Soil respiration—the flow of biologically-generated CO₂ from the soil surface to the atmosphere—is a major component of global carbon cycling, but the long-term response of this flux to altered precipitation regimes remains uncertain, due to different responses of soil respiration in distinct ecosystems with varying degrees of water limitation. We conducted a meta-analysis to determine the role of soil characteristics (organic carbon stock and clay content), study duration, and ecosystem type (e.g., forest, grassland, etc) in modifying the response of soil respiration to precipitation change. In general, decreased precipitation (N = 128 effect size pairs) decreased soil respiration rates. In contrast, increased precipitation (N = 141) had a more variable and on-average weak positive effect on this flux; significantly increasing soil respiration only in desert ecosystems. The long-term response of ecosystems varied, with those that are less constrained by water-availability (e.g., forests) showing acclimation over time to altered precipitation. Soil organic carbon stock strongly modified the response of soil respiration to decreased precipitation (p < 0.0001), but only weakly modified the response to increased precipitation (p < 0.01). Our results suggest that ecosystems with limited soil water-holding capacity and strong inherent water-limitation will show long-term dynamic change in soil respiration regardless of the direction of precipitation change.

Abstract

Climate change is altering global rainfall patterns, which can affect the global carbon cycle via changes in carbon dioxide release from soil (i.e., soil respiration). It is important to understand how carbon cycling in different ecosystems will respond to increased or decreased precipitation to account for soil feedbacks into atmospheric carbon dioxide concentrations. We combined the results of 80 separate studies to determine the effect of altered rainfall on soil respiration. In addition, we looked at how long the changes lasted, and how different soil properties and the intensity of precipitation changes affected the study results. We found that more precipitation resulted in greater amounts of carbon dioxide leaving the soil, and less precipitation resulted in less. However, the changes weakened over time in ecosystems that typically receive plenty of rainfall (e.g., forests), in contrast to ecosystems that typically receive little rainfall (e.g., deserts) where changes strengthened over time. Changes in the amount of carbon dioxide that left the soil were also affected by the amount of organic carbon in the soil, which impacts how much water soil can hold. Our results suggest that typically dry ecosystems will experience long-term changes in their carbon cycling whether precipitation increases or decreases.

1. Introduction

Climate change is modifying the global carbon (C) cycle across multiple fronts, with implications for the role of natural systems in mitigating or exacerbating global warming. A major component of climate change that affects the C cycle is altered precipitation patterns (Trugman et al., 2018). In terrestrial ecosystems, changes in precipitation influence plant C uptake and mortality, soil microbial activity (Schlesinger & Andrews, 2000; Sippel et al., 2018; Trugman et al., 2018), and wildfire occurrence and intensity (Harrison et al., 2021). Increased precipitation has the potential to increase plant productivity, resulting in increased atmospheric C uptake, while reduced precipitation diminishes this potential (Konings et al., 2021). In both instances, microbial responses to both soil moisture changes and plant responses themselves can mitigate or exacerbate the ecosystem-scale effects of changed precipitation.
Soil respiration, the soil-to-atmosphere flux of carbon dioxide (CO₂) generated by plant roots and soil biota, is a critical flux in the global C cycle (Schlesinger & Andrews, 2000) and sensitive to changes in soil moisture (Kim et al., 2012; L. Liu et al., 2016; Ni et al., 2019; Wu et al., 2011). Because soil respiration represents the paired drivers of plant and microbial fluxes, uncertainties about its response to climate change, and specifically changes in soil moisture, limits our ability to model future atmospheric CO₂ concentrations (Hursh et al., 2017; Jia et al., 2021; Z. Liu et al., 2018) and, more generally, the global climate and C cycle. Precipitation is a major source of this uncertainty due to its high spatial and temporal variability; projected changes range from increasing dryness, even drought, in some regions of the world to strongly increasing rainfall in others (Konopala et al., 2020; Trenberth, 2011). Predicting the response of soil respiration to this range of effects within diverse ecosystems represents a major challenge.

The relationship between altered precipitation and soil respiration rates has been studied previously (L. Liu et al., 2016; Ni et al., 2019; Vicca et al., 2014; Wu et al., 2011). For example, Ni et al. (2019) contrasted short-term effects in a field experiment with long-term effects from previous studies on soil respiration responses to increased precipitation, and found that increased precipitation led to increased soil respiration in both cases. Liu et al. (2016) approached this topic by standardizing the effect of precipitation change at 28% above or below ambient (i.e., 28% above or below the mean annual precipitation at a site); their meta-analysis found that soil respiration increased by 16% when precipitation increased and decreased by 17% when precipitation decreased. Liu et al. (2016) also found that increased aridity of biomes was positively correlated with stronger responses to manipulation of precipitation. However, they found few studies that assess longer term trends, consistent with a more general lack of long-term studies addressing the impact of ongoing climate change (Parts et al., 2019; Sánchez-Pinillos et al., 2022; Walker et al., 2020).

Such long-term studies are important, because terrestrial ecosystems are known to acclimate to certain global change forcings, such as increased nitrogen (N) deposition (Lu et al., 2018) and elevated CO₂ (Ainsworth & Long, 2005). Soil respiration itself has been shown to acclimate to experimental warming (Romero-Olivares et al., 2017). In addition to duration of manipulation, antecedent conditions alter the response of soil respiration to changes in precipitation (Broderick et al., 2022), but such legacy effects still represent a major gap in the literature, as well as a statistical and measurement challenge (Ogle et al., 2015, 2021). Intuitively, in arid and semi-arid ecosystems increased precipitation will directly increase both plant growth and C uptake, as well as microbial activity, while decreased precipitation will have the opposite effect. In less water-limited ecosystems, any soil respiration responses to precipitation changes are more likely to be short term. This is because other resources (e.g., C, space, or N) rapidly become limiting (Craine et al., 2012), or acclimation occurs via physiological and/or species-composition shifts (Parts et al., 2019). Such mesic ecosystems are also more likely to have higher soil organic matter content and thus better water holding capacity, which might further buffer against precipitation-driven changes in soil respiration. For these reasons, ecosystems are a logical unit of replication for assessing long-term responses of the earth system to climate change because they include all levels of biological organization and their abiotic context.

Our goal in this study is to conduct a novel meta-analysis to synthesize the effects of precipitation change on soil respiration and the potential of ecosystems to acclimate. By leveraging the unprecedented volume of soil respiration data published over the past decade on this topic (Jian et al., 2021), including an increasing number of long-term studies, we are able to focus in particular on the role of study duration in different ecosystem types. First, we hypothesize that the overall effect of increased precipitation will be an increased soil respiration rate, and that the inverse will also be true. This should occur in the majority of cases because increased soil moisture will increase soil microbes’ access to soil C substrates (Carbone et al., 2011). Second, because the underlying mechanism is increased pore connectivity, we hypothesize that the absolute magnitude of the effect sizes observed in studies will depend on the magnitude (relative to mean annual precipitation, MAP) of precipitation change: stronger manipulations of precipitation will result in stronger changes in soil respiration, in both the positive and negative directions. Finally, we hypothesize that ecosystems that are less water-limited (e.g., forests) will acclimate to changes in precipitation over time: the absolute magnitude of soil respiration responses will approach zero over longer time periods. This should occur because these ecosystems occupy a climatic space where changes in precipitation should not result in substantial shifts in plant community composition or absolute productivity due to light or nutrient limitation being the primary controlling factor. Conversely, water-limited
ecosystems will show persistent responses of soil respiration to precipitation change, with no evidence of acclimation, due to direct relief or exacerbation of their primary limitation.

2. Materials and Methods

2.1. Building the Data Set

We leveraged a pre-existing soil respiration database (SRDB version 5, Jian et al., 2021) and filtered for studies that manipulated precipitation (increase, decrease, or both) and reported at least one of the following for both treatment and control field plots: (a) annual soil respiration, (b) mean growing season soil respiration, or (c) annual soil heterotrophic flux. Although the proportion of annual respiration that growing season respiration comprises varies by ecosystem (Brooks et al., 2005; Hu et al., 2016), the mechanisms underlying responses to precipitation change are the same. Additionally, despite heterotrophic measurements lacking plant root respiration, this flux often represents more than 50% of soil respiration (Jian et al., 2022). In order to directly compare and easily interpret our calculated effect sizes, all fluxes were converted into μmol C m$^{-2}$ s$^{-1}$. We excluded studies that manipulated the timing of precipitation inputs if the total amount of precipitation was not also manipulated, resulting in 80 studies in all being included with 141 paired (manipulation vs. control) datapoints representing increased precipitation and 128 pairs for decreased manipulation (see Tables 1 and 2 for more details).

Following Liu et al. (2016), we calculated the percentage of mean annual precipitation (MAP) that manipulated treatment plots received, using values reported either in SRDB or in the original papers. The studies in our data set were from six distinct ecosystem types (Figure S1 in Supporting Information S1, map produced using the ggmap package version 3.0.0 of Kahle and Wickham (2013)) which together represent 69% of non-urban terrestrial land covers based on the Advanced Very High Resolution Radiometer land cover classification system (Hansen et al., 2000). We collapsed ecosystem types reported in SRDB as pasture or steppe to grassland and combined savannahs with savannas. We used the SoilGrids database (Hengl et al., 2017) for soil clay and organic carbon stock, and extracted values from this database based on study site coordinates. Because of varying levels of coordinate precision, we used a radius of 1000 m to calculate average values for organic carbon stocks (0–30 cm, hereafter OCS) and clay content (15–30 cm). Use of SoilGrids data allowed us to include these soil parameters for all studies in our data set, as only 19 studies included information on soil clay content, and only 16 included sufficient information to calculate OCS. Values from SoilGrids tended to over-estimate the reported values (Figure S2 in Supporting Information S1), but we concluded that the benefit of including these data to capture trends in soil parameters across our data set outweighed a minor loss in accuracy. We focused on soil clay content and OCS as two dominant variables directly influencing soil respiration rates and the response of respiration to changes in precipitation, rather than other soil variables such as pH or inorganic nutrients that would have indirect effects.

2.2. Calculating Effect Sizes

Because the physical processes underlying soil wetting and drying differ fundamentally (Patel et al., 2021), we split the data set into these two categories for analysis. These two datasets are referred to as +P for increased precipitation effect size pairs (i.e., measurement from control plot and measurement from plot with increased precipitation), and −P for decreased precipitation effect size pairs. Regardless of the direction of precipitation change, we used the natural log of the response ratio to calculate the average effect size of treatments on soil respiration (Gurevitch et al., 2001):

$$\ln(RR) = \ln\left(\frac{\bar{X}_T}{\bar{X}_C}\right)$$

and variance as:

$$\text{var}(RR) = \frac{SD_T^2}{N_T X_T^2} + \frac{SD_C^2}{N_C X_C^2}$$

where $\bar{X}_T$, $SD_T$, and $N_T$ are the mean, standard deviation, and sample size of the soil respiration data for the treatment group (i.e., in which precipitation inputs were manipulated), and $\bar{X}_C$, $SD_C$, and $N_C$ are the mean, standard
| Study                        | Doi                                      | Ecosystem(s) | Drought | Irrigation |
|-----------------------------|------------------------------------------|--------------|---------|------------|
| Aronson et al. (2019)       | https://doi.org/10.1016/j.soilbio.2018.12.010 | Grassland    | 1       | 1          |
| Asensio et al. (2007)       | https://doi.org/10.1016/j.atmosenv.2006.05.008 | Forest       | 1       | 0          |
| Bao et al. (2019)           | https://doi.org/10.3390/su11092597        | Grassland    | 1       | 1          |
| Billings et al. (1998)      | https://doi.org/10.1139/x98-145            | Forest       | 4       | 0          |
| Borken et al. (1999)        | https://doi.org/10.2136/sssaj1999.6361848x | Forest       | 1       | 1          |
| Borken et al. (2006)        | https://doi.org/10.1111/j.1365-2486.2005.001058.x | Forest       | 1       | 0          |
| Carter et al. (2012)        | https://doi.org/10.5194/bg-9-3739-2012    | Shrubland    | 4       | 0          |
| Chang et al. (2016)         | https://doi.org/10.3390/f7110263           | Forest       | 2       | 0          |
| Chao et al. (2018)          | https://doi.org/10.1071/RJ16080            | Grassland    | 0       | 1          |
| Chen et al. (2019)          | https://doi.org/10.1016/j.agrformet.2019.03.021 | Forest       | 2       | 0          |
| Chou et al. (2008)          | https://doi.org/10.1111/j.1365-2486.2008.01572.x | Grassland    | 0       | 4          |
| Cotrufo et al. (2011)       | https://doi.org/10.5194/bg-8-2729-2011    | Forest       | 1       | 1          |
| da Costa et al. (2014)      | https://doi.org/10.1080/17550874.2013.798366 | Forest       | 2       | 0          |
| Davidson et al. (2008)      | https://doi.org/10.1111/j.1365-2486.2008.01694.x | Forest       | 1       | 0          |
| de Dato et al. (2010)       | https://doi.org/10.1007/s11104-009-0041-y  | Shrubland    | 3       | 0          |
| Deng et al. (2012)          | https://doi.org/10.1371/journal.pone.0041493 | Forest       | 0       | 3          |
| Deng et al. (2018)          | https://doi.org/10.1016/j.soilbio.2018.02.023 | Shrubland    | 2       | 2          |
| Díaz-Guerra et al. (2018)   | https://doi.org/10.1007/s11104-017-3485-5  | Shrubland    | 1       | 0          |
| Domínguez et al. (2015)     | https://doi.org/10.1007/s10533-014-0059-y  | Shrubland    | 13      | 0          |
| Escolar et al. (2015)       | https://doi.org/10.1016/j.soilbio.2014.09.019 | Grassland    | 2       | 0          |
| Fay et al. (2011)           | https://doi.org/10.5194/bg-8-3053-2011    | Grassland    | 13      | 0          |
| Ford et al. (2012)          | https://doi.org/10.1016/j.agrformet.2011.12.008 | Savanna      | 0       | 2          |
| Garten et al. (2009)        | https://doi.org/10.1007/s11104-008-9851-6  | Grassland    | 2       | 0          |
| Ge et al. (2018)            | https://doi.org/10.1007/s11284-017-1529-1  | Forest       | 1       | 0          |
| Hagedorn and Joos (2014)    | https://doi.org/10.1007/s10533-013-9881-x  | Grassland    | 3       | 0          |
| Han et al. (2017)           | https://doi.org/10.1002/eee3.3536         | Grassland    | 0       | 9          |
| Harper et al. (2005)        | https://doi.org/10.1111/j.1365-2486.2005.00899.x | Grassland    | 1       | 0          |
| Hinko-Najera et al. (2015)  | https://doi.org/10.1016/j.agrformet.2014.09.013 | Forest       | 2       | 0          |
| Hoover et al. (2016)        | https://doi.org/10.1002/2015JG003256       | Grassland    | 3       | 0          |
| Inglima et al. (2009)       | https://doi.org/10.1111/j.1365-2486.2008.01793.x | Forest, Shrubland, Grassland | 0       | 3          |
| Jia et al. (2013)           | https://doi.org/10.1007/s11104-013-1771-4  | Grassland    | 0       | 2          |
| Jia et al. (2013)           | https://doi.org/10.1007/s00374-014-0901-3  | Grassland    | 0       | 4          |
| Jiang et al. (2013)         | https://doi.org/10.5194/bg-10-3963-2013    | Forest       | 3       | 3          |
| Lai et al. (2013)           | https://doi.org/10.1371/journal.pone.0077659 | Shrubland    | 0       | 2          |
| Lellei-Kovács et al. (2008) | https://doi.org/10.1556/comec.9.2008.1.4  | Grassland    | 4       | 0          |
| J. Li et al. (2018)         | https://doi.org/10.1111/1365-2435.13118    | Grassland    | 0       | 1          |
| Y. Li et al. (2020)         | https://doi.org/10.1016/j.agrformet.2020.108126 | Grassland, Desert | 15      | 15         |
| Lu et al. (2017)            | https://doi.org/10.1038/s41598-017-15157-3  | Forest       | 4       | 0          |
| Maier and Kress (2000)      | https://doi.org/10.1139/x99-218             | Forest       | 0       | 2          |
| Maier et al. (2004)         | https://doi.org/10.1111/j.1529-8817.2003.00809.x | Forest       | 0       | 1          |
| Martins et al. (2015)       | https://doi.org/10.1016/j.soilbio.2015.03.012 | Forest       | 0       | 1          |
| McCulley et al. (2007)      | https://doi.org/10.2136/sssaj2006.0303     | Savanna      | 0       | 4          |
| McDaniell et al. (2014)     | https://doi.org/10.1007/s00442-013-2845-y   | Grassland    | 0       | 1          |
deviation, and sample size of the unmanipulated (control) soil respiration values. Using this method, a positive effect size ($\ln[RR]$) indicates that the soil respiration flux increased in the manipulated soil, and a negative effect size means the flux decreased relative to the control.

After visual assessment and direct testing both indicated that the three different dependent variables (annual soil respiration, growing season soil respiration, and annual soil heterotrophic flux) responded similarly to

| Study                        | Doi                                      | Ecosystems | Drought | Irrigation |
|------------------------------|------------------------------------------|------------|---------|------------|
| Metcalfe et al. (2007)       | https://doi.org/10.1029/2007JG000443     | Forest     | 2       | 0          |
| Misson et al. (2009)         | https://doi.org/10.1111/j.1365-2486.2009.02121.x | Forest     | 2       | 0          |
| Moinet et al. (2017)         | https://doi.org/10.1016/j.scitotenv.2016.11.199 | Grassland  | 0       | 1          |
| Munir et al. (2017)          | https://doi.org/10.3390/8030075           | Wetland    | 2       | 0          |
| Ni et al. (2019)             | https://doi.org/10.1016/j.soilbio.2018.11.021 | Forest     | 0       | 3          |
| Ondier et al. (2020)         | https://doi.org/10.1111/aje.12670         | Savanna    | 1       | 1          |
| Reynolds et al. (2015)       | https://doi.org/10.1111/gcb.12732         | Grassland  | 0       | 3          |
| Risch and Frank (2007)       | https://doi.org/10.1007/s10533-007-9148-5 | Grassland  | 0       | 5          |
| Ruehr et al. (2012)          | https://doi.org/10.1016/j.agrformet.2012.05.015 | Forest     | 0       | 1          |
| Schindlbacher et al. (2012)  | https://doi.org/10.1111/j.1365-2486.2012.02696.x | Forest     | 3       | 0          |
| Selmants et al. (2008)       | https://doi.org/10.1111/j.1365-2664.2008.01460.x | Forest     | 0       | 2          |
| Selsted et al. (2012)        | https://doi.org/10.1111/j.1365-2486.2011.02634.x | Shrubland  | 2       | 0          |
| Shen et al. (2015)           | https://doi.org/10.1016/j.apsoil.2015.01.015 | Grassland  | 0       | 2          |
| Silva Júnior et al. (2013)   | https://doi.org/10.1590/S0102-77862013000100009 | Forest     | 1       | 0          |
| Sotta et al. (2007)          | https://doi.org/10.10111/j.1365-2486.2007.01416.x | Forest     | 1       | 0          |
| Sowerby et al. (2008)        | https://doi.org/10.1111/j.1365-2486.2008.01643.x | Shrubland  | 2       | 0          |
| Suseela et al. (2012)        | https://doi.org/10.1111/j.1365-2486.2011.02516.x | Grassland  | 1       | 1          |
| Talmon et al. (2011)         | https://doi.org/10.1111/j.1365-2486.2010.02285.x | Shrubland  | 2       | 2          |
| van Straaten et al., 2010    | https://doi.org/10.5194/bg-7-1223-2010    | Forest     | 1       | 0          |
| Vasconcelos et al. (2004)    | https://doi.org/10.1029/2003GB002210       | Forest     | 0       | 2          |
| Wang et al. (2013)           | NA                                       | Grassland  | 0       | 4          |
| Waring and Powers (2016)     | https://doi.org/10.1088/1748-9326/11/10/105005 | Forest     | 0       | 2          |
| Wu and Lee (2011)            | https://doi.org/10.1007/s11104-010-0548-2 | Forest     | 0       | 2          |
| Xu et al. (2016)             | https://doi.org/10.1038/srep34801          | Grassland  | 0       | 8          |
| L. Yan et al. (2009)         | https://doi.org/10.1111/j.1365-2486.2009.02091.x | Grassland  | 0       | 2          |
| L. Yan et al. (2011)         | https://doi.org/10.1111/j.1365-2486.2010.02365.x | Grassland  | 0       | 2          |
| M. Yan et al. (2014)         | https://doi.org/10.1007/s11104-013-1944-1  | Forest     | 0       | 6          |
| Yang et al. (2020)           | https://doi.org/10.1016/j.agrformet.2020.108039 | Grassland  | 4       | 4          |
| Yu et al. (2019)             | https://doi.org/10.1016/j.scitotenv.2018.08.111 | Grassland  | 0       | 8          |
| Yue et al. (2019)            | https://doi.org/10.5194/bg-15-2007-2018   | Desert     | 0       | 4          |
| Yue et al. (2019)            | https://doi.org/10.5194/bg-15-2007-2018   | Desert     | 0       | 2          |
| X. Zhang et al. (2015)       | https://doi.org/10.1007/s11104-015-2523-4  | Forest     | 1       | 0          |
| L. Zhang et al. (2018)       | https://doi.org/10.1016/j.apsoil.2018.02.005 | Desert     | 2       | 2          |
| B. Zhang et al. (2019)       | https://doi.org/10.1016/j.agrformet.2019.03.019 | Grassland  | 4       | 4          |
| X. Zhou et al. (2006)        | https://doi.org/10.1029/2005GB002526       | Grassland  | 0       | 1          |
| C. Zhou et al. (2019)        | https://doi.org/10.1007/s11104-019-04025-w | Grassland  | 4       | 0          |
| Zou et al. (2018)            | https://doi.org/10.1016/j.agrformet.2018.06.020 | Forest     | 0       | 3          |

Note. Full citation information in Supporting Information S1.
precipitation changes, we combined all three into one data set (Figures S3 and S4 in Supporting Information S1). While growing season and annual fluxes represent two proportions of the same whole, annual heterotrophic fluxes might be anticipated to behave differently. However, there was no evidence for this, and these data represent the minority of our dataset (4% for +P and 9% for −P), making them unsuitable for independent meta-analysis.

2.3. Model Selection and Execution

Potential modifiers—covariates affecting the magnitude and slope of the response of soil respiration to manipulation, *sensu* Viechtbauer 2010—were limited to percent MAP, ecosystem type, soil clay and OCS, and study duration. First, the continuous modifiers (i.e., all except for ecosystem type) were evaluated for collinearity using a correlation matrix via the chart.Correlation function from the PerformanceAnalytics R package version 2.0.4 (Peterson et al., 2014). Significant autocorrelation existed (Figure S5 in Supporting Information S1), and therefore multi-model inference was used to determine which combination of modifiers to include (Burnham & Anderson, 2002) via the multimodel.inference function from the MuMIn package version 1.43.15 (Barton, 2009) which works in conjunction with package dmetar version 0.900 (Harrer et al., 2019). In multi-model inference all possible modifier combinations are modeled—several different meta-regressions are created, and subsequently evaluated. This enables a full examination of all possible modifier combinations and their interactions. A common finding is that there are many different specifications which lead to a good model fit, and the estimated coefficients of modifiers can then be pooled across all fitted models to infer how important certain modifiers are overall. We chose the top four modifiers from this step to go in our final meta-analytical models (Figure 1).

It has been shown that measurement intervals can affect the statistical outcome of manipulative experiments at the ecosystem scale (Vicca et al., 2014). In order to determine the role of measurement timing in our studies we included measurement interval as an additional modifier, first as a continuous variable, and then as a three-leveled factor (frequent (daily to subdaily), intermediate (subweekly to biweekly), and infrequent (monthly plus)), after the initial top four modifiers were identified. Measurement interval was confounded with study duration and ecosystem type in +P studies (Figure S6a in Supporting Information S1), but no direct effect (i.e., with measurement interval as a singular modifier, Figure S6b in Supporting Information S1) was found for either data set. We thus decided to omit measurement interval from our meta-analytical model due the limitations of our data set (for +P) and the lack of evidence of a direct effect (for −P and +P). Code for comparing different meta-regressions using our complete data set are available in the GitHub repository listed below. For both datasets we conducted

| Ecosystem | Sample size | Number of studies |
|-----------|-------------|-------------------|
| Wetland   | 2           | 1                 |
| Forest    | 38          | 36                |
| Shrubland | 27          | 5                 |
| Savanna   | 1           | 7                 |
| Grassland | 53          | 80                |
| Desert    | 7           | 13                |

Note. Sample size is the number of unique effect size pairs and number of studies the number of published articles from which the sample size counts were drawn.

Table 2: Study Number and Sample Sizes by Ecosystem and Manipulation Type, −P Indicates Decreased Precipitation and +P Indicates Increased Precipitation Manipulations

![Figure 1](https://example.com/figure1.png)

**Figure 1.** Flow diagram showing steps taken to determine most important modifiers of the effect of precipitation change on soil respiration for increased and decreased precipitation studies extracted from SRDB v5.
a multivariate mixed effects meta-analytical model using the \texttt{rma.mv} function from the \textit{Metafor} package version 3.0-2 (Viechtbauer, 2010), using the restricted maximum likelihood method to reduce the risk of underestimating variance given multiple modifiers and uneven distribution of effect sizes across modifiers. For both models, study number was treated as a random effect, in order to control for pseudoreplication when we extracted multiple pairs of effect sizes from the same publication (Viechtbauer, 2010), while all other modifiers were treated as fixed effects. Cook's distance was used to check for highly influential data points (Cook, 1977). When such data were found, values were confirmed between SRDB and the original literature (all were correctly entered) and the study design confirmed as meeting our primary criteria. In one instance, this resulted in a study being removed from our data set due to precipitation treatments being a manipulation of precipitation timing, rather than absolute magnitude. For the $-P$ data set, there is a long-term grassland and desert study that was highly influential (Li et al., 2020), but there was no scientific reason to remove it from the data set.

All analyses were conducted in the R statistical computing language version 4.1.1 (R Core Team, 2021). All code and data needed to reproduce the results here are available at https://github.com/COMPASS-DOE/rs-synthesis and permanently archived at https://doi.org/10.5281/zenodo.7054524.

### 3. Results

#### 3.1. Data Overview

Within SRDB there were 80 studies that matched our inclusion criteria (Table 1, see Supporting Information S1 for full citations). These included six distinct ecosystem types: wetland, forest, shrubland, savanna, grassland, and desert. Forest and grassland ecosystems, by far the most common ecosystem types in the data set, were represented by 34 and 32 studies respectively. Nine studies contributed data on shrublands, four on deserts, three on savannas, and one on a wetland. Many studies contained both increased and decreased precipitation manipulations, and the number of studies and effect sizes per ecosystem and manipulation type are summarized in Table 2.

Study sites were distributed across the terrestrial biosphere, but coverage was better in the global north (Figure S1 in Supporting Information S1). Distribution of effect sizes in both models indicated little influence of publication bias (Figure S7 in Supporting Information S1). The majority of studies lasted only one year (53 of 80) and only 16% (13 of 80) were longer than two years (Figure S8 in Supporting Information S1). Manipulation intensity (how much a study increased or decreased precipitation relative to MAP, with 100% meaning the unmanipulated control value) was not evenly distributed among ecosystems (Figure 2), and ranged from 0% to 391% of MAP, with a mean of 145% for $+P$, and 57% for $-P$.

#### 3.2. Model Results

For $+P$ studies, the four highest ranked modifiers were OCS, ecosystem type, study duration, and the interaction between ecosystem type and duration. In contrast, the $-P$ model ranked ecosystem type, OCS, clay, and duration as the top four modifiers (Figure 1). It is worth noting that when the effect of precipitation change is tested without modifiers there is robust evidence of both ($+P$ and $-P$) influencing soil respiration in the expected directions ($+P$, $p < 0.0001$, $-P$, $p < 0.01$). Also, the effect of ecosystem type differs substantially when included as the singular modifier explaining variation in the precipitation change effect (Figures S9a and S9b in Supporting Information S1, see also code in GitHub repo).

While in general soil respiration rates were numerically greater in $+P$ treatments, relative to unmanipulated controls, only desert ecosystems showed a statistically significant increase in soil respiration as a primary effect ($p = 0.017$, Figure 3a). There was a significant interaction (effect size estimate of $-0.18$ for forests, $-0.07$ for grasslands, 0.11 for deserts $p < 0.001$ for all) between the duration of studies and the strength and direction of the respiration response in forest, grassland, and desert ecosystems (Figure 4). The initial increase in soil respiration...
changed over time: decreasing strongly in forests, while increasing slightly in grasslands and strongly in deserts. In contrast, −P treatment plots exhibited lower soil respiration rates relative to control rates (Figure 3b), and nearly all ecosystems were similarly affected by decreased precipitation. Wetlands were an exception, with no significant primary effect for this ecosystem type, but as noted above this was based on a single study.

The duration of manipulation strongly affected the direction and magnitude of response of soil respiration to precipitation change. When the interaction of ecosystem type and duration was included in the meta-analytical model for −P, it was significant for all ecosystems with more than 2 years of data (Figure 4). Its effect diverged depending on the relative water-limitation of the ecosystem: forests, grasslands, and shrublands showed weakening of the manipulation effect over time, leading to reversals of the initial effect (i.e., an initial decrease in soil respiration became an increase over time). In contrast, desert ecosystems had increasingly strong responses to manipulations, whether the change was an increase or decrease in precipitation (Figure 4).

The intensity of the manipulation was more important for −P studies than +P (Figure 5). The relationship is intuitive: the stronger the decrease in precipitation, the stronger the decrease in soil respiration (Figure 5). Manipulation intensity was not included in the primary model for +P (due to being below the top 4 ranking threshold, see Figure 1), if the effect of intensity was included in the +P model, a weak positive relationship exists. This is driven by one very high treatment in a savanna, which we opted to exclude (Figure 5).

3.3. Soil Characteristics

Soil OCS was a highly significant modifier of the soil respiration response for both manipulation types \( (p < 0.001 \text{ for } −P, p = 0.005 \text{ for } +P) \). The overall effect of OCS was positive, meaning that soils with more C had higher respiration rates in response to treatments, regardless of manipulation intensity or ecosystem type. However, when model-predicted effect sizes were plotted against OCS (Figure 6), we found high OCS was associated with a reversal in soil respiration responses to −P treatments, with the predicted effect sizes showing increased rather than decreased respiration rates at highest OCS.

Clay had low modifier importance for +P and was not included in the primary +P model, but was included as a top four modifier in the −P model. The linear regression between effect sizes and clay content supported this divergence (Figure 7), with a positive effect of clay content on effect size, resulting in a similar reversal of treatment effect as seen in the OCS result. Despite this, the primary effect of clay was not significant in the −P model and we observed no significant trend between these variables for +P (Figure 7).

4. Discussion

Using the largest data set ever assembled for this type of analysis, we found that drought and increased precipitation had strongly divergent effects with different primary explanatory variables. Our first hypothesis was thus supported, as we found increased soil respiration rates in +P and decreased rates in −P. However, when accounting for variation amongst ecosystems, only desert ecosystems had significantly increased soil respiration in +P as well as significantly decreased soil respiration in −P. Soil clay content and manipulation intensity were more important for explaining variation in soil respiration responses to drought (see Figures 5 and 7). Conversely, study

Figure 3. Forest plots of mixed-effect meta-regression results for increased precipitation (a) and decreased precipitation (b) manipulations on soil respiration, showing the primary effect of ecosystem type. Values are ln(RR) back-transformed to percent change.

Figure 4. Model-predicted change in effect size (ln(RR)) for different ecosystem types over study duration for decreased precipitation manipulations (−P, left panel), and increased precipitation manipulations (+P, right panel). −P predictions were generated using the +P model (see Figure 1). Linear regression lines show trend in residuals by ecosystem type.
duration and ecosystem type were more important to increased precipitation studies (see Figures 3 and 4). Furthermore, while ecosystem type was statistically significant for both models, there was little variation in the response of soil respiration to precipitation changes among ecosystems (Figure 3), unless study duration was also considered (Figure 4). Interestingly, the exceptions to this occurred in ecosystems at the two extremes of water-availability, deserts and wetlands.

This evidence indicates that the primary factor controlling soil respiration response to precipitation change is the water-limitation status of the ecosystem under consideration. This agrees with the Liu et al. (2016) finding that increased precipitation treatments had the strongest effect on soil respiration in the highest aridity biomes. However, the aridity index used in the Liu et al. (2016) finding suggested that soil respiration in less arid systems was more sensitive to decreases in precipitation (although this effect was not statistically significant). In contrast, we found that reductions in soil respiration were similar regardless of ecosystem (excluding wetlands) type in −P studies (Figure 3b).

Manipulation intensity was significant in −P studies—functioning as drought severity does—but this was not true for +P studies (Figure 5). Therefore, our second hypothesis (that manipulation intensity would be an important modifier for both +P and −P) was only partially supported. This may be due to water-holding limitations of soil: water can run off of saturated soil or pass through soil into groundwater, but there is a lower bound for biologically available water that cannot be circumvented (Liang et al., 2022). Intuitively, we would expect that water-limited ecosystems such as deserts and shrublands would have C cycling responses proportional to increased precipitation intensity, and this is supported by research (Ahlström et al., 2015; Parton et al., 2012). However, extreme precipitation manipulations that might have driven manipulation intensity to greater importance as a modifier of +P soil respiration responses, likely do not reflect the expected trend in precipitation change for these ecosystems (Trenberth, 2011). Additionally, it is also worth noting that our analysis did not include studies that manipulated the timing of precipitation, but not the absolute amount. This type of precipitation change is a different form of disturbance to ecosystem function, and an area of active research (Felton et al., 2021; Griffin-Nolan et al., 2021) which will likely have different short and long-term consequences for soil respiration.

4.1. Soil Characteristics as Modifiers of Respiration Change

Soil organic carbon stock was an important modifier of soil respiration's response to precipitation change in both +P and −P studies. The effect for +P was a modest increase in effect size as OCS increased (Figure 6). In contrast, the effect for −P was dynamic, with low OCS soil showing the strongest decreases in respiration and soils with high OCS responding in the opposite way, with increased soil respiration rates in response to drought treatments. This highlights two key functions of organic matter in driving soil biological processes; the retention of water and a reservoir of nutrients, especially C. From a microbial perspective, C substrate availability determines growth and respiration rates (Soong et al., 2019), with more C leading to more respiration. From a plant perspective, soil organic matter helps hold water, maintaining turgor pressure between rainfall events (Libohova et al., 2018). Similar
sensitivity of modeled decompositions rates to OCS and initial soil moisture was found in a depth-explicit decomposition model (Pallandt et al., 2022). Our results indicate that −P soils with intermediate OCS are buffered against changes in precipitation, and thus had effect sizes near zero, in contrast to −P soils with the highest OCS, where high water-retention may facilitate stimulation of root-growth and associated microbial and autotrophic respiration (Maurel & Nacry, 2020). In the lowest OCS −P soils, both plants and microbes must reduce their respiration rates in response to lower water availability (Carbone et al., 2011) which is a direct consequence of the soil’s low water holding capacity. Desert ecosystems may be an exception to these trends however, with comparatively low soil respiration responses to drought for their OCS (relative to grasslands at similar organic matter contents), and comparatively strong soil respiration responses to increased precipitation for their OCS as well (Figure 6). This is likely due to adaptation of desert organisms to low water availability and a rapid capacity for response when water is available.

Clay content was only important for drought studies. While the effect of clay was positive, it was not statistically significant as a primary factor. Given soil scientists’ recent shifts away from clay as a modifier of soil organic matter distribution (Rasmussen et al., 2018), perhaps the role of water-holding capacity was sufficiently captured by including OCS in our model. A recent meta-analysis found that the SOM impact on soil water-holding capacity was weakest in high clay soils (Minasny & McBratney, 2018), and this likely contributed to the strong model-predicted influence of clay content, especially at the highest percentages, seen in our data set (Figure 7). Furthermore, soil clay content and OCS are strongly correlated in our data set, supporting the idea that clay was a weaker modifier because OCS was also included. Regardless, the stronger effect of OCS on −P and the greater importance of clay to −P both indicate that soil water-holding capacity plays a much stronger role in modifying soil respiration responses to drought than to increased precipitation.

While not all studies reported soil moisture content as part of their results, we were able to further test the idea that OCS and clay content capture the effect of soil moisture in modifying soil respiration responses by graphing these data for the 60% of effect sizes for which it was available. The difference between control and manipulated soil moisture shows no relationship to soil respiration response to precipitation change (Figure S10 in Supporting Information S1). However, percent of soil moisture in the manipulated treatment strongly positively modifies the −P effect and negatively modifies the +P effect (Figure 8), meaning that when manipulated soil had greater soil moisture the effect of precipitation change on soil respiration is smaller, across all ecosystems, study durations, and manipulation strengths.

4.2. Duration and the Potential for Acclimation

Study duration substantially changed the response of soil respiration to treatments and the direction of change was dependent on ecosystem type (Figure 4). Deserts were the most strongly affected, with both increases (+P) and decreases (−P) in soil respiration becoming greater over time. The least water-limited ecosystem type for which we have good long-term data were forests, which had the opposite response, with effect sizes approaching zero over time. Intermediate were grasslands, where soil respiration rates increased with duration regardless of manipulation type, meaning that in +P studies the effect got stronger over time, while in −P studies the effect reversed itself over time. These results confirm our third hypothesis, that the water-limitation status of ecosystems’ controls their ability to acclimate to precipitation change. Moreover, more water-limited ecosystems tend to have lower OCS, and therefore the limited buffering ability of these soils’ organic matter reinforces this pattern.

Intriguingly, there is evidence of this relationship between OCS and ecosystem acclimation: in a long-term grassland irrigation experiment, which was not included in our data set, the long-term increased precipitation treatment had the highest respiration rates (higher than short-term increased precipitation) and increased soil labile C content (Broderick et al., 2022). Additionally, in a dry Scots pine forest irrigated for 17 years, tree responses typically took 4 years to reach a peak value and then stabilized or decreased (Bose et al., 2022). These responses
included increased belowground C inputs. These trends have the potential to lead to higher OCS with time and demonstrate that our results agree with novel data not included in our meta-analysis.

Acclimation of terrestrial C cycle processes is known to affect outcomes of ecosystem C balance models (Lombardozzi et al., 2015; Wythers et al., 2005), and has been long-studied and debated in the soil C cycling literature (e.g., Kirschbaum, 2004). While studies of global change acclimation are limited, temperature acclimation has received the most attention. Ecosystem acclimation to temperature change involves modification of kinetic rates, enzyme structure, and water-use efficiency (Parts et al., 2019; Smith & Keenan, 2020), while acclimation to changes in water-availability are more location-dependent. Water addition can relieve pre-existing soil moisture limitation and push the system toward limitation of another resource (Maurel & Nacry, 2020; Parts et al., 2019). Conversely, exacerbated water-limitation compels organisms to respond by producing osmolytes (Schimel et al., 2007), or growing deeper roots (Fry et al., 2018). While the time-scale and processes of acclimation is poorly understood, our study highlights the need for more long-term studies that pair C cycle fluxes with underlying ecosystem mechanisms (i.e., nutrient-limitation or root growth) that drive the acclimation response.

Figure 8. Effect of study reported soil moisture content (as a percent) on the ln(RR) of soil respiration in decreased (−P, left panel) and increased (+P, right panel) precipitation studies. Soil moisture data were reported for variable depths for about 60% of effect size pairs, thus these data were not included in the primary analytical pipeline.
This is especially true for ecosystems that were not well represented in our data set (Table 2), such as deserts, savannas, shrublands, and wetlands.

4.3. Study Limitations

Meta-analyses by definition aggregate unrelated datasets in order to provide quantitative consensus on research questions. As such, this approach constitutes an important cornerstone of evidence synthesis research and can help summarize evidence as it accumulates in the published literature (Gurevitch et al., 2018). Nonetheless, like any other experimental approach, meta-analysis has limitations, and must be applied with caution (Whittaker, 2010). Most frequently, the biggest limiting factor to meta-analysis is availability of research data (Culina et al., 2018). When data are not archived in a long-term repository, they become increasingly difficult to locate and reuse with each passing year (Vines et al., 2014). Fortunately, more researchers than ever are aware of long-term data archiving options (Tenopir et al., 2020). Advances in data management and data standardization may also enable more efficient data synthesis projects like meta-analysis (Sansone et al., 2019). In addition, newly emerging data standardization tools and reporting formats (Bond-Lamberty et al., 2021) are being created that allow researchers to upload their data to be harmonized in a central data repository (Wicquart et al., 2022). Our work benefited from these positive trends in science.

One limitation to our results was our inability to disentangle the role of measurement interval in +P studies (see Section 2.3, Figure S6 in Supporting Information S1). While previous work has demonstrated the need for manipulative experiments with frequent sampling intervals (Vieca et al., 2014), the mechanism underlying this is not well understood. We strongly encourage new data syntheses explicitly focused on this phenomenon, and field experiments that prioritize measurements at shorter timescales (Bond-Lamberty et al., 2019). Additionally, our results are sensitive to the limited amount of data from long-term experiments, especially in desert ecosystems where only one study (Li et al., 2020) contributed data for more than 1 year. This limitation highlights a well-known need within ecological literature for long-term manipulative studies (Beier et al., 2012; Knapp et al., 2018; Parts et al., 2019; Sánchez-Pinillos et al., 2022; Walker et al., 2020). However, our results indicate the clear potential for differential long-term responses to precipitation of different ecosystem types, which we hope will be further investigated by future studies.

5. Conclusion

By focusing on the effect of study duration on soil respiration's response to manipulated precipitation, we found evidence that in some ecosystems this flux will acclimate to precipitation changes in a matter of years. However, water-limited ecosystems with limited water-holding capacity are likely to continue to change over time. Therefore, these ecosystems should be the target of continued long-term manipulation experiments to further understand the mechanism underlying their response, pairing flux measurements with mechanistic drivers.

Data Availability Statement

All code and data needed to reproduce the results here are available at https://github.com/COMPASS-DOE/rs-synthesis and permanently archived at https://doi.org/10.5281/zenodo.7054524.

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Acknowledgments

The authors thank Ankur Desai, Sigrid Trier Kjær, and one anonymous reviewer for their thoughtful and constructive comments on this work. This research was supported by COMPASS-FMI, a multi-institutional project supported by the U.S. Department of Energy, Office of Science, Biological and Environmental Research as part of the Environmental System Science Program. The Pacific Northwest National Laboratory is operated for DOE by Battelle Memorial Institute under contract DE-AC05-76RL01830. RCO was funded through DOE’s Office of Science Biological and Environmental Science, Biological and Environmental Research under contract DE-AC05-20126280. RCO was funded through DOE’s Office of Science Biological and Environmental Science, Biological and Environmental Research under contract number DE-AC02-05CH11231.
