

Article

Differences in the Sensitivity of Gross Primary Productivity and Ecosystem Respiration to Precipitation

Weirong Zhang ¹, Wenjing Chen ^{1,2}, Mingze Xu ^{3,4}, Kai Di ¹, Ming Feng ¹, Liucui Wu ¹, Mengdie Wang ¹, Wanxin Yang ¹, Heng Xie ¹, Jinkai Chen ¹, Zehao Fan ¹, Zhongmin Hu ¹ and Chuan Jin ^{1,*} 

- ¹ Hainan Baoting Tropical Rainforest Ecosystem Observation and Research Station, School of Ecology, Hainan University, Haikou 570228, China; zhangweirong1@hndx2.wecom.work (W.Z.); throbbmsex@gmail.com (W.C.); dikai@dzu.edu.cn (K.D.); fengming1@hndx2.wecom.work (M.F.); wuliucui1@hndx2.wecom.work (L.W.); wangmengdie2@hndx2.wecom.work (M.W.); yangwanxin@hndx2.wecom.work (W.Y.); xieheng1@hndx2.wecom.work (H.X.); chenjinkai@hndx2.wecom.work (J.C.); 22110713000016@hainanu.edu.cn (Z.F.); huzm@hainanu.edu.cn (Z.H.); ² School of Art and Design, Nanjing Vocational University of Industry Technology, Nanjing 210007, China ³ Observation and Research Station of Ecological Restoration for Chongqing Typical Mining Areas, Ministry of Natural Resources, Chongqing Institute of Geology and Mineral Resources, Chongqing 401120, China; xumingze@cqdky.com ⁴ College of Resources and Environmental Science, China Agricultural University, Beijing 100083, China
* Correspondence: chuanjin@hainanu.edu.cn

Abstract: The spatiotemporal variability of precipitation profoundly influences terrestrial carbon fluxes, driving shifts between carbon source and sink dynamics through gross primary productivity (GPP) and ecosystem respiration (ER). As a result, the sensitivities of GPP and ER to precipitation (S_{GPP} and S_{ER}), along with their differential responses, are pivotal for understanding ecosystem reactions to precipitation changes and predicting future ecosystem functions. However, comprehensive evaluations of the spatiotemporal variability and differences in S_{GPP} and S_{ER} remain notably scarce. In this study, we utilized eddy covariance flux data to investigate the spatial patterns, temporal dynamics, and differences in S_{GPP} and S_{ER} . Spatially, S_{GPP} and S_{ER} were generally strongly correlated. Among different ecosystems, the correlation between S_{GPP} and S_{ER} was lowest in mixed forest and highest in broadleaf and needleleaf forest. Within the same ecosystem, S_{GPP} and S_{ER} exhibited considerable variation but showed no significant differences. In contrast, they differed significantly across ecosystems, with pronounced variability in their magnitudes. For example, shrubland exhibited the highest values for S_{GPP} , whereas needleleaf forest showed the highest values for S_{ER} . Temporally, S_{ER} demonstrated more pronounced changes than S_{GPP} . Different ecosystems displayed distinct trends: shrubland exhibited an upward trend for both metrics, while grassland showed a downward trend in both S_{GPP} and S_{ER} . Forest, on the other hand, maintained stable S_{GPP} but displayed a downward trend in S_{ER} . Additionally, S_{GPP} and S_{ER} exhibited a notable non-linear response to changes in the aridity index (AI), with both showing a rapid decline followed by stabilization. However, S_{ER} demonstrated a wider adaptive range to precipitation changes. Generally, this research enhances our understanding of the spatiotemporal variations in ecosystem carbon fluxes under changing precipitation patterns.



Academic Editors: Dong Kook Woo, Yongwon Seo and Esther Lee

Received: 21 November 2024

Revised: 13 January 2025

Accepted: 14 January 2025

Published: 15 January 2025

Citation: Zhang, W.; Chen, W.; Xu, M.; Di, K.; Feng, M.; Wu, L.; Wang, M.; Yang, W.; Xie, H.; Chen, J.; et al.

Differences in the Sensitivity of Gross Primary Productivity and Ecosystem Respiration to Precipitation. *Forests* **2025**, *16*, 153. <https://doi.org/10.3390/f16010153>

Copyright: © 2025 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

Keywords: sensitivity; precipitation; gross primary productivity; ecosystem respiration; temporal trend; environmental factors; discrepancy

1. Introduction

The carbon dioxide fixed through photosynthesis at the ecosystem level, known as gross primary productivity (GPP), along with the carbon dioxide released via ecosystem respiration (ER), directly governs the global carbon budget balance [1–4]. GPP and ER demonstrate an intertwined and complementary relationship in the ecosystem, showcasing unique dynamic characteristics despite their close interconnection [5–8]. Numerous studies have demonstrated that GPP is predominantly driven by climatic factors, resulting in significant interannual variability [9–12]. Regarding ER, studies have primarily focused on the effects of temperature [13–15], which may be attributed to the inclusion of soil respiration [16,17]. Conversely, ER exhibited a positive relationship with vegetation photosynthetic capacity [13,18,19], suggesting the influence of available carbon substrates on both plant and soil respiration [20]. The sensitivity (S) of ecosystem carbon flux, specifically GPP and ER, to climate change can be understood as the magnitude of its response to these changes [21]. For vegetation productivity, S is generally considered to be an intrinsic characteristic [22,23], with spatial variability primarily driven by differences in ecosystems and local environmental conditions [23,24]. Existing studies have demonstrated that S can also vary in response to various environmental factors, such as drought, heatwaves, and changes in precipitation patterns [11,25,26]. In the context of ER, research has predominantly focused on the temperature sensitivity of soil respiration (Q_{10}), exploring its relationships with climate drivers [27,28] and soil microbial communities [29,30]. Soil respiration exhibits a non-linear relationship with soil temperature, with CO_2 efflux increasing up to a peak (28–30 °C) and decreasing at higher temperatures (>30 °C). Therefore, Q_{10} can accurately represent the temperature dependence of soil respiration for temperatures below 26–28 °C [31].

Precipitation serves as a pivotal environmental driver influencing both GPP and ER. However, their sensitivities to variations in precipitation (S_{GPP} and S_{ER}) can differ markedly [32,33], highlighting the complex interactions within the ecosystems. Numerous studies have investigated the sensitivity of vegetation productivity to precipitation [23–25], yielding a consensus conclusion: S_{GPP} is greater in arid regions and smaller in mesic regions [11,25]. However, there remains a notable gap in the research regarding the spatiotemporal differences between S_{GPP} and S_{ER} , which may be attributed to the intricate nature of ER, involving various underlying processes and factors. For instance, under optimal soil moisture conditions, the respiration of soil microbes and roots is stimulated, whereas excessive water leading to anaerobic conditions can suppress root respiration [31,34,35].

This study directly explores the similarities and differences in the sensitivity of S_{GPP} and S_{ER} , along with their main environmental drivers, using the FLUXNET2015 dataset. The dataset follows a standardized methodology for data processing, which includes rigorous quality control, filtering, the interpolation of meteorological data, and accurate partitioning of flux data [36]. Specifically, the objectives of this study were to (i) examine the spatial distribution and differences of S_{GPP} and S_{ER} ; and (ii) elucidate the temporal trends and variations in S_{GPP} and S_{ER} .

2. Materials and Methods

2.1. Data Collection

To make use of as much observed data as possible, we utilized the FLUXNET2015 dataset to obtain daily mean eddy-covariance carbon dioxide fluxes and meteorological data (<https://fluxnet.org/>, accessed on 1 May 2021) [36]. Initially, we excluded site-years where missing values in the relevant columns exceeded 30% of the total data, obtaining the dataset to 188 sites (Figure 1) and their corresponding Whittaker biomes (Figure 2). We first reclassified global terrestrial ecosystems into five major categories based on the MODIS

IGBP land cover product (0.05°, <https://lpdaac.usgs.gov/products/mcd12q1v006/>, accessed on 11 March 2022): forest, grassland, shrubland, wetland, and cropland [37]. Given that forests encompass various types and are distributed across multiple climate zones globally, we further subdivided the forest category into needleleaf forest, broadleaf forest, and mixed forest. To investigate the relationship between precipitation sensitivity and drought severity, we used the global average aridity index (AI) at a 0.05° resolution from 1970 to 2000. The data were sourced from the Global Aridity Index and Potential Evapotranspiration (ET₀) Database v3 [38], where $AI = MAP_{rec} / MA_{ET_0}$. Here, MAP_{rec} refers to mean annual precipitation (mm year⁻¹), and MA_{ET_0} represents mean annual reference evapotranspiration (mm year⁻¹), which is calculated using the fully parameterized FAO-56 Penman–Monteith formula.

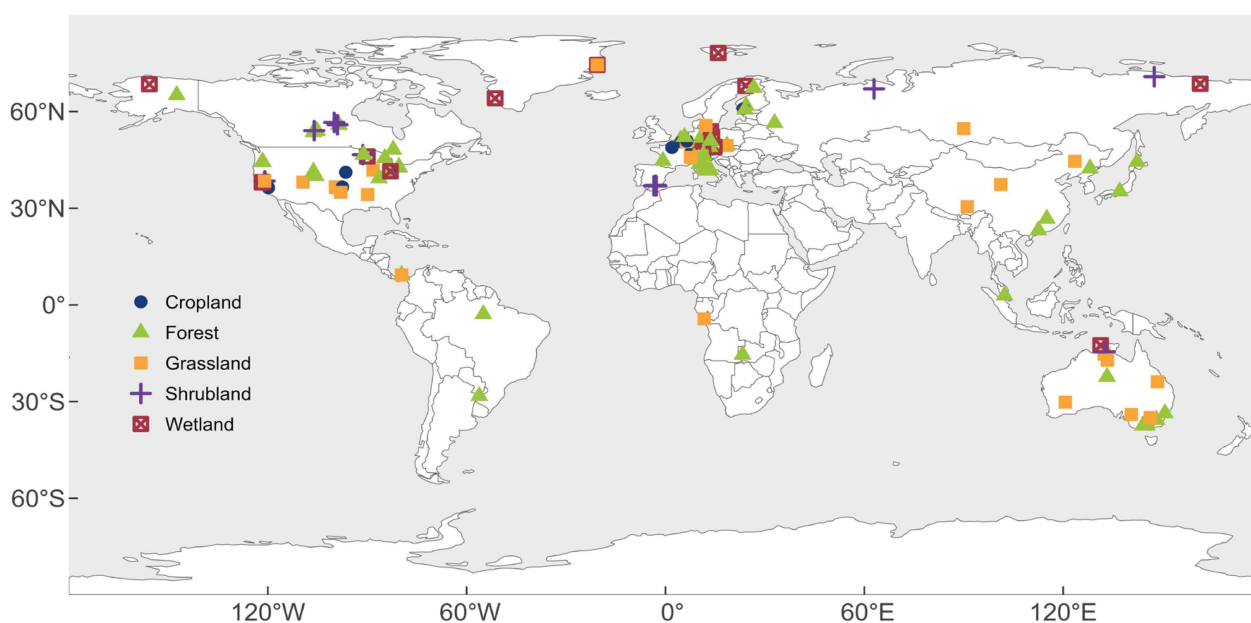


Figure 1. Global distribution of study sites across five ecosystems: cropland, forest, grassland, shrubland, and wetland.

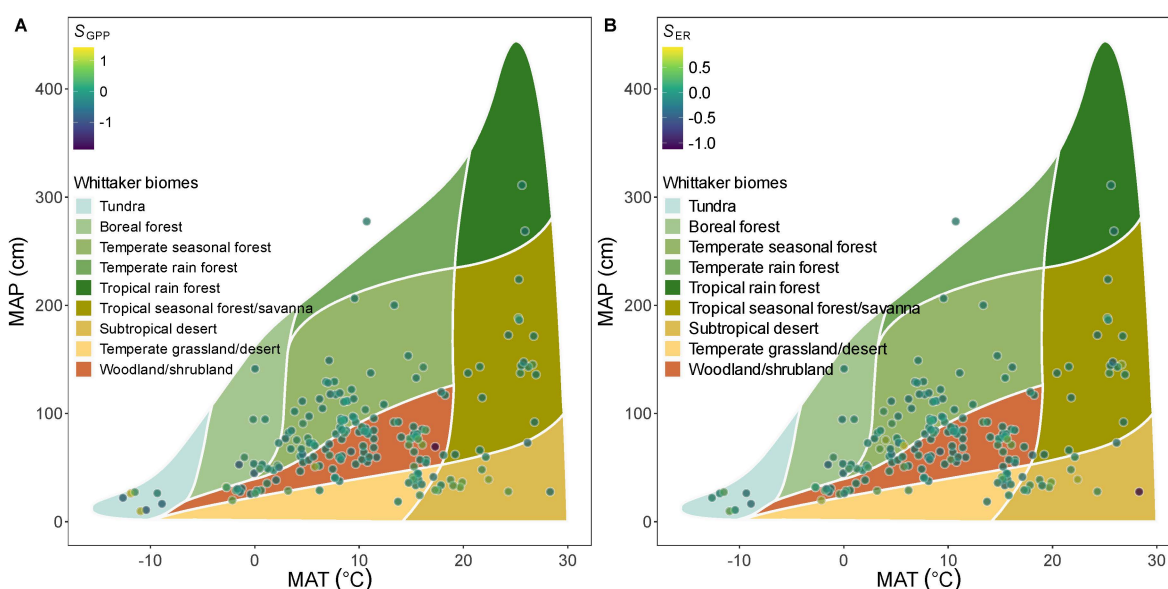


Figure 2. Whittaker biome classification of global distribution of the sensitivity of gross primary productivity and ecosystem respiration to precipitation (S_{GPP} and S_{ER}): (A) S_{GPP} , and (B) S_{ER} .

2.2. Definition and Calculation of S_{GPP} and S_{ER}

Researchers typically represent the sensitivity of carbon dioxide flux to precipitation using the slope of an ordinary least squares (OLS) linear regression [11,23]. Nonetheless, considering that the slope of OLS linear regression is fixed and symmetric, while the actual response of vegetation productivity to changes in environmental factors is often asymmetric [25,39,40], we calculated the sensitivity based on previous studies as the ratio of carbon dioxide flux (GPP and ER) to the net change in precipitation, i.e.,

$$S_{GPP} = \left[\left(\frac{GPP - GPP_{mean}}{GPP} \right) / (P - P_{mean}) \right] \times 100 \quad (1)$$

$$S_{ER} = \left[\left(\frac{ER - ER_{mean}}{ER} \right) / (P - P_{mean}) \right] \times 100 \quad (2)$$

where S_{GPP} and S_{ER} represent the sensitivities of GPP and ER to precipitation, respectively. GPP denotes the gross primary productivity at the site-year, while GPP_{mean} refers to the multi-year average annual total gross primary productivity at the site. P indicates the total annual precipitation at the site-year, and P_{mean} represents the multi-year average annual precipitation at the site. Similarly, ER stands for the annual total ecosystem respiration at the site-year, and ER_{mean} denotes the multi-year average annual total ecosystem respiration at the site. Positive values of S_{GPP} and S_{ER} indicate a direct relationship, where precipitation and GPP or ER increase or decrease together. Negative values reflect an inverse relationship, where increases in precipitation lead to decreases in GPP or ER, and vice versa.

2.3. Data Analysis

We first conducted a paired t -test to assess overall differences between S_{GPP} and S_{ER} , as well as across ecosystems. To explore differences within the same vegetation type, we used one-way ANOVA followed by the least significant difference (LSD) test [41]. ANOVA was performed initially to determine if there were significant differences among group means ($p = 0.05$). The null hypothesis for ANOVA posits that all group means are equal:

$$H_0: \mu_1 = \mu_2 = \mu_3 = \dots = \mu_k \quad (3)$$

If the ANOVA results were significant, indicating that at least one group mean differs, we proceeded with the LSD test. The LSD value was calculated using the following formula:

$$LSD = t_{\alpha/2, df_e} \sqrt{2 \frac{MSE}{n}} \quad (4)$$

where $t_{\alpha/2, df_e}$ is the critical value from the t -distribution for a given significance level α and degrees of freedom df_e from the error term of ANOVA; MSE is the mean square error from the ANOVA; n is the number of observations per group. Given the data limitations, in this study, the significance level for the LSD test was set at $p = 0.05$. We then utilized linear regression to assess the relationship between S_{GPP} and S_{ER} , both overall and within different vegetation functional types.

Additionally, to investigate the range and differences in the degree of variation between S_{GPP} and S_{ER} , we calculated and compared their coefficients of variation (CV).

$$CV = \frac{SD}{MEAN} \quad (5)$$

Linear regression was used to explore the relationships between S_{GPP} , S_{ER} , and their variations with AI and mean annual precipitation (MAP), as well as to examine the influence of environmental factors (mean annual temperature, MAT; MAP; and vapor pressure deficit,

VPD) on S_{GPP} and S_{ER} across each ecosystem. For the temporal variation analysis, we first selected sites within each ecosystem that had data spanning more than 10 years. Then, for each site, we focused on the specific time period (2000–2014) and used the Mann–Kendall test and linear regression to detect trends in S_{GPP} and S_{ER} [42,43].

3. Results

3.1. The Overall Differences and Variability of S_{GPP} and S_{ER} Across Ecosystems

The overall differences between S_{GPP} and S_{ER} were not statistically significant (Figure 3A); however, S_{GPP} exhibited markedly greater variation compared to S_{ER} (Figure 3C). Likewise, no significant differences were observed in S_{GPP} and S_{ER} across ecosystems (Figure 3B), yet their variations differed markedly (Figure 3D). For example, the variation in S_{ER} was greater than that of S_{GPP} in wetland and broadleaf forest, whereas S_{GPP} exhibited considerably greater variation than S_{ER} in grassland and needleleaf forest (Figure 3D). These disparities in S_{GPP} and S_{ER} across ecosystems underscore their distinct responses to changes in precipitation.

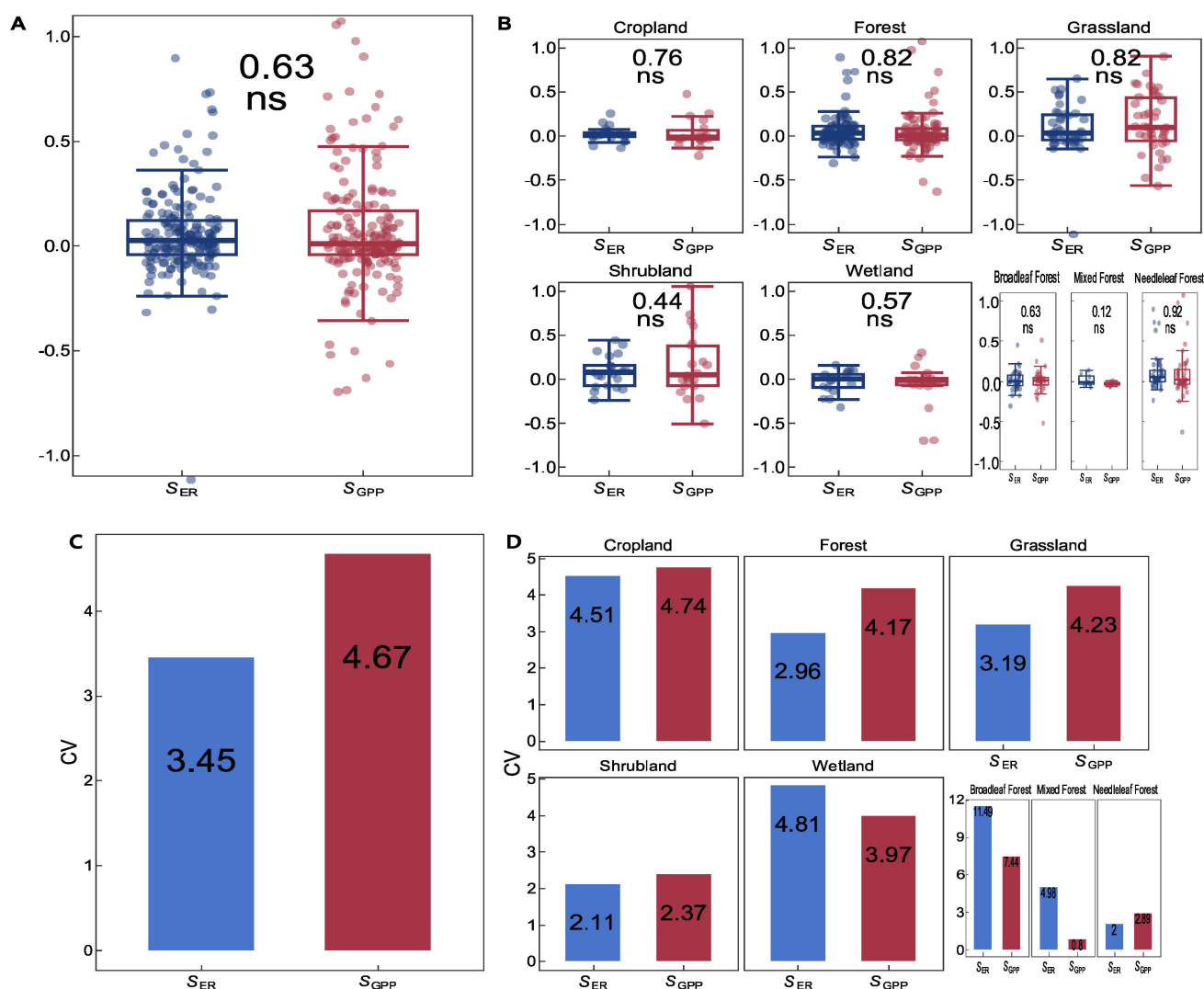


Figure 3. Differences and variability between the sensitivity of gross primary productivity and ecosystem respiration to precipitation (S_{GPP} and S_{ER}): (A) overall differences across all ecosystems, (B) differences among different ecosystems, (C) overall variability across all ecosystems, and (D) variability among different ecosystems.

In addition, our results revealed significant differences in S_{GPP} and S_{ER} across all ecosystems. Specifically, shrublands exhibited the highest S_{GPP} , and wetlands the lowest, while croplands and broadleaf forests showed moderate levels (Figure 4A). For S_{ER} , needleleaf forest exhibited the highest values, broadleaf forest and cropland showed intermediate levels, and wetland had the lowest (Figure 4B). Analysis of the variation in S_{GPP} and S_{ER} across all ecosystems revealed that broadleaf forest exhibited the greatest variation for both metrics, as mixed forest showed the least variation for S_{GPP} and needleleaf forest showed the least variation for S_{ER} (Figure 4C,D).

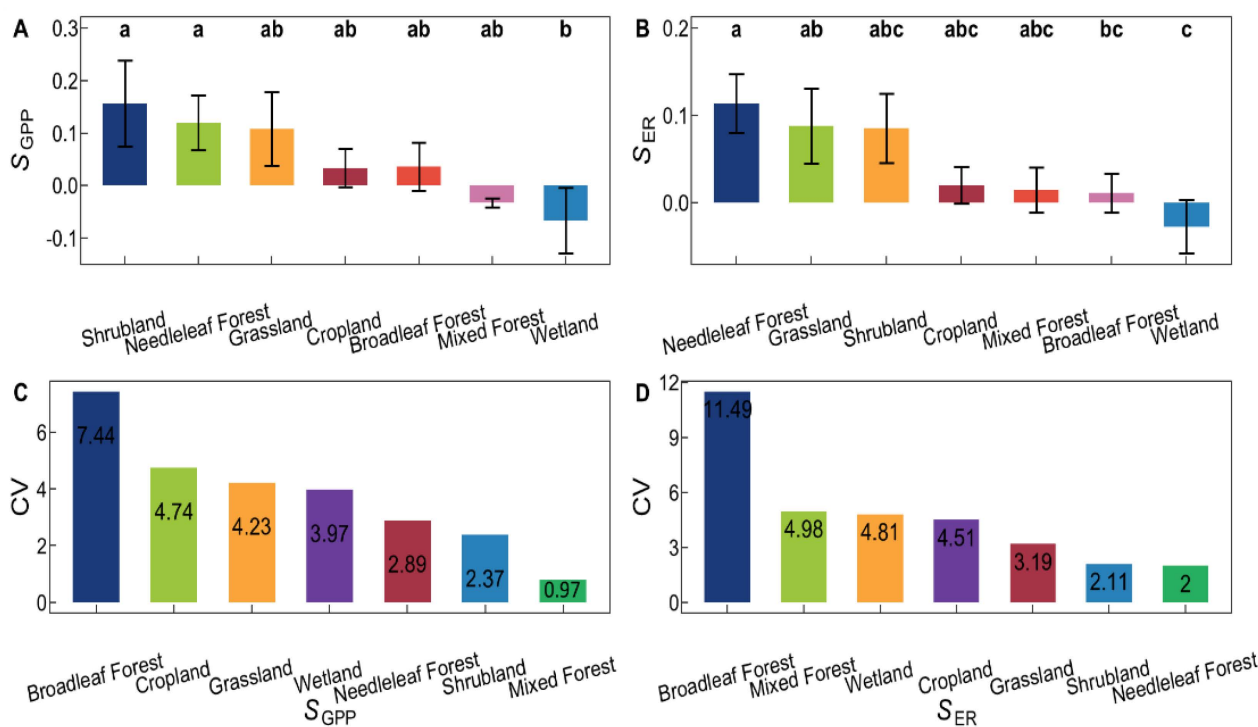


Figure 4. Differences and variability in the sensitivity of gross primary productivity and ecosystem respiration to precipitation (S_{GPP} and S_{ER}) among different ecosystems: (A) S_{GPP} differences, (B) S_{ER} differences, (C) variability in S_{GPP} , and (D) variability in S_{ER} . The letters in panels (A,B) indicate significant differences ($p < 0.05$), while the numbers in panels (C,D) represent the coefficient of variation (CV) for each ecosystem.

3.2. Relationship Between S_{GPP} and S_{ER}

S_{GPP} and S_{ER} exhibited a highly significant positive correlation, $p < 0.001$, $R^2 = 0.27$ (Figure 5A). The slope of the linear regression (slope = 0.31) indicates that S_{ER} was more stable compared to S_{GPP} . This suggests that for every one-unit change in S_{GPP} , S_{ER} changes by 0.31 units.

Furthermore, we examined the relationship between S_{GPP} and S_{ER} across ecosystems. With the exception of mixed forests, all other ecosystems exhibited a significant positive regression relationship between S_{GPP} and S_{ER} . For example, in cropland, forest, and grassland, S_{GPP} and S_{ER} showed significant positive correlations, with p and R^2 of 0.011, 0.32; <0.001 , 0.36; and 0.006, 0.18, respectively (Figure 5B). Broadleaf forest displayed the strongest linear relationship between S_{GPP} and S_{ER} , with $p < 0.001$, $R^2 = 0.61$, while no linear relationship was observed in mixed forest. Furthermore, the regression slopes between S_{GPP} and S_{ER} were less than 1 for all ecosystems, indicating that S_{ER} is more stable than S_{GPP} .

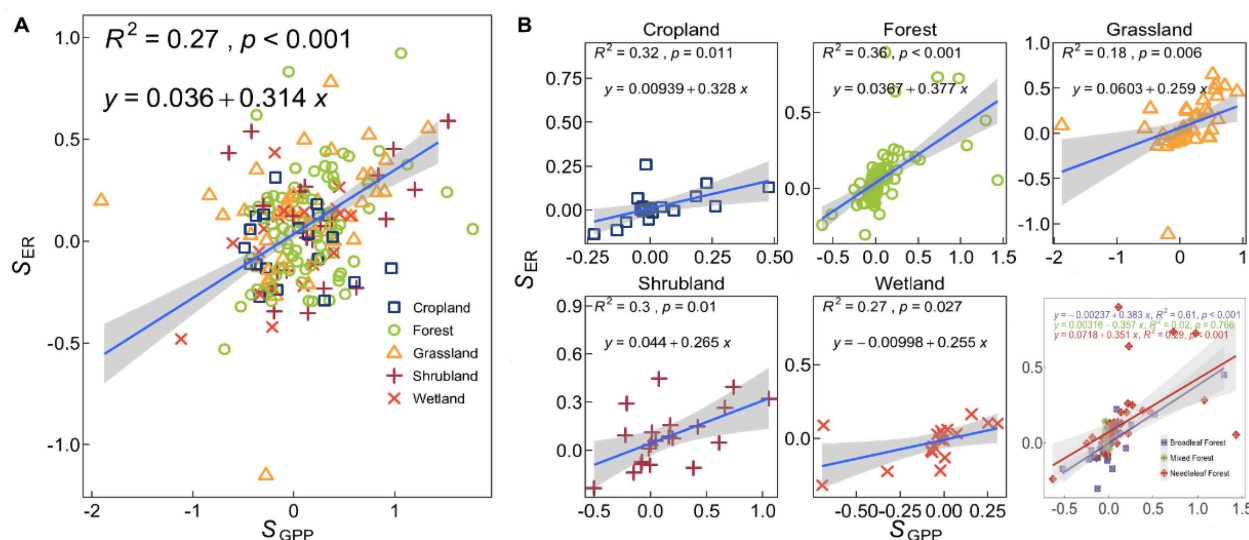


Figure 5. Relationship between the sensitivity of gross primary productivity and ecosystem respiration to precipitation (S_{GPP} and S_{ER}) across different ecosystems: **(A)** regression relationship of S_{GPP} and S_{ER} for all ecosystems, and **(B)** regression relationship of S_{GPP} and S_{ER} across different ecosystems.

3.3. Changes in S_{GPP} and S_{ER} with AI and MAP

Considering the distinct ecological implications of positive and negative values for S_{GPP} and S_{ER} , we delineated these values to examine their variations in response to AI and MAP. When S_{GPP} and S_{ER} were positive, they initially experienced a dramatic decline with increasing AI, followed by stabilization, with critical breakpoints at 0.65 and 0.85 (Figure 6A,B). This suggests that as water availability increases, water no longer acts as a limiting factor for GPP and ER, and their sensitivity to water variations diminishes. Conversely, S_{GPP} and S_{ER} revealed distinct behaviors in response to variations in MAP: S_{GPP} underwent a sharp decrease followed by a continued decline with rising MAP, whereas S_{ER} gradually diminished as MAP increased (Figure 7A,B). When S_{GPP} and S_{ER} were negative, they did not exhibit significant changes in response to variations in AI and MAP (Figures 6C,D and 7C,D).

3.4. Temporal Trends of S_{GPP} and S_{ER}

The MK trend analysis revealed a pronounced difference in the temporal trends in S_{GPP} and S_{ER} across ecosystems. Specifically, the S_{GPP} of shrubland showed a marked increasing trend over time, while grassland exhibited a nearly significant decreasing trend ($p = 0.066$) (Figure 8). No significant changes were observed in the other ecosystems (Figure 8). Regarding S_{ER} , shrubland demonstrated a significant increasing trend (Figure 9), whereas grassland showed a declining trend over time (Figure 9). No significant temporal changes were observed in the other ecosystems. It is important to note that the extent of temporal variation in S_{GPP} and S_{ER} in forests was the smallest, which may be related to the high complexity of forest ecosystems (Figures 8 and 9).

Moreover, even within the same ecosystem type, the direction and extent of temporal changes in S_{GPP} and S_{ER} exhibited certain differences. For example, although both S_{GPP} and S_{ER} in wetland showed non-significant temporal trends, the opposite directions of their changes over time still partially reflect the distinct responses of S_{GPP} and S_{ER} to precipitation variability (Figures 8 and 9).

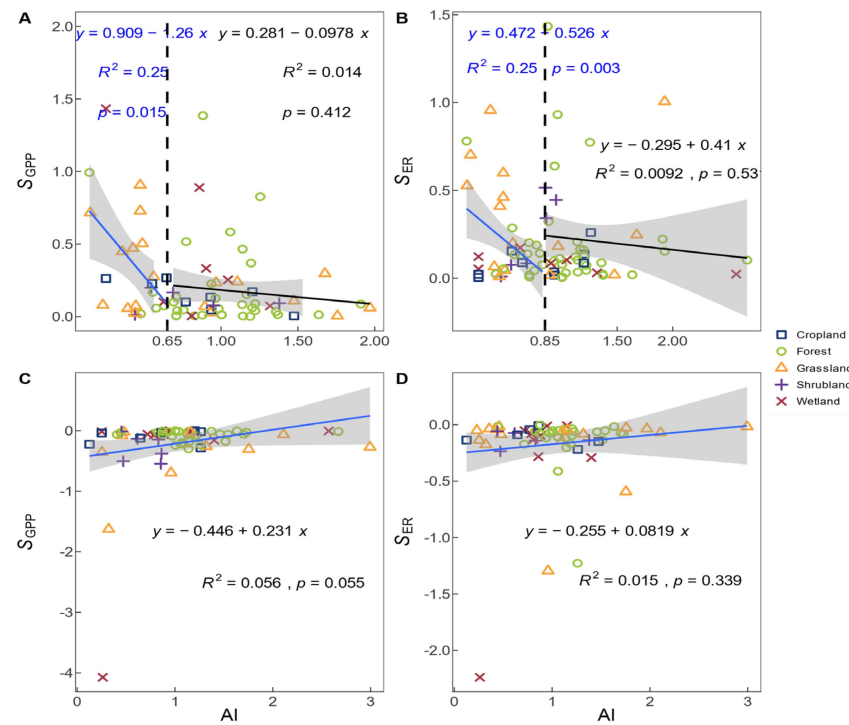


Figure 6. Sensitivity of gross primary productivity and ecosystem respiration to precipitation (S_{GPP} and S_{ER}) across changes in the aridity index (AI): (A) changes in S_{GPP} with AI when S_{GPP} is positive, (B) changes in S_{ER} with AI when S_{ER} is positive, (C) changes in S_{GPP} with AI when S_{GPP} is negative, and (D) changes in S_{ER} with AI when S_{ER} is negative.

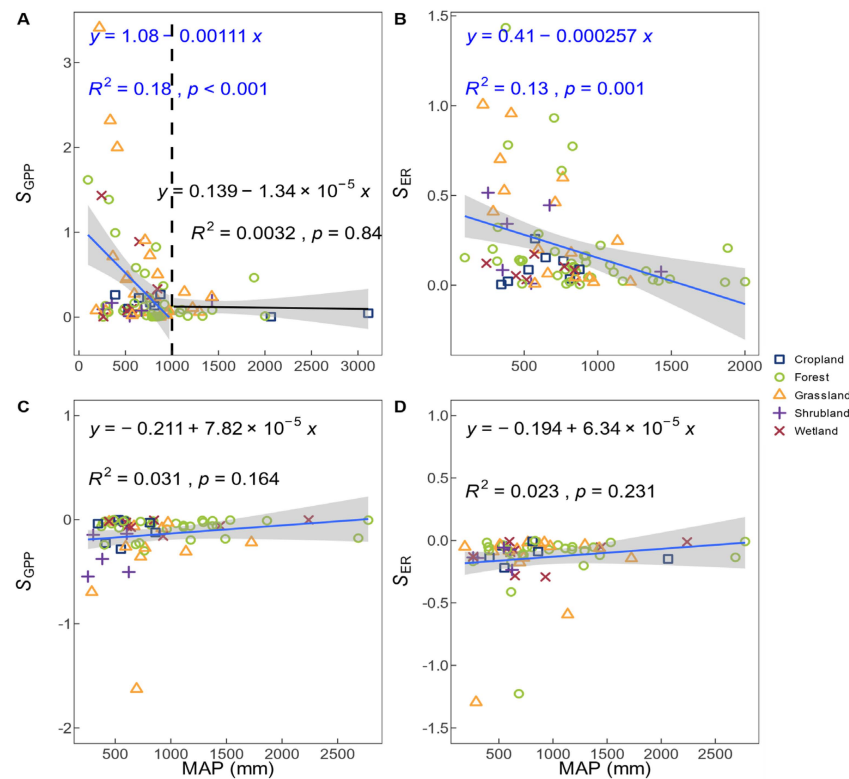


Figure 7. The sensitivity of gross primary productivity and ecosystem respiration to precipitation (S_{GPP} and S_{ER}) across changes in the mean annual precipitation (MAP): (A) changes in S_{GPP} with MAP when S_{GPP} is positive, (B) changes in S_{ER} with MAP when S_{ER} is positive, (C) changes in S_{GPP} with MAP when S_{GPP} is negative, and (D) changes in S_{ER} with MAP when S_{ER} is negative.

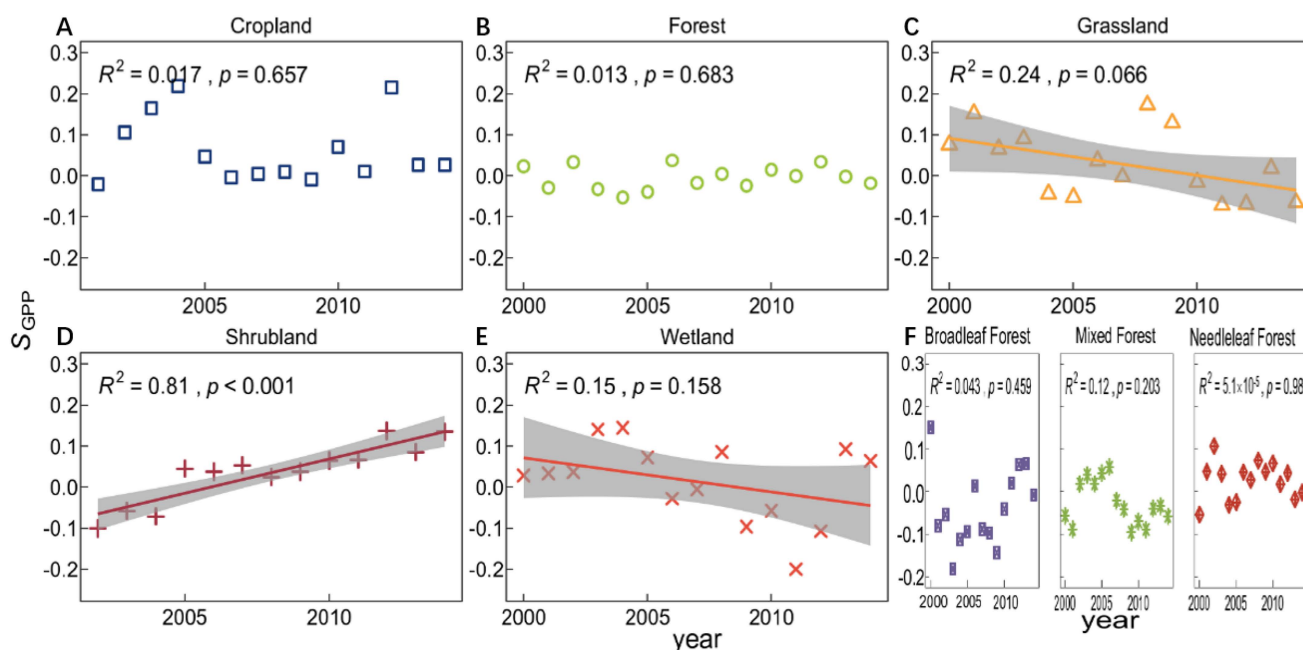


Figure 8. Temporal trends of the sensitivity of gross primary productivity to precipitation (S_{GPP}) across different ecosystems: (A) grassland, (B) cropland, (C) forest, (D) shrubland, (E) wetland, and (F) forest subtypes. Note: For ecosystems with significant linear trends, trend lines and error intervals (in gray, mean $\pm$ SE) were shown. For ecosystems without linear trends, only the distribution of points along with R^2 and p -values were presented to statistically confirm the absence of a linear trend.

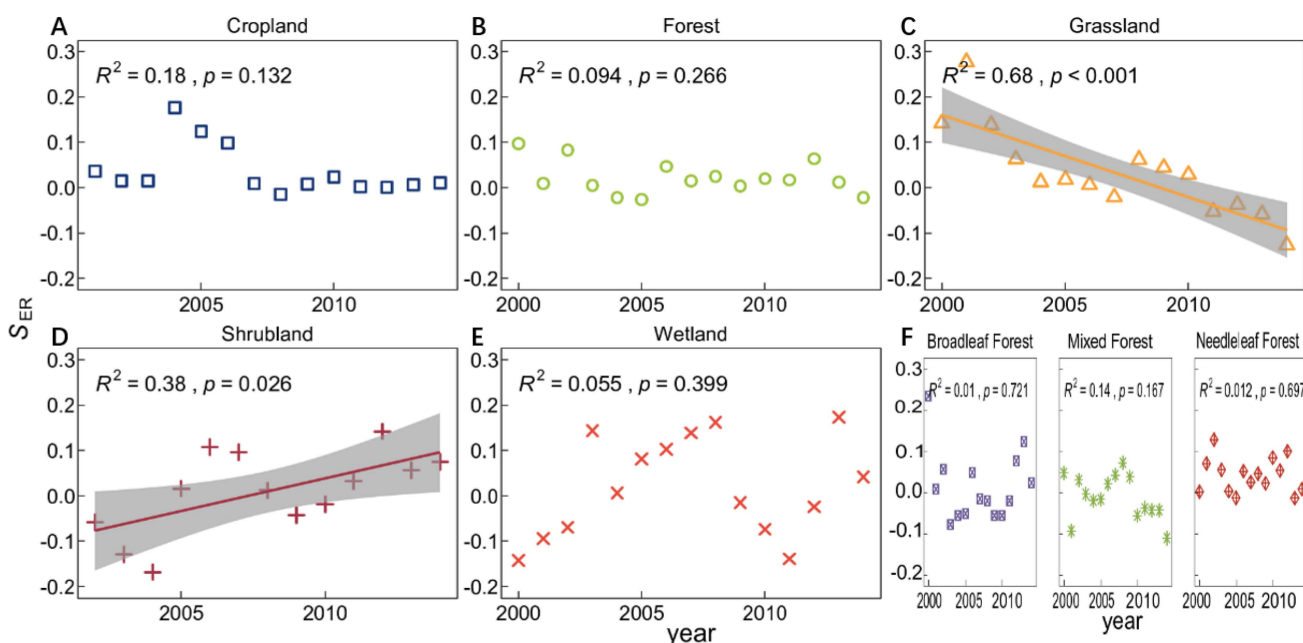


Figure 9. Temporal trends of the sensitivity of ecosystem respiration to precipitation (S_{ER}) across different ecosystems: (A) grassland, (B) cropland, (C) forest, (D) shrubland, (E) wetland, and (F) forest subtypes. Note: For ecosystems with significant linear trends, trend lines and error intervals (in gray, mean $\pm$ SE) were shown. For ecosystems without linear trends, only the distribution of points along with R^2 and p -values were presented to statistically confirm the absence of a linear trend.

3.5. Dominant Factors of S_{GPP} and S_{ER} in Different Ecosystems

Overall, compared to other ecosystem types, S_{GPP} and S_{ER} in grassland were more readily influenced by temperature and precipitation changes. Specifically, the S_{ER} and S_{GPP} in grassland showed a significant declining trend with increasing MAP (Figure 10A,B),

while S_{ER} significantly increased with rising MAT and VPD (Figure 10C,E). Aside from grassland, only the S_{GPP} in wetland significantly decreased with higher MAT (Figure 10D).

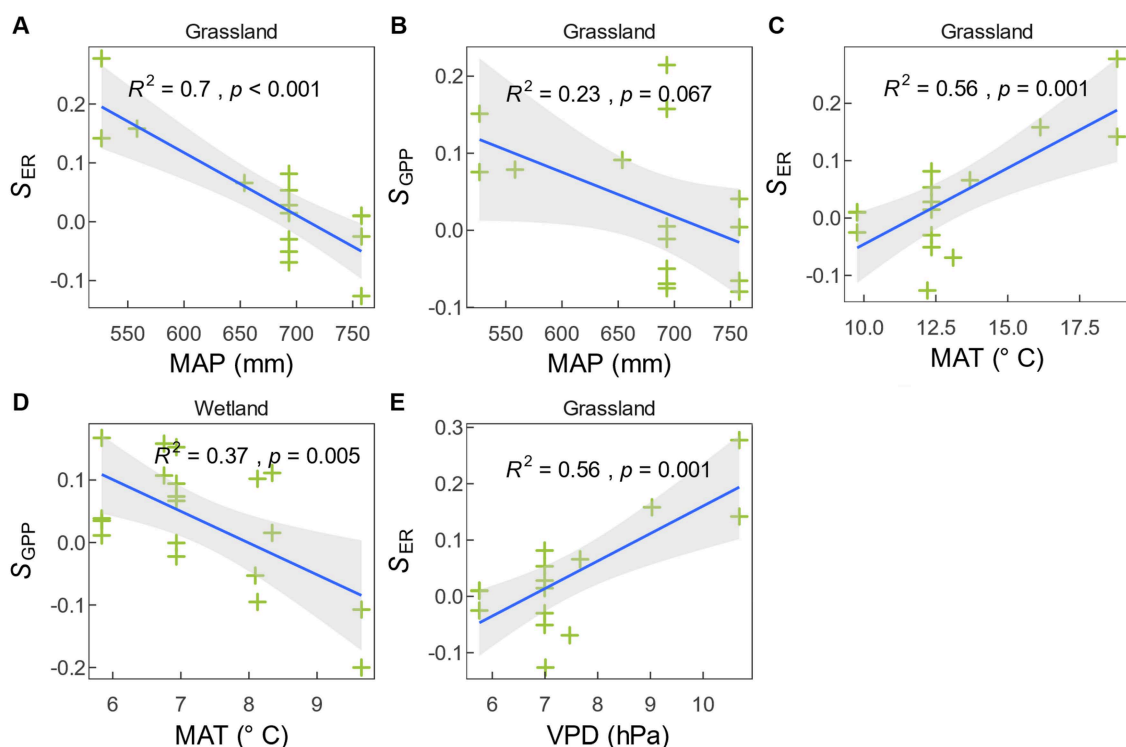


Figure 10. The main factors influencing the sensitivity of gross primary productivity and ecosystem respiration to precipitation (S_{GPP} and S_{ER}) across different ecosystems: (A) grassland S_{ER} and mean annual precipitation (MAP), (B) grassland S_{GPP} and mean annual precipitation, (C) grassland S_{ER} and mean annual temperature (MAT), (D) wetland S_{GPP} and MAT, and (E) grassland S_{ER} and vapor pressure deficit (VPD). Note: for the statistical analysis, we selected sites with at least 10 years of data within each ecosystem, rather than using all available sites within each ecosystem.

4. Discussion

4.1. Differences and Variations Between S_{GPP} and S_{ER}

Our study found no significant differences between S_{GPP} and S_{ER} (Figure 3A,B), indicating a comparable level of responsiveness to changes in precipitation. A precipitation manipulation experiment conducted on the Tibetan Plateau demonstrated that under extreme drought conditions, GPP and ER decreased by 17.26% and 19.05%, respectively, relative to the control, thereby providing indirect support for our findings [44].

The similarity in the responses of GPP and ER to precipitation changes may arise from their intrinsic connection. Physiologically, photosynthesis and respiration in plants are interrelated processes [45,46]. The energy required for photosynthesis, derived from the respiratory breakdown of organic matter, leads to the accumulation of stable compounds when photosynthesis exceeds respiration, thereby providing a consistent substrate for respiration [46–48]. On the other hand, stomatal conductance regulates the exchange of CO_2 , O_2 , and H_2O . Under drought stress, stomata close to reduce transpiration [49–51], impacting gas exchange and consequently affecting both photosynthesis and respiration. Ecologically, studies have confirmed a close relationship between GPP and ER at regional and global scales, primarily because productivity serves as the main and direct substrate supplier for respiration, fundamentally constraining ER [52,53].

However, the overall variation in S_{GPP} was greater than that of S_{ER} (Figure 3C), indicating that GPP was more sensitive to changes in precipitation compared to ER, a conclusion

that was further supported by research on the impact of water availability on carbon dioxide flux in grassland ecosystems [44,54,55]. This may be attributed to several factors. First, the composition of ecosystem ER is complex, consisting of both autotrophic respiration (R_a) and heterotrophic respiration (R_h), which may exhibit different sensitivities to changes in precipitation. This is because R_a is more dependent on photosynthetic products [23] and photosynthesis is easily affected by precipitation [56,57]. Furthermore, existing research indicates that the sensitivity of aboveground plant respiration to precipitation exceeds that of belowground respiration, which is in turn more sensitive than microbial respiration [44]. This suggests that the greater stability of ER in response to water variations, compared to gross primary GPP, was primarily due to the relative stability of soil or heterotrophic respiration. Secondly, multiple researchers have indicated that GPP exhibits a greater response amplitude to precipitation fluctuations. For instance, a controlled experiment conducted in temperate grassland demonstrated that GPP increased more than ER in response to increased precipitation [54]. Additionally, research based on eddy covariance measurements has shown that GPP was more sensitive to precipitation, contributing more to NEE responses than ER [53,58].

GPP is more susceptible to changes in precipitation, which may be attributed to the role of H_2O as a substrate for light reactions. Successful photolysis of water is essential for the proper functioning of electron transport and carbon dioxide fixation during photosynthesis. Existing research indicates that photosynthesis is highly sensitive to drought; when facing drought stress, vegetation may respond by reducing stomatal conductance and the rate of electron transport [59], as well as inhibiting the activity of PS-II and Rubisco [60]. In contrast, ER was influenced not only by aboveground plant activity but also by root systems, soil microorganisms, and enzymatic activities, which are generally less affected by variations in precipitation [44,61].

The variation in S_{GPP} and S_{ER} in cropland and shrubland was the most similar (Figure 3D), likely due to the high sensitivity of R_h to drought in these arid and semi-arid regions [62], where unstable carbon and soil microbes are concentrated in surface layers, causing R_h to react strongly to slight moisture changes [63]. Across ecosystems, shrubland, grassland, and needleleaf forest exhibited higher S_{GPP} and S_{ER} (Figure 4A,B), likely because these ecosystems are globally water-limited [64] and the impact of global warming on ER is more pronounced in colder regions [65]. In arid ecosystems, higher water-use efficiency [23] likely increases the sensitivity of productivity to precipitation changes compared to humid regions, and the close link between GPP and ER contributes to the elevated S_{ER} .

4.2. The Response of S_{GPP} and S_{ER} to Changes in Water Availability

In our study, a positive sensitivity of carbon dioxide flux to precipitation signifies a synchronous relationship, whereas a negative value indicates an inverse correlation. When S_{GPP} and S_{ER} are positive, S_{GPP} shows a marked non-linear response to changes in AI and MAP (Figures 6A and 7A). Specifically, S_{GPP} and S_{ER} are highest in arid and semi-arid regions. S_{GPP} and S_{ER} decline rapidly with increasing AI when $AI < 0.65$ and 0.85 , but they stabilize when $AI > 0.65$ and 0.85 . It is widely recognized that S_{GPP} is typically higher in arid regions and lower in more mesic ecosystems [11,25,66]. This may be attributed to the fact that water availability is a key limiting factor for vegetation growth in these areas [67,68], coupled with the higher water-use efficiency of local vegetation [69]. In contrast, in humid regions, factors such as light and soil nutrients may play a more significant role in limiting vegetation growth [70].

Regarding non-linearity, Knapp and Smith (2001) were the first to find that vegetation productivity responds to precipitation in a non-linear manner [71]. With further research,

an increasing body of evidence supports the idea that grassland ecosystems exhibit positive asymmetry in their response to precipitation, meaning that productivity increases in wet years exceed declines in dry years [39,72], which is beneficial for the ecosystem's carbon sink [73]. Conversely, negative asymmetry is observed in dry years [74], which is detrimental to the carbon sink. On the other hand, experiments in grassland have also shown that ER and its components exhibit asymmetric responses to changes in precipitation [39,44].

The asymmetry between carbon dioxide flux and precipitation may be attributed to two main factors: firstly, the asymmetric response of ANPP to precipitation was a key reason for the non-linear nature of carbon dioxide flux in response to precipitation changes [40,44]; secondly, the asymmetric relationship between soil moisture and precipitation exacerbates the non-linear relationship of carbon dioxide flux. Experimental studies have shown that reduced precipitation significantly decreases surface soil water content (SWC), while increased precipitation has limited effects, further intensifying the non-linear response of carbon dioxide flux across different precipitation gradients [44]. Moreover, overall, S_{ER} exhibits a significant decreasing trend over a wider range of AI and MAP changes (Figures 6B and 7B), indicating that ER is more sensitive to variations in moisture while possessing some regulatory capacity. This phenomenon may be attributed to the soil's ability to store and buffer water [75] and to the effective utilization of deep moisture by plant roots [76,77], which together enhance the ecosystem's adaptability to changes in moisture.

4.3. Temporal Trend Pattern of S_{GPP} and S_{ER} Across Ecosystems

For S_{GPP} , only shrubland showed a significant increase, while wetland exhibited a non-significant decrease (Figure 8), and grassland showed a non-significant downward trend. In contrast, for S_{ER} , grassland exhibited a highly significant downward trend, while shrubland showed a significant increase over time (Figure 9). The temporal variations in S_{GPP} and S_{ER} between grassland and shrubland were notably different, which is a noteworthy observation. As global warming advances, total precipitation has increased [78]. Coupled with the CO_2 fertilization effect, this has contributed to the rise in global vegetation productivity [79–81]. Concurrently, the expansion of leaf area in vegetation has led to higher water consumption [82], establishing a balance between the increased availability of water and the elevated demand for it.

Studies have shown that grassland exhibits a broadly positive, symmetric response to precipitation changes [39], indicating a reduced water limitation on carbon dioxide flux. In contrast, the temporal trend of S_{GPP} in forest remains more stable, likely due to multiple factors. First, rising atmospheric CO_2 concentrations have enhanced forest water-use efficiency [83]. Additionally, the complex vertical structure of forest provides resilience to environmental changes [84]. These factors collectively contribute to the stability of forest S_{GPP} trends. For S_{ER} , the increased precipitation enhances soil respiration due to the strong water retention capacity of the soil [28,85]. Studies show that moderate increases in precipitation significantly boost microbial respiration, while root and microbial respiration only decline significantly under extreme precipitation increases [86]. Therefore, in ecosystems with relatively mild water resource limitations, an increase in precipitation results in a more pronounced declining trend in S_{ER} . It is noteworthy that while both S_{GPP} and S_{ER} in shrubland exhibit a consistent upward trend over time, the increase in S_{GPP} is markedly more pronounced than that of S_{ER} . This discrepancy may be attributed to the higher water use efficiency of vegetation in water-limited areas [87], as GPP typically responds more rapidly to changes in precipitation compared to ER [58].

4.4. Uncertainty Analysis

Eddy covariance offers a direct technique for assessing trace gas and energy fluxes between the surface and the atmosphere at an ecosystem level, usually within a 1 km radius of the measurement site [36]. This makes it difficult to directly compare it with other methods. Campioli et al. assessed eddy covariance (EC) data by comparing them with other methods, such as inventory and chamber techniques, and found that EC biases are not evident across sites, which indicates the effectiveness of the standard post-processing procedures and enhances confidence in the reliability of EC data [88]. Pastorello and the eddy covariance site teams further compared and technically validated their measurements based on their in-depth knowledge of the respective sites [36]. While measurement and processing uncertainties are inevitable and can be significant for certain sites and ecosystem conditions, the flux values in this dataset generally align with expectations. Overall, eddy covariance continues to be one of the most dependable methods for evaluating land–atmosphere exchanges at the ecosystem scale. The widespread use of eddy covariance data in many scientific studies indirectly confirms its reliability and value.

On the other hand, CO₂ flux (net ecosystem exchange, NEE) is primarily partitioned into GPP and ER using two methods: the nighttime flux method and the daytime flux method [36]. The nighttime flux method estimates ER by constructing a respiration–temperature model using nighttime data and calculates GPP based on NEE. The parameterization process accounts for dynamic factors such as water availability, substrate, and phenology [89]. The daytime flux method, which combines both daytime and nighttime data, estimates GPP through a light-response curve and vapor pressure deficit, while ER is estimated using a respiration–temperature relationship [90]. Compared to the nighttime flux method, the daytime flux method is more widely used in research, which is consistent with this study.

5. Conclusions

This study, using the FLUXNET2015 dataset, examined the spatiotemporal variations in S_{GPP} and S_{ER} and identified the primary environmental factors driving these variations. Our results show that S_{GPP} and S_{ER} were generally strongly correlated spatially. The correlation was weakest in mixed forests and strongest in broadleaf and needleleaf forests. While S_{GPP} and S_{ER} displayed notable variation within the same ecosystem, no significant differences were observed. In contrast, significant differences were found across ecosystems, with marked variability in their magnitudes. For instance, shrubland had the highest S_{GPP} values, while needleleaf forest had the highest S_{ER} values. Temporally, S_{ER} showed more pronounced changes than S_{GPP} . Ecosystem temporal trends varied: shrubland displayed an increasing trend for both metrics, grassland showed a decreasing trend in both S_{GPP} and S_{ER} , and forest maintained stable S_{GPP} but showed a downward trend in S_{ER} . Moreover, S_{GPP} exhibited a clear non-linear response to changes in the aridity index (AI), with both metrics rapidly declining before stabilizing. However, S_{ER} had a broader adaptive range to precipitation changes. Overall, this study improves our understanding of the spatiotemporal variations in ecosystem carbon dioxide fluxes under changing precipitation patterns.

Author Contributions: Methodology, M.X., K.D., Z.F., Z.H. and C.J.; Software, W.Z., W.C., M.X., K.D., M.F., L.W., M.W., W.Y., H.X., J.C. and Z.F.; Validation, M.X. and M.F.; Formal analysis, M.F.; Resources, K.D., M.W., W.Y. and Z.F.; Data curation, W.Z., W.C., L.W., W.Y., H.X. and J.C.; Writing—original draft, W.Z. and W.C.; Writing—review & editing, Z.H. and C.J.; Visualization, Z.H.; Supervision, C.J. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the Second Tibetan Plateau Scientific Expedition and Research Program (Grant No. 2019QZKK0405), the National Natural Science Foundation of China (Grant No. 62472216), the Hainan Provincial Natural Science Foundation of China (Grant No. 423RC432), and the Start-up Fund for New Talented Researchers of Nanjing Vocational University of Industry Technology (Grant No. YK23-08-01). This work was also promoted by the U.S.–China Carbon Consortium (USCCC).

Data Availability Statement: The raw data are available upon request to the authors. Please contact C. Jin (chuanjin@hainanu.edu.cn) to access the data of this study.

Conflicts of Interest: The authors declare no conflicts of interest.

References

- Griffis, T.J.; Black, T.A.; Gaumont-Guay, D.; Drewitt, G.B.; Nesic, Z.; Barr, A.G.; Morgenstern, K.; Kljun, N. Seasonal variation and partitioning of ecosystem respiration in a southern boreal aspen forest. *Agric. For. Meteorol.* **2004**, *125*, 207–223. [\[CrossRef\]](#)
- Taillardat, P.; Thompson, B.S.; Garneau, M.; Trottier, K.; Friess, D.A. Climate change mitigation potential of wetlands and the cost-effectiveness of their restoration. *Interface Focus* **2020**, *10*, 20190129. [\[CrossRef\]](#) [\[PubMed\]](#)
- Wang, S.; Chen, W.; Fu, Z.; Li, Z.; Wang, J.; Liao, J.; Niu, S. Seasonal and inter-annual variations of carbon dioxide fluxes and their determinants in an Alpine meadow. *Front. Plant Sci.* **2022**, *13*, 894398. [\[CrossRef\]](#)
- Jin, C.; Zha, T.; Bourque, C.P.A.; Liu, P.; Jia, X.; Zhang, F.; Wang, N. Multi-year trends and interannual variation in ecosystem resource use efficiencies in a young mixedwood plantation in northern China. *Agric. For. Meteorol.* **2023**, *330*, 109318. [\[CrossRef\]](#)
- Field, C.B.; Behrenfeld, M.J.; Randerson, J.T.; Falkowski, P. Primary Production of the Biosphere: Integrating Terrestrial and Oceanic Components. *Science* **1998**, *281*, 237–240. [\[CrossRef\]](#) [\[PubMed\]](#)
- Luyssaert, S.; Inglima, I.; Jung, M.; Richardson, A.D.; Reichstein, M.; Papale, D.; Piao, S.L.; Schulze, E.-D.; Wingate, L.; Matteucci, G.; et al. CO₂ balance of boreal, temperate, and tropical forests derived from a global database. *Glob. Change Biol.* **2007**, *13*, 2509–2537. [\[CrossRef\]](#)
- Chapin, F.S.; Matson, P.A.; Vitousek, P.M. *Principles of Terrestrial Ecosystem Ecology*; Springer: New York, NY, USA, 2011. [\[CrossRef\]](#)
- Jin, C.; Jian, J.; Bourque, C.P.A.; Zha, T.; Dai, L.; Yang, Y.; Hu, Z. Soil autotrophic-to-heterotrophic-respiration ratio and its controlling factors across several terrestrial biomes: A global synthesis. *Catena* **2024**, *242*, 108118. [\[CrossRef\]](#)
- Piao, S.; Wang, X.; Wang, K.; Li, X.; Bastos, A.; Canadell, J.G.; Ciais, P.; Friedlingstein, P.; Sitch, S. Interannual variation of terrestrial carbon cycle: Issues and perspectives. *Glob. Chang. Biol.* **2020**, *26*, 300–318. [\[CrossRef\]](#) [\[PubMed\]](#)
- Wang, M.; Wang, S.; Zhao, J.; Ju, W.; Hao, Z. Global positive gross primary productivity extremes and climate contributions during 1982–2016. *Sci. Total Environ.* **2021**, *774*, 145703. [\[CrossRef\]](#) [\[PubMed\]](#)
- Zeng, X.; Hu, Z.; Chen, A.; Yuan, W.; Hou, G.; Han, D.; Liang, M.; Di, K.; Cao, R.; Luo, D. The global decline in the sensitivity of vegetation productivity to precipitation from 2001 to 2018. *Glob. Chang. Biol.* **2022**, *28*, 6823–6833. [\[CrossRef\]](#) [\[PubMed\]](#)
- Jin, C.; Zha, T.; Bourque, C.P.; Jia, X.; Tian, Y.; Liu, P.; Hu, Z. Ecosystem-scale carbon dynamics in desert Shrublands: Unraveling the complex interplay among leaf functional and physiological traits and environment. *Agric. For. Meteorol.* **2024**, *355*, 110133. [\[CrossRef\]](#)
- Chen, W.; Wang, S.; Wang, J.; Xia, J.; Luo, Y.; Yu, G.; Niu, S. Evidence for widespread thermal optimality of ecosystem respiration. *Nat. Ecol. Evol.* **2023**, *7*, 1379–1387. [\[CrossRef\]](#) [\[PubMed\]](#)
- Perkins, D.M.; Yvon-Durocher, G.; Demars, B.O.L.; Reiss, J.; Pichler, D.E.; Friberg, N.; Trimmer, M.; Woodward, G. Consistent temperature dependence of respiration across ecosystems contrasting in thermal history. *Glob. Chang. Biol.* **2012**, *18*, 1300–1311. [\[CrossRef\]](#)
- Yvon-Durocher, G.; Caffrey, J.M.; Cescatti, A.; Dossena, M.; del Giorgio, P.; Gasol, J.M.; Montoya, J.M.; Pumpanen, J.; Staehr, P.A.; Trimmer, M. Reconciling the temperature dependence of respiration across timescales and ecosystem types. *Nature* **2012**, *487*, 472–476. [\[CrossRef\]](#)
- Kirschbaum, M.U. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biol. Biochem.* **1995**, *27*, 753–760. [\[CrossRef\]](#)
- Yuste, J.C.; Janssens, I.A.; Carrara, A.; Meiresonne, L.; Ceulemans, R. Interactive effects of temperature and precipitation on soil respiration in a temperate maritime pine forest. *Tree Physiol.* **2003**, *23*, 1263–1270. [\[CrossRef\]](#)
- Janssens, I.A.; Lankreijer, H.; Matteucci, G.; Kowalski, A.S.; Buchmann, N.; Epron, D.; Pilegaard, K.; Kutsch, W.; Longdoz, B.; Grünwald, T.; et al. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Glob. Chang. Biol.* **2001**, *7*, 269–278. [\[CrossRef\]](#)
- Luo, X.; Keenan, T.F. Global evidence for the acclimation of ecosystem photosynthesis to light. *Nat. Ecol. Evol.* **2020**, *4*, 1351–1357. [\[CrossRef\]](#) [\[PubMed\]](#)

20. Flanagan, L.B.; Johnson, B.G. Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland. *Agric. For. Meteorol.* **2005**, *130*, 237–253. [\[CrossRef\]](#)
21. Seddon, A.W.; Macias-Fauria, M.; Long, P.R.; Benz, D.; Willis, K.J. Sensitivity of global terrestrial ecosystems to climate variability. *Nature* **2016**, *531*, 229–232. [\[CrossRef\]](#)
22. Hu, Z.; Guo, Q.; Li, S.; Piao, S.; Knapp, A.K.; Ciais, P.; Li, X.; Yu, G. Shifts in the dynamics of productivity signal ecosystem state transitions at the biome-scale. *Ecol. Lett.* **2018**, *21*, 1457–1466. [\[CrossRef\]](#)
23. Huxman, T.E.; Smith, M.D.; Fay, P.A.; Knapp, A.K.; Shaw, M.R.; Loik, M.E.; Smith, S.D.; Tissue, D.T.; Zak, J.C.; Weltzin, J.F.; et al. Convergence across biomes to a common rain-use efficiency. *Nature* **2004**, *429*, 651–654. [\[CrossRef\]](#) [\[PubMed\]](#)
24. Liu, Y.; Wu, C.; Liu, L.; Gu, C.; Andrew Black, T.; Jassal, R.S.; Hörtnagl, L.; Montagnani, L.; Moyano, F.; Varlagin, A.; et al. Interannual and spatial variability of net ecosystem production in forests explained by an integrated physiological indicator in summer. *Ecol. Indic.* **2021**, *129*, 107982. [\[CrossRef\]](#)
25. Knapp, A.K.; Ciais, P.; Smith, M.D. Reconciling inconsistencies in precipitation–productivity relationships: Implications for climate change. *New Phytol.* **2017**, *214*, 41–47. [\[CrossRef\]](#) [\[PubMed\]](#)
26. Wilcox, K.R.; Blair, J.M.; Smith, M.D.; Knapp, A.K. Does ecosystem sensitivity to precipitation at the site-level conform to regional-scale predictions? *Ecology* **2016**, *97*, 561–568. [\[CrossRef\]](#)
27. Peng, S.; Piao, S.; Wang, T.; Sun, J.; Shen, Z. Temperature sensitivity of soil respiration in different ecosystems in China. *Soil Biol. Biochem.* **2009**, *41*, 1008–1014. [\[CrossRef\]](#)
28. Zhang, Z.; Li, Y.; Williams, R.A.; Chen, Y.; Peng, R.; Liu, X.; Qi, Y.; Wang, Z. Responses of soil respiration and its sensitivities to temperature and precipitation: A meta-analysis. *Ecol. Inform.* **2023**, *75*, 102057. [\[CrossRef\]](#)
29. Karhu, K.; Auffret, M.D.; Dungait, J.A.J.; Hopkins, D.W.; Prosser, J.I.; Singh, B.K.; Subke, J.-A.; Wookey, P.A.; Ågren, G.I.; Sebastià, M.-T.; et al. Temperature sensitivity of soil respiration rates enhanced by microbial community response. *Nature* **2014**, *513*, 81–84. [\[CrossRef\]](#)
30. Tong, D.; Li, Z.; Xiao, H.; Nie, X.; Liu, C.; Zhou, M. How do soil microbes exert impact on soil respiration and its temperature sensitivity? *Environ. Microbiol.* **2021**, *23*, 3048–3058. [\[CrossRef\]](#) [\[PubMed\]](#)
31. Davidson, E.A.; Janssens, I.A. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* **2006**, *440*, 165–173. [\[CrossRef\]](#)
32. Jiang, M.; Liu, X.; Liu, L. Different Responses of Terrestrial Carbon Fluxes to Environmental Changes in Cold Temperate Forest Ecosystems. *Forests* **2024**, *15*, 1340. [\[CrossRef\]](#)
33. Oleksy, I.A.; Jones, S.E.; Solomon, C.T. Hydrologic Setting Dictates the Sensitivity of Ecosystem Metabolism to Climate Variability in Lakes. *Ecosystems* **2022**, *25*, 1328–1345. [\[CrossRef\]](#)
34. Li, J.-T.; Zhang, Y.; Chen, H.; Sun, H.; Tian, W.; Li, J.; Liu, X.; Zhou, S.; Fang, C.; Li, B.; et al. Low soil moisture suppresses the thermal compensatory response of microbial respiration. *Glob. Chang. Biol.* **2023**, *29*, 874–889. [\[CrossRef\]](#) [\[PubMed\]](#)
35. Orchard, V.A.; Cook, F.J. Relationship between soil respiration and soil moisture. *Soil Biol. Biochem.* **1983**, *15*, 447–453. [\[CrossRef\]](#)
36. Pastorello, G.; Trotta, C.; Canfora, E.; Chu, H.; Christianson, D.; Cheah, Y.-W.; Poindexter, C.; Chen, J.; Elbashandy, A.; Humphrey, M.; et al. The FLUXNET2015 dataset and the ONEFlux processing pipeline for eddy covariance data. *Sci. Data* **2020**, *7*, 225. [\[CrossRef\]](#) [\[PubMed\]](#)
37. Friedl, M.A.; McIver, D.K.; Hodges, J.C.F.; Zhang, X.Y.; Muchoney, D.; Strahler, A.H.; Woodcock, C.E.; Gopal, S.; Schneider, A.; Cooper, A.; et al. Global land cover mapping from MODIS: Algorithms and early results. *Remote Sens. Environ.* **2002**, *83*, 287–302. [\[CrossRef\]](#)
38. Zomer, R.J.; Xu, J.; Trabucco, A. Version 3 of the Global Aridity Index and Potential Evapotranspiration Database. *Sci. Data* **2022**, *9*, 409. [\[CrossRef\]](#) [\[PubMed\]](#)
39. Dai, L.; Yang, Y.; Wang, X. Positive asymmetric responses indicate larger carbon sink with increase in precipitation variability in global terrestrial ecosystems. *Innov. Geosci.* **2024**, *2*, 100060. [\[CrossRef\]](#)
40. Wilcox, K.R.; Shi, Z.; Gherardi, L.A.; Lemoine, N.P.; Koerner, S.E.; Hoover, D.L.; Bork, E.; Byrne, K.M.; Cahill, J., Jr.; Collins, S.L.; et al. Asymmetric responses of primary productivity to precipitation extremes: A synthesis of grassland precipitation manipulation experiments. *Glob. Chang. Biol.* **2017**, *23*, 4376–4385. [\[CrossRef\]](#)
41. Piepho, H.P.; Edmondson, R.N. A tutorial on the statistical analysis of factorial experiments with qualitative and quantitative treatment factor levels. *J. Agron. Crop Sci.* **2018**, *204*, 429–455. [\[CrossRef\]](#)
42. Mann, H.B. Nonparametric tests against trend. *Econom. J. Econom. Soc.* **1945**, *13*, 245–259. [\[CrossRef\]](#)
43. Kendall, M.G. *Rank Correlation Methods*; Griffin: London, UK, 1948.
44. Zhang, F.; Quan, Q.; Ma, F.; Tian, D.; Zhou, Q.; Niu, S. Differential responses of ecosystem carbon flux components to experimental precipitation gradient in an alpine meadow. *Funct. Ecol.* **2019**, *33*, 889–900. [\[CrossRef\]](#)
45. Sharkey, T.D. Advances in photosynthesis and respiration. *Photosynth. Res.* **2012**, *111*, 327–329. [\[CrossRef\]](#)
46. Yamori, W. Chapter 12—Photosynthesis and respiration. In *Plant Factory*, 2nd ed.; Kozai, T., Niu, G., Takagaki, M., Eds.; Academic Press: Cambridge, MA, USA, 2020; pp. 197–206. [\[CrossRef\]](#)

47. Atkin, O.K.; Millar, A.H.; Gardeström, P.; Day, D.A. Photosynthesis, Carbohydrate Metabolism and Respiration in Leaves of Higher Plants. In *Photosynthesis: Physiology and Metabolism*; Leegood, R.C., Sharkey, T.D., von Caemmerer, S., Eds.; Springer: Dordrecht, The Netherlands, 2000; pp. 153–175. [\[CrossRef\]](#)
48. Noguchi, K.; Yoshida, K. Interaction between photosynthesis and respiration in illuminated leaves. *Mitochondrion* **2008**, *8*, 87–99. [\[CrossRef\]](#)
49. Chaves, M.M. Effects of water deficits on carbon assimilation. *J. Exp. Bot.* **1991**, *42*, 1–16. [\[CrossRef\]](#)
50. Cornic, G.; Massacci, A. Leaf Photosynthesis Under Drought Stress. In *Photosynthesis and the Environment*; Baker, N.R., Ed.; Springer: Dordrecht, The Netherlands, 1996; pp. 347–366. [\[CrossRef\]](#)
51. Pirasteh-Anosheh, H.; Saed-Moucheshi, A.; Pakniyat, H.; Pessarakli, M. Stomatal responses to drought stress. In *Water Stress and Crop Plants*; John Wiley & Sons, Ltd.: Hoboken, NJ, USA, 2016; pp. 24–40. [\[CrossRef\]](#)
52. Baldocchi, D.; Sturtevant, C.; Contributors, F. Does day and night sampling reduce spurious correlation between canopy photosynthesis and ecosystem respiration? *Agric. For. Meteorol.* **2015**, *207*, 117–126. [\[CrossRef\]](#)
53. Chen, Z.; Yu, G.; Zhu, X.; Wang, Q.; Niu, S.; Hu, Z. Covariation between gross primary production and ecosystem respiration across space and the underlying mechanisms: A global synthesis. *Agric. For. Meteorol.* **2015**, *203*, 180–190. [\[CrossRef\]](#)
54. Li, G.; Han, H.; Du, Y.; Hui, D.; Xia, J.; Niu, S.; Li, X.; Wan, S. Effects of warming and increased precipitation on net ecosystem productivity: A long-term manipulative experiment in a semiarid grassland. *Agric. For. Meteorol.* **2017**, *232*, 359–366. [\[CrossRef\]](#)
55. Niu, S.; Wu, M.; Han, Y.; Xia, J.; Li, L.; Wan, S. Water-mediated responses of ecosystem carbon fluxes to climatic change in a temperate steppe. *New Phytol.* **2008**, *177*, 209–219. [\[CrossRef\]](#)
56. Resco, V.; Ignace, D.D.; Sun, W.; Huxman, T.E.; Weltzin, J.F.; Williams, D.G. Chlorophyll fluorescence, predawn water potential and photosynthesis in precipitation pulse-driven ecosystems—implications for ecological studies. *Funct. Ecol.* **2008**, *22*, 479–483. [\[CrossRef\]](#)
57. Stefanski, A.; Bermudez, R.; Sendall, K.M.; Montgomery, R.A.; Reich, P.B. Surprising lack of sensitivity of biochemical limitation of photosynthesis of nine tree species to open-air experimental warming and reduced rainfall in a southern boreal forest. *Glob. Change Biol.* **2020**, *26*, 746–759. [\[CrossRef\]](#) [\[PubMed\]](#)
58. Shi, Z.; Thomey, M.L.; Mowll, W.; Litvak, M.; Brunsell, N.A.; Collins, S.L.; Pockman, W.T.; Smith, M.D.; Knapp, A.K.; Luo, Y. Differential effects of extreme drought on production and respiration: Synthesis and modeling analysis. *Biogeosciences* **2014**, *11*, 621–633. [\[CrossRef\]](#)
59. Flexas, J.; Bota, J.; Escalona, J.M.; Sampol, B.; Medrano, H. Effects of drought on photosynthesis in grapevines under field conditions: An evaluation of stomatal and mesophyll limitations. *Funct. Plant Biol.* **2002**, *29*, 461–471. [\[CrossRef\]](#) [\[PubMed\]](#)
60. Cavender-Bares, J.; Bazzaz, F.A. From Leaves to Ecosystems: Using Chlorophyll Fluorescence to Assess Photosynthesis and Plant function in Ecological Studies. In *Chlorophyll a Fluorescence: A Signature of Photosynthesis*; Papageorgiou, G.C., Govindjee, Eds.; Springer: Dordrecht, The Netherlands, 2004; pp. 737–755. [\[CrossRef\]](#)
61. Bell, C.W.; Acosta-Martinez, V.; McIntyre, N.E.; Cox, S.; Tissue, D.T.; Zak, J.C. Linking Microbial Community Structure and Function to Seasonal Differences in Soil Moisture and Temperature in a Chihuahuan Desert Grassland. *Microb. Ecol.* **2009**, *58*, 827–842. [\[CrossRef\]](#)
62. Chen, S.; Lin, G.; Huang, J.; Jenerette, G.D. Dependence of carbon sequestration on the differential responses of ecosystem photosynthesis and respiration to rain pulses in a semiarid steppe. *Glob. Change Biol.* **2009**, *15*, 2450–2461. [\[CrossRef\]](#)
63. Moyano, F.E.; Manzoni, S.; Chenu, C. Responses of soil heterotrophic respiration to moisture availability: An exploration of processes and models. *Soil Biol. Biochem.* **2013**, *59*, 72–85. [\[CrossRef\]](#)
64. Knapp, A.K.; Briggs, J.M.; Koelliker, J.K. Frequency and Extent of Water Limitation to Primary Production in a Mesic Temperate Grassland. *Ecosystems* **2001**, *4*, 19–28. [\[CrossRef\]](#)
65. Niu, B.; Zhang, X.; Piao, S.; Janssens, I.A.; Fu, G.; He, Y.; Zhang, Y.; Shi, P.; Dai, E.; Yu, C.; et al. Warming homogenizes apparent temperature sensitivity of ecosystem respiration. *Sci. Adv.* **2021**, *7*, eabc7358. [\[CrossRef\]](#)
66. Sala, O.E.; Gherardi, L.A.; Reichmann, L.; Jobbágy, E.; Peters, D. Legacies of precipitation fluctuations on primary production: Theory and data synthesis. *Philos. Trans. R. Soc. B Biol. Sci.* **2012**, *367*, 3135–3144. [\[CrossRef\]](#)
67. Berdugo, M.; Vidiella, B.; Solé, R.V.; Maestre, F.T. Ecological mechanisms underlying aridity thresholds in global drylands. *Funct. Ecol.* **2022**, *36*, 4–23. [\[CrossRef\]](#)
68. Running, S.W.; Nemani, R.R.; Heinsch, F.A.; Zhao, M.; Reeves, M.; Hashimoto, H. A continuous satellite-derived measure of global terrestrial primary production. *Bioscience* **2004**, *54*, 547–560. [\[CrossRef\]](#)
69. Bai, Y.; Zha, T.; Bourque, C.P.-A.; Jia, X.; Ma, J.; Liu, P.; Yang, R.; Li, C.; Du, T.; Wu, Y. Variation in ecosystem water use efficiency along a southwest-to-northeast aridity gradient in China. *Ecol. Indic.* **2020**, *110*, 105932. [\[CrossRef\]](#)
70. Dalling, J.W.; Heineman, K.; Lopez, O.R.; Wright, S.J.; Turner, B.L. Nutrient Availability in Tropical Rain Forests: The Paradigm of Phosphorus Limitation. In *Tropical Tree Physiology*; Goldstein, G., Santiago, L.S., Eds.; Springer International Publishing: Cham, Switzerland, 2016; Volume 6, pp. 261–273. [\[CrossRef\]](#)

71. Knapp, A.K.; Smith, M.D. Variation Among Biomes in Temporal Dynamics of Aboveground Primary Production. *Science* **2001**, *291*, 481–484. [[CrossRef](#)] [[PubMed](#)]
72. Ahlström, A.; Raupach, M.R.; Schurgers, G.; Smith, B.; Arneth, A.; Jung, M.; Reichstein, M.; Canadell, J.G.; Friedlingstein, P.; Jain, A.K.; et al. The dominant role of semi-arid ecosystems in the trend and variability of the land CO₂ sink. *Science* **2015**, *348*, 895–899. [[CrossRef](#)] [[PubMed](#)]
73. Rudgers, J.A.; Chung, Y.A.; Maurer, G.E.; Moore, D.I.; Muldavin, E.H.; Litvak, M.E.; Collins, S.L. Climate sensitivity functions and net primary production: A framework for incorporating climate mean and variability. *Ecology* **2018**, *99*, 576–582. [[CrossRef](#)] [[PubMed](#)]
74. Knapp, A.K.; Carroll, C.J.W.; Denton, E.M.; La Pierre, K.J.; Collins, S.L.; Smith, M.D. Differential sensitivity to regional-scale drought in six central US grasslands. *Oecologia* **2015**, *177*, 949–957. [[CrossRef](#)] [[PubMed](#)]
75. Vereecken, H.; Kama, T.; Harter, T.; Kasteel, R.; Hopmans, J.; Vanderborght, J. Explaining soil moisture variability as a function of mean soil moisture: A stochastic unsaturated flow perspective. *Geophys. Res. Lett.* **2007**, *34*, 2007GL031813. [[CrossRef](#)]
76. Caldwell, M.M.; Richards, J.H. Hydraulic lift: Water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia* **1989**, *79*, 1–5. [[CrossRef](#)] [[PubMed](#)]
77. Lindh, M.; Zhang, L.; Falster, D.; Franklin, O.; Brännström, Å. Plant diversity and drought: The role of deep roots. *Ecol. Model.* **2014**, *290*, 85–93. [[CrossRef](#)]
78. Lambert, F.H.; Stine, A.R.; Krakauer, N.Y.; Chiang, J.C.H. How Much Will Precipitation Increase With Global Warming? *Eos Trans. Am. Geophys. Union* **2008**, *89*, 193–194. [[CrossRef](#)]
79. Piao, S.; Fang, J.; Zhou, L.; Ciais, P.; Zhu, B. Variations in satellite-derived phenology in China's temperate vegetation. *Glob. Chang. Biol.* **2006**, *12*, 672–685. [[CrossRef](#)]
80. Sitch, S.; Friedlingstein, P.; Gruber, N.; Jones, S.D.; Murray-Tortarolo, G.; Ahlström, A.; Doney, S.C.; Graven, H.; Heinze, C.; Huntingford, C.; et al. Recent trends and drivers of regional sources and sinks of carbon dioxide. *Biogeosciences* **2015**, *12*, 653–679. [[CrossRef](#)]
81. Yan, Y.; Piao, S.; Hammond, W.M.; Chen, A.; Hong, S.; Xu, H.; Munson, S.M.; Myneni, R.B.; Allen, C.D. Climate-induced tree-mortality pulses are obscured by broad-scale and long-term greening. *Nat. Ecol. Evol.* **2024**, *8*, 912–923. [[CrossRef](#)] [[PubMed](#)]
82. Jiao, W.; Wang, L.; Smith, W.K.; Chang, Q.; Wang, H.; D'Odorico, P. Observed increasing water constraint on vegetation growth over the last three decades. *Nat. Commun.* **2021**, *12*, 3777. [[CrossRef](#)] [[PubMed](#)]
83. Keenan, T.F.; Hollinger, D.Y.; Bohrer, G.; Dragoni, D.; Munger, J.W.; Schmid, H.P.; Richardson, A.D. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. *Nature* **2013**, *499*, 324–327. [[CrossRef](#)]
84. Turner, M.G. Disturbance and landscape dynamics in a changing world. *Ecology* **2010**, *91*, 2833–2849. [[CrossRef](#)] [[PubMed](#)]
85. Jiang, H.; Deng, Q.; Zhou, G.; Hui, D.; Zhang, D.; Liu, S.; Chu, G.; Li, J. Responses of soil respiration and its temperature/moisture sensitivity to precipitation in three subtropical forests in southern China. *Biogeosciences* **2013**, *10*, 3963–3982. [[CrossRef](#)]
86. Du, Y.; Wang, Y.-P.; Su, F.; Jiang, J.; Wang, C.; Yu, M.; Yan, J. The response of soil respiration to precipitation change is asymmetric and differs between grasslands and forests. *Glob. Change Biol.* **2020**, *26*, 6015–6024. [[CrossRef](#)]
87. Ehleringer, J.R.; Monson, R.K. Evolutionary and Ecological Aspects of Photosynthetic Pathway Variation. *Annu. Rev. Ecol. Syst.* **1993**, *24*, 411–439. [[CrossRef](#)]
88. Campioli, M.; Malhi, Y.; Vicca, S.; Luyssaert, S.; Papale, D.; Peñuelas, J.; Reichstein, M.; Migliavacca, M.; Arain, M.A.; Janssens, I.A. Evaluating the convergence between eddy-covariance and biometric methods for assessing carbon budgets of forests. *Nat. Commun.* **2016**, *7*, 13717. [[CrossRef](#)]
89. Reichstein, M.; Falge, E.; Baldocchi, D.; Papale, D.; Aubinet, M.; Berbigier, P.; Bernhofer, C.; Buchmann, N.; Gilmanov, T.; Granier, A.; et al. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: Review and improved algorithm. *Glob. Chang. Biol.* **2005**, *11*, 1424–1439. [[CrossRef](#)]
90. Lasslop, G.; Reichstein, M.; Papale, D.; Richardson, A.D.; Arneth, A.; Barr, A.; Stoy, P.; Wohlfahrt, G. Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: Critical issues and global evaluation. *Glob. Chang. Biol.* **2010**, *16*, 187–208. [[CrossRef](#)]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.