, E.: Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils, Global Change Biol., 15, 808–824, 2009.

Bryla, D. R., Bouma, T. J., Hartmond, U., and Eissenstat, D. M.: Influence of temperature and soil drying on respiration of individual roots in citrus: integrating greenhouse observations into a predictive model for the field, Plant Cell Environ., 24, 781–790, 2001.

Burton, A. J., Pregitzer, K. S., Zogg, G. P., and Zak, D. R.: Drought reduces root respiration in sugar maple forests, Ecol. Appl., 8, 771–778, 1998.

Chapin, F. S., Matson, P. A., and Mooney, H. A.: Principles of Terrestrial Ecosystem Ecology, Springer-Verlag, New York, 2002.

Cotrufo, M. F., Alberti, G., Inglima, I., Marjanović, H., LeCain, D., Zaldei, A., Peressotti, A., and Miglietta, F.: Decreased summer drought affects plant productivity and soil carbon dynamics in a Mediterranean woodland, Biogeosciences, 8, 2729–2739, doi:10.5194/bg-8-2729-2011, 2011.

Curiel Yuste, J., Janssens, I. A., Carrara, A., Meiresonne, L., and Ceulemans, R.: Interactive effects of temperature and precipitation on soil respiration in a temperate maritime pine forest, Tree Physiol., 23, 1263–1270, 2003.

Curiel Yuste, J., Barba, J., Jose Fernandez-Gonzalez, A., Fernandez-Lopez, M., Mattana, S., Martinez-Vilalta, J., Nolis, P., and Lloret, F.: Changes in soil bacterial community triggered by drought-induced gap succession preceded changes in soil C stocks and quality, Evol. Ecol., 2, 3016–3031, 2012.

Davidson, E. A. and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, Nature, 440, 165–173, 2006.

Davis, J. C.: Statistics and Data Analysis in Geology, 3rd edn., John Wiley and Sons, 2002.

de Dato, G., Pellizzaro, G., Cesaraccio, C., Sirca, C., De Angelis, P., Duce, P., Spano, D., and Mugnozza, G. S.: Effects of warmer and drier climate conditions on plant composition and biomass production in a Mediterranean shrubland community, iFor. Biogeosci. For., 1, 39–48, 2008.

de Dato, G. D., De Angelis, P., Sirca, C., and Beier, C.: Impact of drought and increasing temperatures on soil CO_2 emissions in a Mediterranean shrubland (gariga), Plant Soil, 327, 153–166, 2010.

cc BY

Denef, K., Six, J., Paustian, K., and Merckx, R.: Importance of macroaggregate dynamics in controlling soil carbon stabilization: short-term effects of physical disturbance induced by dry-wet cycles, Soil Biol. Biochem., 33, 2145–2153, 2001.

Eissenstat, D. M., Whaley, E. L., Volder, A., and Wells, C. E.: Recovery of citrus surface roots following prolonged exposure to dry soil, J. Exp. Bot., 50, 1845–1854, 1999.

Escolar, C., Martinez, I., Bowker, M. A., and Maestre, F. T.: Warming reduces the growth and diversity of biological soil crusts in a semi-arid environment: implications for ecosystem structure and functioning, Philos. T. Roy. Soc. B, 367, 3087–3099, 2012.

Evans, S. E. and Wallenstein, M. D.: Soil microbial community response to drying and rewetting stress: does historical precipitation regime matter?, Biogeochemistry, 109, 101–116, 2012.

Fay, P. A., Blair, J. M., Smith, M. D., Nippert, J. B., Carlisle, J. D., and Knapp, A. K.: Relative effects of precipitation variability and warming on tallgrass prairie ecosystem function, Biogeosciences, 8, 3053–3068, doi:10.5194/bg-8-3053-2011, 2011.

Friedlingstein, P., Cox, P., Betts, R., Bopp, L., Von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H. D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K. G., Schnur, R., Strassmann, K., Weaver, A. J., Yoshikawa, C., and Zeng, N.: Climate-carbon cycle feedback analysis: results from the C^{4}MIP model intercomparison, J. Climate, 19, 3337–3353, 2006.

Goebel, M.-O., Bachmann, J., Reichstein, M., Janssens, I. A., and Guggenberger, G.: Soil water repellency and its implications for organic matter decomposition – is there a link to extreme climatic events?, Global Change Biol., 17, 2640–2656, 2011.

Hanson, P. J. and Weltzin, J. F.: Drought disturbance from climate change: response of United States forests, Sci. Total Environ., 262, 205–220, 2000.

Hanson, P. J., Wullschleger, S. D., Norby, R. J., Tschaplinski, T. J., and Gunderson, C. A.: Importance of changing CO$_2$, temperature, precipitation, and ozone on carbon and water cycles of an upland-oak forest: incorporating experimental results into model simulations, Global Change Biol., 11, 1402–1423, 2005.

Heinemeyer, A., Wilkinson, M., Vargas, R., Subke, J.-A., Casella, E., Morison, J. I. L., and Ineson, P.: Exploring the "overflow tap" theory: linking forest soil CO$_2$ fluxes and individual mycorrhizosphere components to photosynthesis, Biogeosciences, 9, 79–95, doi:10.5194/bg-9-79-2012, 2012.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and Jarvis, A.: Very high resolution interpolated climate surfaces for global land areas, Int. J. Climatol., 15, 1965–1978, 2005.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Högberg, M. N., Nyberg, G., Ottosson-Lofvenius, M., and Read, D. J.: Large-scale forest girdling shows that current photosynthesis drives soil respiration, Nature, 411, 789–792, 2001.

Huang, X. M., Lakso, A. N., and Eissenstat, D. M.: Interactive effects of soil temperature and moisture on concord grape root respiration, J. Exp. Bot., 56, 2651–2660, 2005.

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 CO_2 efflux, Global Change Biol., 15, 1289–1301, 2009.

Janssens, I. A., Lankreijer, H., Matteucci, G., Kowalski, A. S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grunwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E. J., Grelle, A., Rannik, U., 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, Global Change Biol., 7, 269–278, 2001.

Jarvis, P., Rey, A., Petsikos, C., Wingate, L., Rayment, M., Pereira, J., Banza, J., David, J., Miglietta, F., Borghetti, M., Manca, G., and Valentini, R.: Drying and wetting of mediterranean soils stimulates decomposition and carbon dioxide emission: the “Birch effect”, Tree Physiol., 27, 929–940, 2007.

Jentsch, A., Kreyling, J., and Beierkuhnlein, C.: A new generation of climate-change experiments: events, not trends, Front. Ecol. Environ., 5, 365–374, 2007.

Jentsch, A., Kreyling, J., Elmer, M., Gellesch, E., Glaser, B., Grant, K., Hein, R., Lara, M., Mirzae, H., Nadler, S. E., Nagy, L., Otieno, D., Pritsch, K., Rascher, U., Schadler, M., Schloter, M., Singh, B. K., Stadler, J., Walter, J., Wellstein, C., Wollecke, J., and Beierkuhnlein, C.: Climate extremes initiate ecosystem-regulating functions while maintaining productivity, J. Ecol., 99, 689–702, 2011.

Joos, O., Hagedorn, F., Heim, A., Gilgen, A. K., Schmidt, M. W. I., Siegwolf, R. T. W., and Buchmann, N.: Summer drought reduces total and litter-derived soil CO_2 effluxes in temperate grassland – clues from a $_{13}C$ litter addition experiment, Biogeosciences, 7, 1031–1041, doi:10.5194/bg-7-1031-2010, 2010.

CC BY

Jungkunst, H. F. and Fiedler, S.: Latitudinal differentiated water table control of carbon dioxide, methane and nitrous oxide fluxes from hydromorphic soils: feedbacks to climate change, Global Change Biol., 13, 2668–2683, 2007.

Jungkunst, H. F., Flessa, H., Scherber, C., and Fiedler, S.: Groundwater level controls CO_2, N_2O and CH_4 fluxes of three different hydromorphic soil types of a temperate forest ecosystem, Soil Biol. Biochem., 40, 2047–2054, 2008.

Kahmen, A., Perner, J., and Buchmann, N.: Diversity-dependent productivity in semi-natural grasslands following climate perturbations, Funct. Ecol., 19, 594–601, 2005.

Kim, D.-G., Vargas, R., Bond-Lamberty, B., and Turetsky, M. R.: Effects of soil rewetting and thawing on soil gas fluxes: a review of current literature and suggestions for future research, Biogeosciences, 9, 2459–2483, doi:10.5194/bg-9-2459-2012, 2012.

Kljun, N., Black, T. A., Griffis, T. J., Barr, A. G., Gaumont-Guay, D., Morgenstern, K., McCaughey, J. H., and Nesic, Z.: Response of net ecosystem productivity of three boreal forest stands to drought, Ecosystems, 9, 1128–1144, 2006.

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.

Kopittke, G. R., van Loon, E. E., Tietema, A., and Asscheman, D.: Soil respiration on an aging managed heathland: identifying an appropriate empirical model for predictive purposes, Biogeosciences, 10, 3007–3038, doi:10.5194/bg-10-3007-2013, 2013.

Kuzyakov, Y. and Gavrichkova, O.: Time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls, Global Change Biol., 16, 3386–3406, 2010.

Larcher, W.: Physiological plant ecology, 4th edn., Springer-Verlag, Berlin, Heidelberg, New York, 2003.

Lellei-Kovacs, E., Kovacs-Lang, E., Botta-Dukat, Z., Kalapos, T., Emmett, B., and Beier, C.: Thresholds and interactive effects of soil moisture on the temperature response of soil respiration, Eur. J. Soil Biol., 47, 247–255, 2011.

MacKay, S. L., Arain, M. A., Khomik, M., Brodeur, J. J., Schumacher, J., Hartmann, H., and Peichl, M.: The impact of induced drought on transpiration and growth in a temperate pine plantation forest, Hydrol. Process., 26, 1779–1791, 2012.

Maestre, F. T., Escolar, C., Ladrón de Guevara, M., Quero, J. L., Lázaro, R., Delgado-Baquerizo, M., Ochoa, V., Berdugo, M., Gozalo, B., and Gallardo, A.: Changes in biocrust

cc BY

cover drive carbon cycle responses to climate change in drylands, Global Change Biol., 19, 3835–3847, 2013.

Mäkiranta, P., Minkkinen, K., Hytonen, J., and Laine, J.: Factors causing temporal and spatial variation in heterotrophic and rhizospheric components of soil respiration in afforested organic soil croplands in finland, Soil Biol. Biochem., 40, 1592–1600, 2008.

Morecroft, M. D., Masters, G. J., Brown, V. K., Clarke, I. P., Taylor, M. E., and Whitehouse, A. T.: Changing precipitation patterns alter plant community dynamics and succession in an ex-arable grassland, Funct. Ecol., 18, 648–655, 2004.

Moyano, F. E., Manzoni, S., and Chenu, C.: Responses of soil heterotrophic respiration to moisture availability: an exploration of processes and models, Soil Biol. Biochem., 59, 72–85, 2013.

Muhr, J. and Borken, W.: Delayed recovery of soil respiration after wetting of dry soil further reduces c losses from a Norway spruce forest soil, J. Geophys. Res.-Biogeo., 114, G04023, doi:10.1029/2009JG000998, 2009.

Muhr, J., Franke, J., and Borken, W.: Drying-rewetting events reduce C and N losses from a Norway spruce forest floor, Soil Biol. Biochem., 42, 1303–1312, 2010.

Ogaya, R., Peñuelas, J., Asensio, D., and Llusia, J.: Chlorophyll fluorescence responses to temperature and water availability in two co-dominant Mediterranean shrub and tree species in a long-term field experiment simulating climate change, Environ. Exp. Bot., 71, 123–127, 2011.

Orlowsky, B. and Seneviratne, S. I.: Global changes in extreme events: regional and seasonal dimension, Clim. Change, 110, 669–696, 2012.

Patrick, L., Cable, J., Potts, D., Ignace, D., Barron-Gafford, G., Griffith, A., Alpert, H., Van Gestel, N., Robertson, T., Huxman, T. E., Zak, J., Loik, M. E., and Tissue, D.: Effects of an increase in summer precipitation on leaf, soil, and ecosystem fluxes of CO_2 and H_2O in a sotol grassland in big bend national park, Texas, Oecologia, 151, 704–718, 2007.

Piani, C., Weedon, G. P., Best, M., Gomes, S. M., Viterbo, P., Hagemann, S., and Haerter, J. O.: Statistical bias correction of global simulated daily precipitation and temperature for the application of hydrological models, J. Hydrol., 395, 199–215, 2010.

Poll, C., Marhan, S., Back, F., Niklaus, P. A., and Kandeler, E.: Field-scale manipulation of soil temperature and precipitation change CO_2 flux in a temperate agricultural ecosystem, Agr. Ecosyst. Environ., 165, 88–97, 2013.

cc BY

Priestley, C. H. B. and Taylor, R. J.: Assessment of surface heat-flux and evaporation using large-scale parameters, Mon. Weather Rev., 100, 81–92, 1972.

Raich, J. W. and Schlesinger, W. H.: The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate, Tellus B, 44, 81–99, 1992.

Reichstein, M., Bahn, M., Ciais, P., Frank, D., M. D., Mahecha, Seneviratne, S. I., Zscheischler, J., Beer, C., Buchmann, N., Frank, D. C., Papale, D., Rammig, A., Smith, P., Thonicke, K., van der Velde, M., Vicca, S., Walz, A., and Wattenbach, M.: Climate extremes and the carbon cycle, Nature, 500, 287–295, 2013.

Sanaullah, M., Blagodatskaya, E., Chabbi, A., Rumpel, C., and Kuzyakov, Y.: Drought effects on microbial biomass and enzyme activities in the rhizosphere of grasses depend on plant community composition, Appl. Soil Ecol., 48, 38–44, 2011.

Schimel, J., Balser, T. C., and Wallenstein, M.: Microbial stress-response physiology and its implications for ecosystem function, Ecology, 88, 1386–1394, 2007.

Schindlbacher, A., Wunderlich, S., Borken, W., Kitzler, B., Zechmeister-Boltenstern, S., and Jandl, R.: Soil respiration under climate change: prolonged summer drought offsets soil warming effects, Global Change Biol., 18, 2270–2279, 2012.

Selsted, M. B., van der Linden, L., Ibrom, A., Michelsen, A., Larsen, K. S., Pedersen, J. K., Mikkelsen, T. N., Pilegaard, K., Beier, C., and Ambus, P.: Soil respiration is stimulated by elevated CO_2 and reduced by summer drought: three years of measurements in a multifactor ecosystem manipulation experiment in a temperate heathland (Climaite), Global Change Biol., 18, 1216–1230, 2012.

Sotta, E. D., Veldkamp, E., Schwendenmann, L., Guimaraes, B. R., Paixao, R. K., Ruivo, M. D. L. P., Lola Da Costa, A. C., and Meir, P.: Effects of an induced drought on soil carbon dioxide (CO_2) efflux and soil CO_2 production in an eastern Amazonian rainforest, Brazil, Global Change Biol., 13, 2218–2229, 2007.

Sowerby, A., Emmett, B. A., Tietema, A., and Beier, C.: Contrasting effects of repeated summer drought on soil carbon efflux in hydric and mesic heathland soils, Global Change Biol., 14, 2388–2404, 2008.

Suseela, V., Conant, R. T., Wallenstein, M. D., and Dukes, J. S.: Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment, Global Change Biol., 18, 336–348, 2012.

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, Global Change Biol., 17, 1505–1515, 2011.

Thorne, M. A. and Frank, D. A.: The effects of clipping and soil moisture on leaf and root morphology and root respiration in two temperate and two tropical grasses, Plant Ecol., 200, 205–215, 2009.

Tian, J., Zhu, Y., Kang, X., Dong, X., Li, W., Chen, H., and Wang, Y.: Effects of drought on the archaeal community in soil of the zoige wetlands of the Qinghai-Tibetan plateau, Eur. J. Soil Biol., 52, 84–90, 2012.

van der Molen, M. K., Dolman, A. J., Ciais, P., Eglin, T., Gobron, N., Law, B. E., Meir, P., Peters, W., Phillips, O. L., Reichstein, M., Chen, T., Dekker, S. C., Doubkova, M., Friedl, M. A., Jung, M., van den Hurk, B. J. J. M., de Jeu, R. A. M., Kruijt, B., Ohta, T., Rebel, K. T., Plummer, S., Seneviratne, S. I., Sitch, S., Teuling, A. J., van der Werf, G. R., and Wang, G.: Drought and ecosystem carbon cycling, Agr. Forest Meteorol., 151, 765–773, 2011.

van Straaten, O., Veldkamp, E., Köhler, M., and Anas, I.: Spatial and temporal effects of drought on soil CO_2 efflux in a cacao agroforestry system in Sulawesi, Indonesia, Biogeosciences, 7, 1223–1235, doi:10.5194/bg-7-1223-2010, 2010.

van Straaten, O., Veldkamp, E., and Corre, M. D.: Simulated drought reduces soil CO_2 efflux and production in a tropical forest in Sulawesi, Indonesia, Ecosphere, 2, 119, doi:doi:10.1890/ES11-00079.1, 2011.

Vargas, R., Baldocchi, D. D., Allen, M. F., Bahn, M., Black, T. A., Collins, S. L., Yuste, J. C., Hirano, T., Jassal, R. S., Pumpanen, J., and Tang, J.: Looking deeper into the soil: Biophysical controls and seasonal lags of soil CO_2 production and efflux, Ecol Appl, 20, 1569–1582, 2010.

Vargas, R., Collins, S. L., Thomey, M. L., Johnson, J. E., Brown, R. F., Natvig, D. O., and Friggens, M. T.: Precipitation variability and fire influence the temporal dynamics of soil CO_2 efflux in an arid grassland, Global Change Biol., 18, 1401–1411, 2012.

Vicca, S., Fivez, L., Kockelbergh, F., Van Pelt, D., Segers, J. R., Meire, P., Ceulemans, R., and Janssens, I. A.: No signs of thermal acclimation of heterotrophic respiration from peat soils exposed to different water levels, Soil Biol. Biochem., 41, 2014–2016, 2009.

Vicca, S., Gilgen, A. K., Serrano, M. C., Dreesen, F. E., Dukes, J. S., Estiarte, M., Gray, S. B., Guidolotti, G., Hoeppner, S. S., Leakey, A. D. B., Ogaya, R., Ort, D. R., Ostrogovic, M. Z., Rambal, S., Sardans, J., Schmitt, M., Siebers, M., van der Linden, L., van Straaten, O., and

Granier, A.: Urgent need for a common metric to make precipitation manipulation experiments comparable, New Phytol., 195, 518–522, 2012a.

Vicca, S., Luyssaert, S., Penuelas, J., Campioli, M., Chapin III, F. S., Ciais, P., Heinemeyer, A., Högberg, P., Kutsch, W. L., Law, B. E., Malhi, Y., Papale, D., Piao, S. L., Reichstein, M., Schulze, E. D., and Janssens, I. A.: Fertile forests produce biomass more efficiently, Ecol. Lett., 15, 520–526, 2012b.

Weedon, G. P., Gomes, S., Viterbo, P., Shuttleworth, W. J., Blyth, E., Österle, H., Adam, J. C., Bellouin, N., Boucher, O., and Best, M.: Creation of the WATCH forcing data and its use to assess global and regional reference crop evaporation over land during the twentieth century, J. Hydrometeorol., 12, 823–848, 2011.

Wieder, W. R., Bonan, G. B., and Allison, S. D.: Global soil carbon projections are improved by modelling microbial processes, Nat. Clim. Change, 3, 909–912, 2013.

Wood, J. M., Bremer, E., Csonka, L. N., Kraemer, R., Poolman, B., van der Heide, T., and Smith, L. T.: Osmosensing and osmoregulatory compatible solute accumulation by bacteria, Comp. Bioch. Phys. A, 130, 437–460, 2001.

Wu, Z., 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, Global Change Biol., 17, 927–942, 2011.

CC BY

Table A1. Information about the precipitation manipulation experiments: latitude (Lat), longitude (Long), mean annual precipitation (MAP; mm), mean annual temperature (MAT; °C), vegetation type, Köppen classification (Köppen class.), hydrology (Hydr.), manipulation type (Manip. type; drying experiment (–), irrigation experiment (+) or experiment in which the pattern of precipitation was altered, but not the total amount of precipitation (0)), duration of the manipulation (episodic manipulation during few weeks while the rest of the year is unaltered (Epis) vs. continuous drying/irrigation during entire growing season or year (Cont) vs. altered rainfall pattern during entire year (ContAlt)), the % clay in the soil, the depth of SWC measurements (cm) and a key reference for each experiment (if available). Species composition for all sites is given in Table S1. We distinguish between sites used only for Fig. 1 (not used for further analysis because there were not enough data points to generate reliable model fits ($n \leq 10$)), sites discarded from further analyses because of non-robust results (see Table C1), and sites used for all analyses.

Experiment	Lat	Long	MAP	MAT	Köppen class.	Vegetation	Hydr.	Manip. type	Duration manip.	% clay	SWC depth	Key reference
Sites included in Fig. 1, but excluded from other analyses because of too few data or non-normal distribution of model residuals for $SCE_{control}$												
Almería	37.09	−2.08	274	17	BSk	shrubland	xeric	–	Cont	7	0–5	Maestre et al. (2013)
Achenkirch	47.58	11.64	1480	5.7	Cfb	forest	mesic	–	Epis	28	5	Schindlbacher et al. (2012)
BigBend_S	29.30	−103.17	370	24.2	BWh	shrubland	xeric	+	Epis	8	15	Patrick et al. (2007)
BigBend_W	29.30	−103.17	370	24.2	BWh	shrubland	xeric	+	Epis	8	15	
BigBend_SW	29.30	−103.17	370	24.2	BWh	shrubland	xeric	+	Epis	8	15	
Garraf	41.30	1.82	552	15.6	Csa	shrubland	xeric	+	Epis	18	0–15	Beier et al. (2004)
Prades	41.35	1.03	663	11.7	Csa	forest	xeric	–	Epis	21	0–25	Ogaya et al. (2011)
RaMPs_Alt	39.10	−96.60	835	13	Cfa	grassland	mesic	0	ContAlt	32	0–15	Fay et al. (2011)
ThuringerSchiefer5	50.48	11.60	1000	6.5	Cfb	grassland	mesic	–	Epis	25	0–10	Kahmen et al. (2005)
ThuringerSchiefer6	50.48	11.58	1000	6.5	Cfb	grassland	mesic	–	Epis	25	0–10	
ThuringerSchiefer19	50.48	11.26	1000	6.5	Cfb	grassland	mesic	–	Epis	22	0–10	
Tolfa_Dry	42.15	11.93	729	13	Csa	forest	xeric	–	Cont	6	0–10	Cotrufo et al. (2011)
Tolfa_Wet	42.15	11.93	729	13	Csa	forest	xeric	+	Epis	6	0–10	

Table A1. Continued.

Experiment	Lat	Long	MAP	MAT	Köppen class.	Vegetation	Hydr.	Manip. type	Duration manip.	% clay	SWC depth	Key reference
Sites included in Fig. 1and hypothesis tests, but excluded from CART-analysis because of non-robust results (see Table C1)												
Boston_dry	42.39	−71.22	1063	10.3	Dfa	grassland	mesic	–	Cont	9	0–30	Suseela et al. (2012)
Caxiuana	−1.73	−51.46	2314	26.9	Af	forest	mesic	–	Cont	10	0–30	Sotta et al. (2007)
Hohenheim_LALF	48.70	9.18	679	8.7	Cfb	agriculture	mesic	–	Epis	22	0–15	
Oldebroek	52.40	5.90	1042	10.1	Cfb	shrubland	mesic	–	Epis	8	0–50	Kopittke et al. (2013)
SulawesiCacao	−1.55	120.02	2092	25.5	Af	forest	mesic	–	Cont	14	5	van Straaten et al. (2010)
ThuringerSchiefer2	50.41	11.63	1000	6.5	Cfb	grassland	mesic	–	Epis	24	0–10	Kahmen et al. (2005)
ThuringerSchiefer3	50.41	11.63	1000	6.5	Cfb	grassland	mesic	–	Epis	23	0–10	
Sites included in all analyses												
Aranjuez	40.03	−3.54	349	15	Csa	grassland	xeric	–	Cont	6	0–5	Escolar et al. (2012)
Boston_wet	42.39	−71.22	1063	10.3	Dfa	grassland	mesic	+	Cont	9	0–30	Suseela et al. (2012)
Brandbjerg	55.88	11.97	613	8	Cfb	shrubland	mesic	–	Epis	2	20	Selsted et al. (2012)
Clocaenog	53.05	−3.47	1550	8.2	Cfb	shrubland	hydric	–	Epis	50	7	Sowerby et al. (2008)
Coulissenhieb	50.14	11.87	1160	5.3	Cfb	forest	mesic	–	Epis	19	10	Muhr and Borken (2009)
Duolun_20	42.02	116.17	385	2.1	Dwb	grassland	mesic	–	Cont	17	0–10	
Duolun_40	42.02	116.17	385	2.1	Dwb	grassland	mesic	–	Cont	17	0–10	
Duolun_60	42.02	116.17	385	2.1	Dwb	grassland	mesic	–	Cont	17	0–10	
HarvardForest	42.54	−72.17	1100	6	Dfb	forest	mesic	+	Epis	18	5	Borken et al. (2006)
Hohenheim_LA	48.70	9.18	679	8.7	Cfb	agriculture	mesic	–	Epis	22	0–15	Poll et al. (2013)
Hohenheim_LF	48.70	9.18	679	8.7	Cfb	agriculture	mesic	0	ContAlt	22	0–15	
Kiskunsag	46.88	19.38	505	10.4	Cfb	shrubland	xeric	–	Epis	2	0–20	Lellei-Kovacs et al. (2011)
Mols	56.38	10.95	550	7.7	Cfb	shrubland	mesic	–	Epis	6	0–40	Beier et al. (2004)
PortoConte	40.62	8.17	640	16.8	Csa	shrubland	xeric	–	Epis	13	0–10	de Dato et al. (2010)
RaMPs_Dry	39.10	−96.60	835	13	Cfa	grassland	mesic	–	Cont	32	0–15	
RaMPs_DryAlt	39.10	−96.60	835	13	Cfa	grassland	mesic	–	ContAlt	32	0–15	
Sevilleta_Wet1	34.34	−106.73	250	13.2	BSk	grassland	xeric	+	ContAlt	10	0–15	Thomey et al. (2011)
Sevilleta_Wet2	34.34	−106.73	250	13.2	BSk	grassland	xeric	+	ContAlt	10	0–15	
Solling	51.52	9.56	1090	6.4	Cfb	forest	mesic	–	Epis	32	10	Borken et al. (1999)
Stubai	47.13	11.31	915	6.3	Dfc	grassland	mesic	–	Epis	16	5	
SulawesiForest	−1.49	120.05	2901	20.6	Af	forest	mesic	–	Cont	39	5	van Straaten et al. (2011)
ThuringerSchiefer1	50.41	11.63	1000	6.5	Cfb	grassland	mesic	–	Epis	24	0–10	Kahmen et al. (2005)
ThuringerSchiefer4	50.46	11.59	1000	6.5	Cfb	grassland	mesic	–	Epis	25	0–10	
ThuringerSchiefer7	50.48	11.56	1000	6.5	Cfb	grassland	mesic	–	Epis	25	0–10	
ThuringerSchiefer8	50.47	11.50	1000	6.5	Cfb	grassland	mesic	–	Epis	22	0–10	
ThuringerSchiefer9	50.43	11.51	1000	6.5	Cfb	grassland	mesic	–	Epis	23	0–10	
ThuringerSchiefer10	50.40	11.45	1000	6.5	Cfb	grassland	mesic	–	Epis	27	0–10	
ThuringerSchiefer11	50.38	11.45	1000	6.5	Cfb	grassland	mesic	–	Epis	23	0–10	
ThuringerSchiefer12	50.41	11.38	1000	6.5	Cfb	grassland	mesic	–	Epis	32	0–10	
ThuringerSchiefer13	50.42	11.39	1000	6.5	Cfb	grassland	mesic	–	Epis	31	0–10	
ThuringerSchiefer14	50.45	11.41	1000	6.5	Cfb	grassland	mesic	–	Epis	27	0–10	
ThuringerSchiefer15	50.45	11.41	1000	6.5	Cfb	grassland	mesic	–	Epis	25	0–10	
ThuringerSchiefer16	50.44	11.36	1000	6.5	Cfb	grassland	mesic	–	Epis	25	0–10	
ThuringerSchiefer17	50.44	11.34	1000	6.5	Cfb	grassland	mesic	–	Epis	28	0–10	
ThuringerSchiefer18	50.46	11.35	1000	6.5	Cfb	grassland	mesic	–	Epis	24	0–10	
TurkeyPoint	42.72	−80.37	1010	7.8	Dfb	forest	mesic	–	Epis	1	0–5	MacKay et al. (2012)
WalkerBranch_Dry	35.97	−84.28	1352	14.2	Cfa	forest	mesic	–	Cont	6	0–35	Hanson et al. (2005)
WalkerBranch_Wet	35.97	−84.28	1352	14.2	Cfa	forest	mesic	+	Cont	6	0–35	

Table B1. For each experiment, the % change in precipitation is given, along with the average of observed and predicted soil CO_2 efflux (SCE; µmol $CO_2\,m^{-2}\,s^{-1}$) for control and treatment in all experiments. Sign. level indicates whether the difference between treatment and control SCE measurements was significant at $p < 0.01$ (**), at $p < 0.05$ (*) or not significant (ns) according to repeated measures ANOVA. For the treatment, averages are also shown for the subset including only days where $SWC_{treatment}$ is within the range of SWC observed in the control (common-SWC-subset). Averages were computed over the entire measurement period. Predictions are based on the model parameterized by the control data (model 4, see Methods and Table S2 for details). The % difference between predicted and observed is calculated as 100*(average predicted - average observed)/average observed. Positive values indicate overestimates, whereas negative values indicate that predicted SCE underestimated observed SCE. The % change in precipitation was calculated from precipitation data, averaged for the entire duration of the experiment. Negative values indicate a reduction of precipitation, while positive numbers indicate an increase in precipitation. When only the timing of precipitation was altered, this is indicated as “timing”.

Table B1. Continued.

Experiment	% change in precip.	OBSERVED control	treatment	Sign. level	PREDICTED control	treatment	treatment	% difference control common-SWC-subset	treatment	treatment common-SWC-subset
Achenkirch	−15.44	2.45	2.11	ns	2.47	2.29	2.41	0.87	8.75	11.86
Aranjuez	−30.00	0.72	0.73	**	0.67	0.67	0.69	−5.77	−8.39	−7.77
Boston_dry	−51.89	3.58	3.07	**	3.64	11.34	1.91	1.72	269.39	−17.35
Boston_wet	20.00	3.58	3.29	**	3.64	3.87	3.38	1.72	17.58	−2.37
Brandbjerg	−7.64	1.60	1.46	**	1.52	1.37	1.35	−4.98	−5.84	−9.86
Caxiuana	−50.00	3.70	3.00	**	3.68	2.82	3.59	−0.45	−5.89	2.87
Clocaenog	−22.04	1.33	1.62	ns	1.21	1.42	1.39	−9.14	−12.46	−13.64
Coulissenhieb	6.68	2.65	2.02	*	2.62	2.51	2.54	−1.09	24.23	27.67
Duolun_20	−20.00	1.54	1.26	**	1.43	1.24	1.32	−7.00	−1.15	−1.66
Duolun_40	−40.00	1.54	1.07	ns	1.43	1.14	1.17	−7.00	6.47	6.71
Duolun_60	−60.00	1.54	0.84	**	1.43	0.83	1.06	−7.00	−2.07	2.82
HarvardForest	−32.55	3.05	2.25	ns	2.98	2.77	2.77	−2.14	23.19	23.19
Hohenheim_LA	−11.73	1.08	1.00	**	1.01	1.06	1.04	−6.45	6.45	4.67
Hohenheim_LALF	−11.00	1.08	0.94	ns	1.01	1.07	1.02	−6.45	13.71	10.94
Hohenheim_LF	0.85	1.08	1.13	*	1.01	1.05	1.02	−6.45	−7.75	−9.88
Kiskunsag	−21.38	0.53	0.43	**	0.50	0.47	0.48	−5.76	7.79	7.12
Mols	−23.18	2.45	1.63	ns	2.41	2.65	1.10	−1.56	63.23	21.50
Oldebroek	−19.03	0.80	0.68	**	0.77	0.57	0.61	−3.59	−15.55	−8.63
PortoConte	−16.24	2.86	2.63	ns	2.74	2.61	2.66	−4.30	−0.67	−0.17
RaMPs_Alt	13.13	9.37	8.35	ns	9.16	8.47	8.49	−2.25	1.48	1.41
RaMPs_Dry	−17.59	9.57	8.88	ns	9.29	8.98	9.04	−2.90	1.16	0.88
RaMPs_DryAlt	−17.19	9.67	7.93	ns	9.39	9.03	9.19	−2.88	13.81	13.37
Sevilleta_Wet1	26.38	0.70	0.83	*	0.69	0.67	0.68	−1.85	−18.91	−18.34
Sevilleta_Wet2	15.63	0.70	1.02	ns	0.69	0.66	0.66	−1.85	−35.37	−35.29
Solling	−28.37	1.07	1.48	ns	1.06	0.98	0.99	−0.83	−33.30	−33.29
Stubai	−31.42	4.33	2.73	**	4.26	2.36	4.35	−1.60	−13.36	25.49
SulawesiCacao	−60.09	2.83	2.81	ns	2.79	1.40	2.90	−1.39	−50.28	−8.39
SulawesiForest	−53.91	3.07	1.94	ns	3.05	1.79	2.58	−0.85	−7.69	4.34
ThuringerSchiefer1	−11.11	4.77	4.11	ns	4.67	4.11	4.14	−2.09	0.01	−1.08
ThuringerSchiefer2	−11.11	5.82	3.50	ns	5.65	4.71	5.07	−2.82	34.47	34.39
ThuringerSchiefer3	−11.11	6.10	4.89	**	5.77	4.91	5.35	−5.35	0.35	2.21
ThuringerSchiefer4	−11.11	5.81	4.70	**	5.49	4.86	5.10	−5.51	3.54	4.06
ThuringerSchiefer5	−11.11	6.28	4.36	*	6.11	5.20	5.44	−2.69	19.02	18.38
ThuringerSchiefer6	−11.11	6.36	6.24	**	6.13	4.96	5.53	−3.62	−20.57	−15.36
ThuringerSchiefer7	−11.11	8.12	6.09	**	7.86	6.44	6.73	−3.16	5.79	4.73
ThuringerSchiefer8	−11.11	5.96	6.10	ns	5.84	5.85	6.14	−2.13	−4.05	−3.87
ThuringerSchiefer9	−11.11	4.36	4.12	**	4.25	4.00	4.00	−2.50	−2.96	−2.96
ThuringerSchiefer10	−11.11	4.30	4.18	**	4.18	4.06	4.06	−2.92	−2.72	−2.72
ThuringerSchiefer11	−11.11	6.41	5.61	**	6.15	5.54	5.54	−4.04	−1.36	−1.36
ThuringerSchiefer12	−11.11	5.17	4.24	**	4.61	4.08	4.35	−10.81	−3.64	−4.11
ThuringerSchiefer13	−11.11	5.93	6.46	**	5.65	5.58	5.79	−4.64	−13.68	−14.41
ThuringerSchiefer14	−11.11	4.26	3.84	**	4.24	3.80	3.96	−0.63	−1.05	−3.01
ThuringerSchiefer15	−11.11	5.99	4.56	**	5.93	4.87	5.08	−1.00	6.91	7.03
ThuringerSchiefer16	−11.11	4.54	3.91	**	4.39	3.78	3.91	−3.29	−3.50	−3.80
ThuringerSchiefer17	−11.11	4.42	4.01	**	4.37	4.15	4.71	−1.32	3.70	5.63
ThuringerSchiefer18	−11.11	4.62	4.35	**	4.54	4.29	4.29	−1.83	−1.38	−1.38
ThuringerSchiefer19	−11.11	4.12	4.98	**	4.03	3.79	3.84	−2.32	−24.02	−26.46
Tolfa	−21.44	3.22	3.81	**	3.00	3.27	3.27	−6.87	−14.23	−14.23
Tolfa_Wet	69.00	3.05	4.90	**	2.88	3.43	3.43	−5.54	−30.00	−29.98
TurkeyPoint	−23.20	2.14	1.54	**	2.10	2.65	2.48	−1.95	72.17	62.92
WalkerBranch_Dry	−33.00	3.59	3.81	**	3.52	3.05	3.11	−2.11	−20.05	−20.29
WalkerBranch_Wet	33.00	3.68	3.62	**	3.60	3.61	3.53	−1.96	−0.23	−0.33

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◀| |▶
◀ ▶
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

Table C1. For each experiment, we present the R^2 of the model fitted to the data of the control plots, the number of data points (N), and the median interval (in days) between two consecutive measurements of soil CO_2 efflux (I). We also show the results of the two tests that we performed to test our hypothesis. For both the entire dataset and the common-SWC-subset, “h1” is the p value of the Lilliefors test for normality, “h2” shows the ratio of $RMSE_{treatment}$ to $RMSE_{control}$ and ‘H’ indicates whether or not H1 was rejected (see Fig. 2 and Methods for details). Experiments for which both the entire dataset and the common-SWC-subset gave the same result are indicated with “yes” in the column “Robust?”. The weight (W) used in this CART-analysis is given (W is calculated as 1/number of experiments per site that are used in CART). The results of the trend analysis on the time course of the predictability index of $SCE_{treatment}$ (Pi; runs test dichotomized around the median) are presented in the column “Trend”, with 0 indicating that no trend was detected, and 1 indicating a significant trend for Pi vs. time. When the rainfall manipulation was initiated more than one year before the start of SCE measurements, trend analysis is considered irrelevant. This is indicated as NA, followed by the result of the trend analysis in parenthesis. Note that this table includes only results for experiments with > 10 data points and for which residuals of the control were normally distributed.

CC BY

Table C1. Continued.

				entire dataset			common-SWC-subset					
Experiment	R^2	N	I	h1	h2	H	h1	h2	H	Robust?	W	Trend
Aranjuez	0.37	29	35	0.50	1.06	0	0.50	1.06	0	Yes	1	0
Boston_dry	0.93	11	31	0.50	4.29	1	0.50	1.12	0	No	NA	NA(0)
Boston_wet	0.93	11	31	0.50	1.74	0	0.50	1.22	0	Yes	1	NA(0)
Brandbjerg	0.60	173	16	0.08	1.30	0	0.50	1.10	0	Yes	1	0
Caxiuana	0.49	22	15	0.15	2.35	1	0.50	1.55	0	No	NA	0
Clocaenog	0.59	90	15	0.50	1.09	0	0.50	1.09	0	Yes	1	NA(0)
Coulissenhieb	0.86	35	9	0.09	**2.41**	1	0.13	**2.43**	1	Yes	1	0
Duolun_20	0.53	23	8	**0.04**	1.06	1	**0.01**	1.05	1	Yes	0.33	0
Duolun_40	0.53	23	8	0.07	1.09	0	0.08	1.09	0	Yes	0.33	0
Duolun_60	0.53	23	8	0.17	1.29	0	0.32	1.26	0	Yes	0.33	0
HarvardForest	0.82	43	7	0.50	1.72	0	0.50	1.72	0	Yes	1	0
Hohenheim_LA	0.71	38	7	0.50	1.20	0	0.50	1.21	0	Yes	0.5	0
Hohenheim_LALF	0.71	38	7	0.06	1.14	0	**0.02**	1.13	1	No	NA	0
Hohenheim_LF	0.71	38	7	0.50	0.91	0	0.50	0.92	0	Yes	0.5	0
Kiskunsag	0.34	66	27	0.50	0.99	0	0.50	1.04	0	Yes	1	NA(0)
Mols	0.80	18	24	0.18	1.67	0	0.50	1.44	0	Yes	1	NA(0)
Oldebroek	0.73	73	15	**0.03**	1.36	1	0.50	1.07	0	No	NA	1
PortoConte	0.30	47	36	0.50	0.97	0	0.37	0.98	0	Yes	1	0
RaMPs_Dry	0.47	74	5	0.50	0.94	0	0.50	0.92	0	Yes	0.5	0
RaMPs_DryAlt	0.45	73	5	0.50	1.29	0	0.50	1.26	0	Yes	0.5	0
Sevilleta_Wet1	0.38	163	1	**0.00**	1.47	1	**0.01**	1.39	1	Yes	0.5	1
Sevilleta_Wet2	0.38	163	1	0.50	**2.53**	1	0.42	**2.53**	1	Yes	0.5	1
Solling	0.85	264	1	0.00	**2.60**	1	0.00	**2.59**	1	Yes	1	1
Stubai	0.66	309	1	0.00	**4.92**	1	0.06	**2.08**	1	Yes	1	1
SulawesiCacao	0.37	46	14	0.00	**13.14**	1	0.50	1.29	0	No	NA	1
SulawesiForest	0.39	59	14	0.50	1.73	0	0.33	0.89	0	Yes	1	1
ThuringerSchiefer1	0.72	14	22	0.11	1.28	0	0.30	1.45	0	Yes	0.07	0
ThuringerSchiefer2	0.81	13	24	0.17	1.95	0	**0.03**	**2.38**	1	No	NA	0
ThuringerSchiefer3	0.35	13	24	**0.04**	0.87	1	0.11	0.72	0	No	NA	0
ThuringerSchiefer4	0.59	14	22	0.50	0.85	0	0.50	0.88	0	Yes	0.07	0
ThuringerSchiefer7	0.72	14	22	0.50	1.53	0	0.50	1.47	0	Yes	0.07	0
ThuringerSchiefer8	0.75	15	24	0.33	1.57	0	0.50	1.62	0	Yes	0.07	0
ThuringerSchiefer9	0.83	15	24	0.32	1.26	0	0.32	1.26	0	Yes	0.07	0
ThuringerSchiefer10	0.76	14	22	0.34	1.12	0	0.34	1.12	0	Yes	0.07	0
ThuringerSchiefer11	0.67	13	27	0.13	1.14	0	0.13	1.14	0	Yes	0.07	0
ThuringerSchiefer12	0.52	14	23	0.50	0.88	0	0.50	0.94	0	Yes	0.07	0
ThuringerSchiefer13	0.73	14	23	0.13	1.18	0	0.20	1.37	0	Yes	0.07	0
ThuringerSchiefer14	0.86	12	26	0.22	1.13	0	0.08	1.18	0	Yes	0.07	0
ThuringerSchiefer15	0.96	14	26	0.50	1.44	0	0.50	1.47	0	Yes	0.07	0
ThuringerSchiefer16	0.73	15	24	0.14	0.95	0	0.27	0.95	0	Yes	0.07	0
ThuringerSchiefer17	0.83	14	22	0.13	1.86	0	0.38	1.62	0	Yes	0.07	0
ThuringerSchiefer18	0.83	14	22	0.50	1.18	0	0.50	1.18	0	Yes	0.07	0
TurkeyPoint	0.85	106	1	**0.04**	**3.59**	1	**0.04**	**3.63**	1	Yes	1	1
WalkerBranch_Dry	0.59	20	38	0.50	1.46	0	0.50	1.42	0	Yes	0.5	0
WalkerBranch_Wet	0.63	21	33	0.45	1.13	0	0.47	1.13	0	Yes	0.5	0

Table D1. Nomenclature.

CART	classification and regression tree
H1	hypothesis that the relationship between SCE and ST and SWC observed from fluctuations over time in the control plots can be extrapolated to predict SCE in plots exposed to a different precipitation regime
MAP	mean annual precipitation
MAT	mean annual temperature
Pi	predictability index, calculated as the absolute error of predicted soil CO_2 efflux in the treatment reduced by the absolute error of predicted soil CO_2 efflux in the control at a specific moment (see Eq. 5). Pi values close to zero indicate that $SCE_{treatment}$ was predicted similarly well as $SCE_{control}$, whereas values substantially below or above zero indicate the difference in predictability of $SCE_{treatment}$ relative to $SCE_{control}$. Negative values indicate that the prediction of $SCE_{treatment}$ was less good than that of $SCE_{control}$, and vice versa for positive values
SCE	soil CO_2 efflux
$SCE_{control}$	soil CO_2 efflux in the control
$SCE_{treatment}$	soil CO_2 efflux in the treatment
SWC	volumetric soil water content
$SWC_{control}$	volumetric soil water content in the control
$SWC_{treatment}$	volumetric soil water content in the treatment
common-SWC-subset	dataset using only dates when $SWC_{treatment}$ was within the range of $SWC_{control}$
ST	soil temperature.

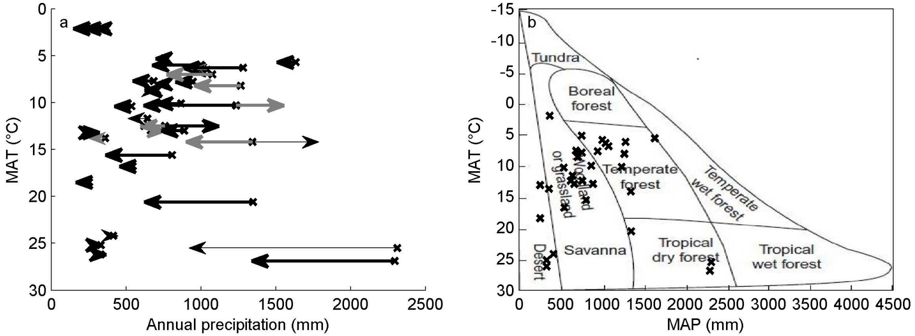

Fig. 1. (a) Overview of the magnitude and direction of precipitation effect on soil CO_2 efflux (SCE) for the different experiments. Arrows point from control precipitation to treatment precipitation (averaged over different years in case of multi-year data). Crosses localize control conditions in terms of annual precipitation and mean annual temperature (MAT). Black arrows indicate a positive correlation between precipitation manipulation and SCE, i.e., an increase of SCE when precipitation increases, or a decrease of SCE when precipitation is reduced. Gray arrows indicate negative correlations (which could be considered to reflect somewhat unexpected results). Bold arrows represent significant differences between SCE treatment and SCE control ($p < 0.05$), while thin arrows reflect non-significant differences (repeated measures ANOVA). Panel b shows the biomes that are represented by our dataset (biome figure adapted from Chapin et al., 2002).

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

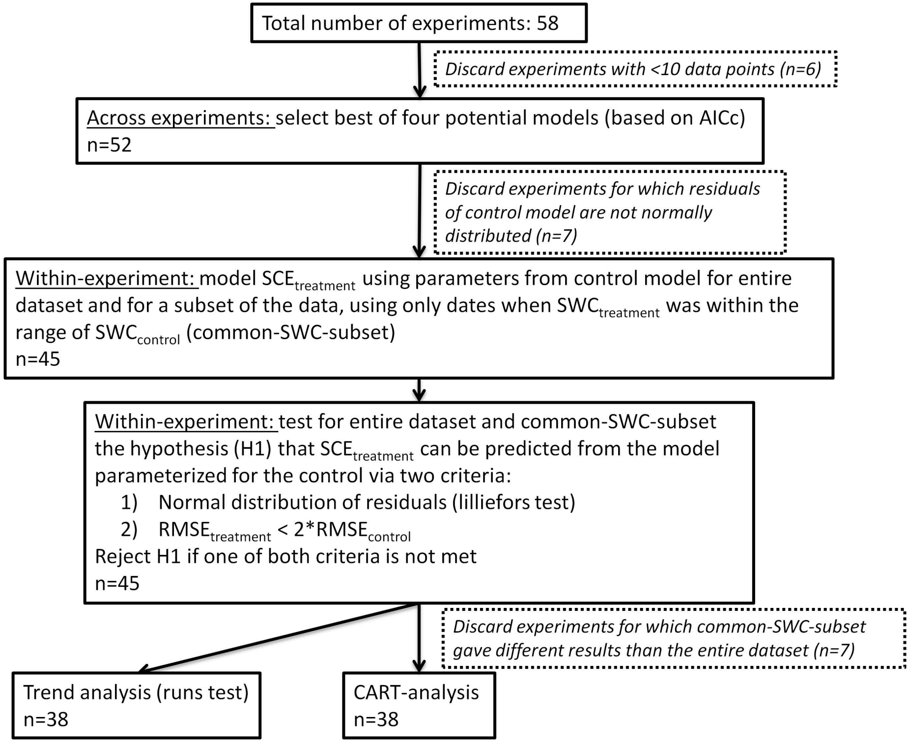

Fig. 2. Protocol of the analyses performed to test the hypothesis (H1) whether the moisture response of soil CO_2 efflux as observed in the control plots ($SCE_{control}$) can be used to predict soil CO_2 efflux in the precipitation manipulation treatment ($SCE_{treatment}$). The number of sites for each step and the reasons for discarding experiments from further analyses are displayed.

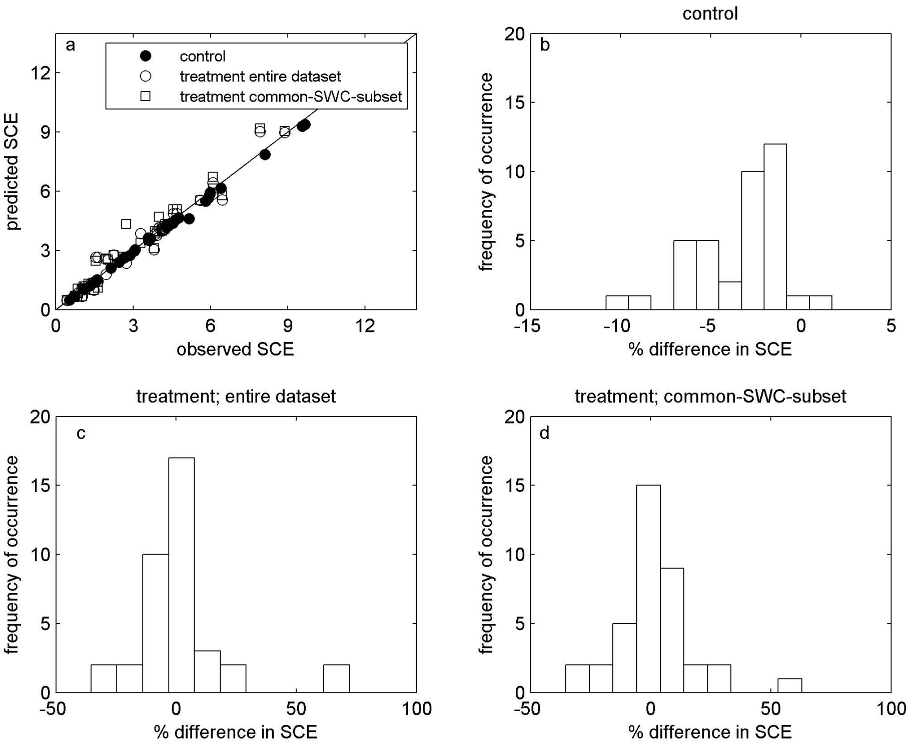

Fig. 3. **(a)** Predicted soil CO_2 efflux (SCE; µmol $CO_2\,m^{-2}\,s^{-1}$) vs. observed SCE for control, for the treatment when using the entire dataset, and for the treatment when using the common-SWC-subset. Predictions of treatment SCE were based on the model parameterized for the control. **(b–d)** histograms showing the frequency of occurrence for the % difference between observed and predicted for control, for the treatment when using the entire dataset and for the treatment when using the common-SWC-subset. The % difference was calculated as 100 · (average predicted – average observed)/average observed. For details, see Table C1.

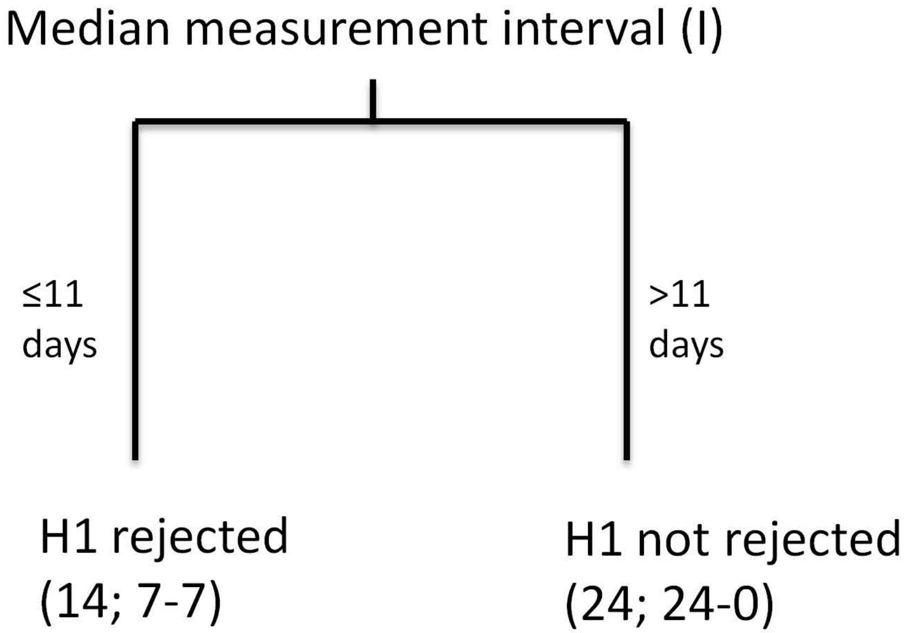

Fig. 4. Classification and regression tree (CART) showing for which groups of experiments our hypothesis (H1: the relationship of soil CO_2 efflux (SCE) to fluctuations in soil temperature and soil water content observed in the controls can be used to predict SCE in the treatment) could and could not be rejected. The key predictor variable (the median measurement interval) is depicted at the top, and predictor variable thresholds are at the side of each branch. Below the terminal nodes, the values between brackets display *total number of experiments; number of experiments for which H1 was not rejected – number of experiments for which H1 was rejected*. A list of all predictor variables included in the CART-analysis is given in the Methods section.

cc BY

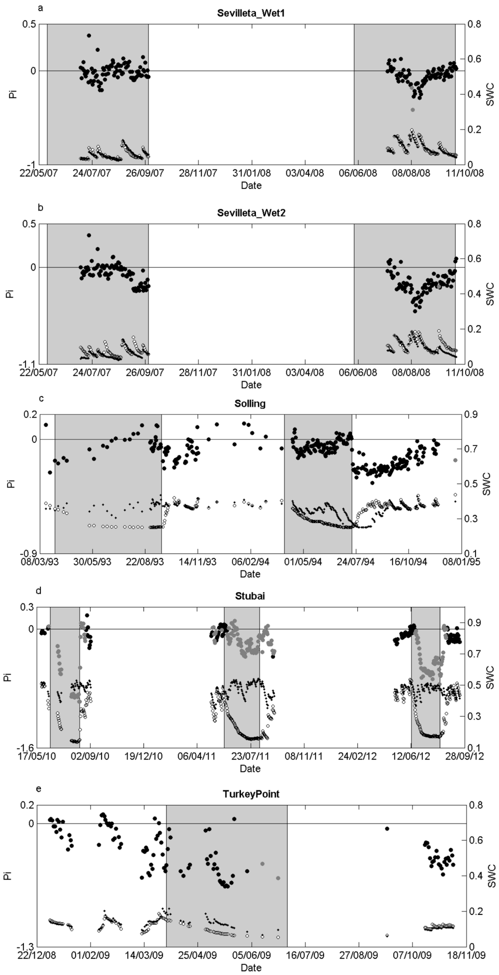

Fig. 5. Caption on next page.

Title Page
Abstract
Introduction
Conclusions
References
Tables
Figures
◀|
|▶
◀
▶
Back
Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

Fig. 5. Time course of Pi (predictability index; large black and gray circles) for the six experiments for which our hypothesis was rejected and for which a significant trend was detected: **(a)** Sevilleta_Wet1, **(b)** Sevilleta_Wet2, **(c)** Solling, **(d)** Stubai, **(e)** TurkeyPoint. Pi values close to zero indicate that $SCE_{treatment}$ was predicted similarly well as $SCE_{control}$, whereas values substantially below or above zero indicate the difference in predictability of $SCE_{treatment}$ relative to $SCE_{control}$. Negative values indicate that the prediction of $SCE_{treatment}$ was less good than that of $SCE_{control}$, and vice versa for positive values. Large gray circles indicate when $SWC_{treatment}$ was outside the range of $SWC_{control}$. Small black and white circles represent the soil water content (SWC), for control and treatment plots, respectively. Gray areas indicate the time that water inputs were manipulated.