

1 **Variations in diurnal and seasonal net ecosystem carbon dioxide**
2 **exchange in a semiarid sandy grassland ecosystem in China's Horqin**
3 **Sandy Land**

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16

17 Abstract

18 Grasslands are major terrestrial ecosystems in arid and semiarid regions, and play
19 important roles in the regional carbon dioxide (CO₂) balance and cycles. Sandy
20 grasslands are sensitive to climate change, yet the magnitudes, patterns, and
21 environmental controls of their CO₂ flows are poorly understood. Here, we report the
22 results from continuous year-round **CO₂ flux measurements** in 5 years from a sandy
23 grassland in China's Horqin Sandy Land. The grassland was a net CO₂ source at an
24 annual scale, with a mean annual net ecosystem CO₂ exchange (NEE) of $49 \pm 8 \text{ g C m}^{-2}$
25 yr^{-1} in the years for which a complete dataset was available (2015, 2016, and 2018);
26 **Annual precipitation had the strongest effect on annual NEE. The grassland's carbon**
27 **sequestration increased with increasing precipitation. In the spring, NEE increased with**
28 **increasing soil temperature (T_{soil}) and increasing precipitation. In the summer, NEE was**
29 **dominated by the frequency and amount of effective precipitation events. In the autumn,**
30 **NEE increased with increasing T_{soil} and near-surface soil water content (SWC), but**
31 **decreased with increased SWC deeper in the soil. In the winter, NEE decreased with**
32 **increasing T_{soil} and SWC. The sandy grassland was a net annual CO₂ source at an annual**
33 **scale. On the one hand, this is because drought decreased carbon sequestration by the**
34 **annual plants. On the other hand, the study site is recovering from degradation, so**
35 **vegetation productivity is still low.** Therefore, the ecosystem has not yet transitioned to
36 a CO₂ sink and long-term observations will be necessary to reveal the true source or
37 sink intensity and its response to environmental and biological factors.

38 **Keywords:** Net ecosystem CO₂ exchange (NEE); Gross primary productivity (GPP);
39 ecosystem respiration (R_{ec}); Eddy covariance; Horqin Sandy Land

40 1 Introduction

41 Arid and semiarid ecosystems cover 30 to 40 % of the global terrestrial surface
42 (Poulter et al., 2014). The extent and distribution of these areas are increasing in
43 response to factors such as climate change, changes in wildfire frequency and intensity,
44 and changes in land use (Asner et al., 2003; Hastings et al., 2010). These ecosystems
45 are important because they account for 30 to 35 % of terrestrial net primary productivity

46 (Gao et al., 2012; Liu et al., 2016a) and approximately 15 % of the global soil organic
47 carbon pool (Lal, 2004; Liu et al., 2016a). Thus, these areas are important contributors
48 to the global carbon budget due to their wide distribution (Emmerich, 2003; Noso et
49 al., 2006; Poulter et al., 2014; Zhou et al., 2020), and arid and semiarid ecosystems will
50 have significant effects on the global carbon cycle and carbon balance (Lal, 2004;
51 Biederman et al., 2017). However, the availability of continuous, long-term
52 measurements of water and net ecosystem CO₂ exchange (NEE) has lagged in arid and
53 semiarid ecosystems (Baldocchi et al., 2001; Hastings et al., 2010; Biederman et al.,
54 2017). Recent research on the relationship between NEE and water in drylands has
55 focused on the southwestern United States (Scott et al., 2015; Biederman et al., 2016,
56 2017) and Australia (Cleverly et al., 2016; Li et al., 2017). For instance, Biederman et
57 al. (2016) showed that across a climatic and ecological gradient in semiarid North
58 American ecosystems, photosynthesis showed a saturating spatial relationship to
59 precipitation, and evapotranspiration was a better proxy for the water available to drive
60 NEE after accounting for hydrologic losses. Both photosynthesis and respiration
61 showed similar site-level sensitivity to interannual changes in evapotranspiration
62 among the studied ecosystems. Compared with the more constant sink that is typically
63 measured in mesic ecosystems, dryland ecosystems showed a wide range of carbon sink
64 or source functions for diverse vegetation types (Biederman et al., 2017). However, to
65 our knowledge, there has been no report on the intra-annual and interannual variation
66 of ecosystem-scale NEE and its components in China's Horqin Sandy Land, an
67 important dryland ecosystem in northern China.

68 Desertification occurs in more than two-thirds of the area of arid and semiarid
69 ecosystems (Lal, 2001). This may cause a serious imbalance in the structure and
70 function of these ecosystems (Huenneke et al., 2002; Vest et al., 2011), especially in
71 terms of whether the ecosystem functions as a carbon source or sink (Shachak et al.,
72 1998; Gang et al., 2011). Grazing exclusion is a common method used to combat
73 desertification in the world's arid and semiarid areas (Mureithi et al., 2010; Sousa et al.,
74 2012). For example, Sun et al. (2015) suggested that proper enclosures promoted the

75 recovery of degraded sandy grassland and more sustainable use of sandy grassland
76 resources.

77 The Horqin Sandy Land is the largest sandy land in China, and nearly 80 % of the
78 area has been desertified (Li et al., 2019). Here, we define “sandy land” as land covered
79 by a sandy soil, with a vegetation cover less than 5%, which includes areas of sandy
80 desert (Yan et al., 2003). Sandy land includes multiple overlapping ecotones, including
81 transition zones between areas with different population pressures, between semi-
82 humid and semiarid areas, and in typical agro-pastoral ecotones. The ecological
83 environment is fragile and extremely sensitive to climate change and human activities
84 (Bagan et al., 2010; Zhao et al., 2015). The region’s sandy grassland grows on aeolian
85 sandy soils or areas with sandy soils as the substrate, and is typical of the grassland
86 vegetation that develops in sandy land (Munkhdalai et al., 2007). This grassland
87 ecosystem is widespread in the Horqin Sandy Land (Zhao et al., 2007).

88 Research showed that the restoration of degraded sandy grassland can increase its
89 productivity and carbon sequestration, and that the ecosystem can begin to act as a
90 carbon sink (Ruiz-Jaen and Aide, 2005; Zhao et al., 2016). However, other studies
91 showed that it was a carbon source (Li et al., 2012; Niu et al., 2018). There have been
92 relatively few long-term studies of sandy grassland at the ecosystem level, so we do not
93 yet fully understand the characteristic of NEE and its components, gross primary
94 productivity (GPP) and ecosystem respiration (R_{ec}), at an ecosystem scale, particularly
95 for sandy grassland protected by grazing exclosures, and more data are needed,
96 particularly for semiarid sandy land (Barrett, 1968; Czobel et al., 2012).

97 Precipitation is one of the factors that most strongly affects NEE in arid and semiarid
98 areas (Scott et al. 2015; Biederman et al. 2016). Slight changes to the amount and
99 frequency of precipitation may trigger complex interactions among biochemical
100 processes at the ecosystem level (Emmerich and Verdugo, 2008; Cleverly et al., 2016).
101 Small precipitation amounts can improve the near-surface (<10 cm) soil water content
102 (SWC) and stimulate ecosystem carbon emission, mainly by promoting microbial
103 respiration, in arid and semiarid areas (Schwinning and Sala, 2004). Larger

104 precipitation amounts can increase SWC in deeper levels of the soil and trigger
105 sequestration processes (Hao et al., 2010). To better understand the effects of
106 precipitation on NEE, we asked the following question: Is there a threshold of “effective
107 precipitation” that determines whether ecosystem carbon fluxes will lead to net
108 sequestration or net emission in sandy grasslands?

109 Precipitation is characterized by discrete events in arid and semiarid regions, with
110 high variability in the amount, duration, and frequency of precipitation at intra-annual
111 (e.g., seasonal) and inter-annual scales (Hao et al., 2010; Ponce Campos et al., 2013).
112 These discrete and largely unpredictable events may lead to pulsed availability of soil
113 water and nutrients, with both spatial and temporal variation (Zhao and Liu, 2011). The
114 response of photosynthesis and respiration to precipitation is seasonally specific
115 because of differences in the depth of soil water infiltration and because these processes
116 differ in their sensitivity to temperature (Li and Zhou, 2012). Spring and autumn
117 precipitation are important controls on the beginning and end dates of the growing
118 season, so the ability of these events to change carbon accumulation or emission should
119 not be ignored, especially in semiarid and arid regions (Prev éy et al., 2014; Shen et al.,
120 2015). This is particularly true when relatively low temperatures limit soil microbial
121 respiration during certain periods (Knorr et al., 2005). Summer precipitation is thought
122 to primarily influence shallow soil moisture, thereby stimulating the activity of
123 shallowly rooted plants, whereas a combination of high temperatures and high soil
124 moisture stimulate the respiratory response by soil microbes (Sponseller, 2006). The
125 amount and frequency of summer precipitation may therefore play an important role in
126 regulating inter-annual variations of the ecosystem carbon balance (Scott et al., 2009;
127 Wu et al., 2012). Moreover, we found no reports on the response of ecosystem-scale
128 NEE and its components to seasonal and annual precipitation, and the response
129 mechanisms are uncertain for the sandy grassland in the Horqin region. Therefore, long-
130 term data are required to fully understand how changes in seasonal and annual
131 precipitation influence NEE, GPP, and R_{ec} in grassland ecosystems such as those in the
132 Horqin Sandy Land. Understanding the consequences of climate change that are

133 associated with changes in precipitation patterns, and that affect soil water regimes,
134 may be critical for developing strategies to preserve or restore these sandy grasslands.

135 In this paper, we present the results from continuous (14 September 2014 to 31
136 December 2018) *in situ* monitoring of CO₂ dynamics in the Horqin Sandy Land's sandy
137 grassland using the eddy covariance technique, and quantify the temporal variation of
138 NEE and the factors that control it. We had the following goals: (1) To quantify the
139 annual, seasonal, and diurnal variation in NEE, GPP, and R_{ec}. We hypothesized that the
140 sandy grassland is a carbon source at the ecosystem scale, because the sandy grassland
141 is dominated by annual plants that are vulnerable to drought (Li et al., 2016; Kang et
142 al., 2018), and because the ecosystem is recovering from degradation, leading to low
143 vegetation productivity (Sun et al., 2015). (2) To explore the effects of changes in
144 precipitation amount and frequency on seasonal and annual NEE, GPP, and R_{ec}. Based
145 on the response thresholds of shrubs and herbs to precipitation in arid and semiarid
146 areas (Hao et al., 2010; Zhou et al., 2020), we hypothesized that an “effective
147 precipitation” threshold would exist at around 5 mm, which could alter soil moisture in
148 deeper layer and affect carbon fluxes in the sandy grassland ecosystem. We also
149 hypothesized that spring, summer, and autumn precipitation would have different
150 impacts on the ecosystem CO₂ exchange through differential effects on plant
151 photosynthesis and soil microbial respiration (Scott et al., 2009).

152 **2 Materials and methods**

153 **2.1 Experimental site**

154 Our study was conducted in a sandy grassland in the southern part of the Horqin
155 Sandy Land, Inner Mongolia, China, at the Naiman Desertification Research Station of
156 the Chinese Academy of Sciences (42°55' N, 120°42' E) (Fig. 1). The terrain is flat,
157 and it evolved from reclamation of sandy grassland for agriculture to severe
158 desertification, after which cultivation was abandoned and grazing exclosures were
159 established to allow natural recovery of the vegetation, starting in 1985 (Zhao et al.,
160 2007). Thus, the grassland had been recovering naturally for nearly 30 years when our
161 study began. At an elevation of 377 m a.s.l., the study area has a continental semiarid

162 monsoon temperate climate regime. The mean annual temperature is 6.8 °C, with mean
163 monthly temperatures ranging from -9.63 °C in January to 24.58 °C in July. Average
164 annual precipitation is approximately 360 mm, with 70 % of the precipitation occurring
165 during the growing season, between June and August. Annual mean potential
166 evaporation is approximately 1973 mm. The annual frost-free period is 130 to 150 days.
167 The **most common soil type in the study region** is a sandy chestnut soil, but most of the
168 soil has been degraded by a combination of climate change and anthropogenic activity
169 (unsustainable grazing or agriculture) into an aeolian sandy soil under the action of
170 wind erosion (Zhao et al., 2007), with coarse sand, fine sand, and clay-silt contents of
171 92.7, 3.3, and 4.0 % in the topsoil to a depth of 20 cm. The contents of soil organic
172 carbon and total nitrogen were 1.27 and 0.21 g kg⁻¹, respectively. Vegetation cover in
173 the study area ranged from 50 to 70 %. The dominant plant species were annual herbs,
174 including *Artemisia scoparia*, *Setaria viridis*, *Salsola collina*, and *Corispermum*
175 *hysopifolium* (Niu et al., 2018).

176 **2.2 Eddy covariance observations**

177 An eddy covariance flux tower (2.0 m high) was installed at the center of the
178 observation field (Fig. 1b, c). We have continuously monitored CO₂, water, and heat
179 fluxes at the tower using the eddy covariance system since late 2014. **The site was flat**
180 **and comprised homogeneous vegetation. The upwind fetch was about 200 m under**
181 **unstable atmospheric conditions, which was greater than the flux footprint** (Schmid,
182 1997; Xu and Baldocchi, 2004). The eddy covariance system consisted of an LI-7500
183 infrared gas analyzer (Li-Cor Inc., Lincoln, NE, USA), with a precision of 0.01 μmol
184 m⁻² s⁻¹ and an accuracy within 1 % of the reading for measurements at 30-min mean
185 intervals, and a CSAT-3 three-dimensional ultrasonic anemometer (Campbell Scientific,
186 Inc., Logan, UT, USA), with a precision of 0.1 °C and an accuracy of 1 % for the
187 readings at 30-min mean intervals. Raw 10-Hz data were recorded by a CR3000
188 datalogger (Campbell Scientific, Logan, UT, USA). The operation, calibration, and
189 maintenance of the eddy covariance system followed the manufacturers' standard
190 procedures. The LI-7500 was calibrated every 6 months for CO₂, water vapor, and dew

191 point values using calibration gases and dew point generator measurements supported
192 by the China Land–Atmosphere Coordinated Observation System (Yun et al., 2018).
193 We cleaned the mirror of the LI-7500 every 15 days to maintain the automatic gain
194 control value below its threshold (55 to 65). All of the instruments were powered by
195 solar panels connected to a battery.

196 **2.3 Micrometeorological measurements**

197 Along with the flux measurements obtained by the eddy covariance equipment, we
198 measured standard meteorological and soil parameters continuously with an array of
199 sensors. A propeller anemometer was installed at the top of the meteorological tower to
200 measure the wind speed and direction. Net solar radiation (R_n , $W\ m^{-2}$) was measured
201 by a four-component radiometer (CNR-1, Kipp and Zonen, Delft, the Netherlands)
202 installed at 1 m above the ground. The air temperature (T_{air} , °C) and relative humidity
203 (%) instruments (HMP45C, Vaisala Inc., Helsinki, Finland) were mounted at 2 m above
204 the ground to measure the T_{air} , relative humidity, and atmospheric pressure (kPa).
205 Precipitation (mm) measurements were obtained from a meteorological station 400 m
206 from the study site. **Total daily precipitation was treated as a single event rather than a**
207 **series of events. The daily events were separated into size classes for evaluation of the**
208 **number of events per class and the effect on CO₂ fluxes (Emmerich and Verdugo, 2008).**

209 We installed five CS109 temperature probes (Campbell Scientific) and five CS616
210 moisture probes (Campbell Scientific) in the soil at depths of 10, 20, 30, 40, and 50 cm
211 to measure soil temperature (T_{soil} , °C) and soil water content (SWC, %). Two self-
212 calibrating HFP01 soil heat flux (SHF, $W\ m^{-2}$) sensors (Hukseflux, Delft, the
213 Netherlands) were buried 5 and 10 cm below the ground to obtain the SHF data. All of
214 the environmental parameters were measured simultaneously with the eddy covariance
215 measurements, and all data were recorded as 30-min mean values with a CR3000
216 datalogger.

217 **2.4 Data quality and gap-filling method**

218 We used the EddyPro 6.2.0 software (Li-Cor, Lincoln, NE, USA) to process the 10-
219 Hz raw eddy covariance data. Processing included spike removal, lag correction,

220 secondary coordinate rotation, Webb–Pearman–Leuning correction, and sonic virtual
221 temperature conversion (Webb et al., 1980). We used the data processing method of Lee
222 et al. (2004) to process the 30-min mean raw flux measurements to ensure their quality.
223 Processed data were further corrected for weather effects and sensor uncertainty using
224 the following procedure: (1) We removed data gathered during precipitation events,
225 power failures, and sensor maintenance or malfunction. (2) We excluded unrealistic
226 CO₂ flux data (values outside the range of –2.0 to 2.0 mg CO₂ m⁻² s⁻¹). (3) **We rejected**
227 **data collected during periods of insufficient turbulent mixing using a friction-velocity**
228 **filter ($u^* < 0.1 \text{ m s}^{-1}$) for data collected at night (Reichstein et al., 2005; Scott et al.,**
229 **2009).** Based on the R_n, NEE was classified as the daytime exchange (NEE_{day}; R_n ≥ 1
230 W m⁻²) or the night-time exchange (NEE_{night}; R_n < 1 W m⁻²). This screening resulted in
231 the rejection of 20 to 30 % of the flux data, depending on the period.

232 We used several strategies to compensate for missing data. We used linear
233 interpolation to fill gaps that were shorter than 2 h. For longer gaps, we handled the gap
234 in the NEE_{day} using the mean diurnal variation with a 7-day window (Falge et al., 2001),
235 and handled the gap in the NEE_{night} **using the following equation 1, the parameter values**
236 **were calculated with a 7-day moving window using version 22 of the SPSS software**
237 **(IBM, Armonk, NY, USA) (Lloyd and Taylor, 1994; Reichstein et al., 2005).**

$$238 \quad \text{NEE}_{\text{night}} = R_0 \exp(b T_{10}) \quad (1)$$

239 R₀ is the base ecosystem respiration rate when the soil temperature is 0 °C, b is an
240 empirically determined coefficient, and T₁₀ is the soil temperature at a depth of 10 cm.
241 Daytime ecosystem respiration can be estimated by extrapolation from the
242 parameterization derived from Eq. (1). We did not attempt to fill in gaps longer than 7
243 days, and treated those gaps as missing data. Gross primary productivity (GPP) was
244 obtained as follows:

$$245 \quad \text{GPP} = R_{\text{ec}} - \text{NEE} \quad (2)$$

246 **We used the standard sign convention for NEE, with NEE > 0 indicating a net loss**
247 **of CO₂ to the atmosphere (source) and NEE < 0 indicating net CO₂ uptake by the**
248 **ecosystem (sink).**

249 We evaluated the data quality based on the degree of energy closure (sensible heat
250 + latent heat – net radiation – soil heat flux). The energy closure values for the sandy
251 grassland from 2015 to 2018 were 86.5, 82.1, 57.7, and 85.2 %, respectively.

252 **2.5 Statistical analyses**

253 We performed correlation analysis (Pearson's r) and **regression analysis** using the
254 SPSS software. Unless otherwise noted, we defined statistical significance at $p < 0.05$.
255 Pearson's r was applied to confirm the strength of the relationships between parameters.
256 Before **regression analysis**, we tested for collinearity (using a variance inflation factor
257 of $0 < VIF < 10$) using the Kaiser–Meyer–Olkin (KMO) test and Bartlett's sphericity
258 test. Collinearity was used to repartition the T_{soil} and SWC data. We considered KMO
259 values > 0.50 and $p < 0.05$ for Bartlett's sphericity test to indicate acceptable data (Hair
260 et al., 2005). The KMO value ranged from 0.52 to 0.78 and $p < 0.001$ for all Bartlett's
261 sphericity test results for our data.

262 **3 Results**

263 **3.1 Meteorological conditions**

264 **Figures S1 to S5 show the diurnal and seasonal variation of the meteorological**
265 **factors during the observation period. The mean daily T_{air} , R_n , SHF at all depths, and**
266 **T_{soil} at depths of 10, 20, 30, 40, and 50 cm showed unimodal seasonal variations in all**
267 **4 years. These parameters were therefore largely stable and did not differ greatly**
268 **between years, except for the precipitation and SWC at all depths (Fig. S4b). Thus,**
269 **precipitation and SWC were the main factors that influenced NEE, and we focused on**
270 **them in our analysis. The annual precipitation totaled 212 mm in 2015, 277 mm in 2016,**
271 **313 mm in 2017, and 351 mm in 2018 (Fig. S4b). Yearly and seasonal variability in the**
272 **total number of precipitation events and number of precipitation events within each size**
273 **class was large, and the 0 to 5 mm size class was by far the dominant size class (Table**
274 **1). Zhao and Liu (2010) showed that precipitation less than 5 mm in arid and semiarid**
275 **areas changes SWC primarily in the near-surface soil, and that precipitation events**
276 **greater than 5 mm can effectively supplement root layer moisture at greater depths; it**
277 **is therefore called “effective precipitation”. Our result was consistent with this view**

278 (Fig. 2). The essence of effective precipitation is that precipitation enters the soil below
279 the surface layer, and becomes part of the soil water; that soil water is used either
280 directly or indirectly by the vegetation, and has an impact on other ecological links
281 (Joseph Turk et al., 2012). Therefore, we studied the influence of precipitation on NEE
282 and its components in each season from the perspective of SWC. The climate was drier
283 in 2015, 2016, and 2017 than in a normal year (based on the mean annual precipitation
284 of 360 mm from 1960 to 2014), whereas 2018 was close to a normal year. The variation
285 in soil water content was related to precipitation patterns. During the spring (March,
286 April, and May), precipitation was relatively abundant, with mean precipitation of
287 about 42 mm, which accounted for 12 to 20 % of the total annual precipitation. The
288 majority of the precipitation (about 65 %) occurred in the summer (June, July, and
289 August), with mean precipitation of about 197 mm. The autumn (September, October,
290 and November) precipitation was similar to that in spring, with a mean precipitation of
291 about 49 mm, which accounted for 14 to 23 % of the annual total. During the winter
292 (December, January, and February), the mean precipitation of 0.6 mm accounted for
293 only 1 to 6 % of the annual total, and was largely stable, with small differences among
294 the years.

295 **3.2 Annual, seasonal, and diurnal variability of NEE, GPP and R_{ec} .**

296 We also observed clear seasonal variations in daily mean NEE, GPP, and R_{ec} from
297 2014 to 2018 (Fig. 3). Our results suggests that the sandy grassland was a net CO₂
298 source, with an annual mean NEE, GPP, and R_{ec} of 49 ± 8 , 303 ± 29 , and 352 ± 21 g C
299 $m^{-2} yr^{-1}$, respectively, in the years for which a complete dataset was available (2015,
300 2016, and 2018) (Fig. 3f). (We omitted 2017 from this calculation because of large gaps
301 in the data, described below.) NEE ranged from 35 g C $m^{-2} yr^{-1}$ in 2018 to 63 g C m^{-2}
302 yr^{-1} in 2015, whereas GPP ranged from 256 g C $m^{-2} yr^{-1}$ in 2015 to 356 g C $m^{-2} yr^{-1}$ in
303 2018 and R_{ec} ranged from 319 g C $m^{-2} yr^{-1}$ in 2015 to 391 g C $m^{-2} yr^{-1}$ in 2018. From
304 15 September to 23 December 2014, we measured a cumulative carbon release of 47 g
305 C m^{-2} , with cumulative GPP and R_{ec} of 25 and 72 g C m^{-2} , respectively. From 15
306 February to 26 April 2017 and from 14 October to 6 November 2017, approximately 3

307 months of data were missing due to instrument maintenance and calibration, and the
308 cumulative NEE, GPP, and R_{ec} were 64, 274, and 338 g C m⁻², respectively, for the
309 remaining 9 months of the year. Note that the periods covered by the data are therefore
310 not identical.

311 Figures 4 and 5 show the seasonal NEE, GPP, and R_{ec} and their diurnal cycles,
312 respectively. In the spring, the sandy grassland was an atmospheric CO₂ source in all
313 years, with NEE, GPP, and R_{ec} averaging 0.14 ± 0.04 , 0.60 ± 0.06 , and 0.74 ± 0.02 g C
314 m⁻² d⁻¹, respectively (Fig. 4a). The diurnal NEE cycle was characterized by a single
315 peak, and between 7:30 and 16:30, the ecosystem showed CO₂ absorption (Fig. 5a); the
316 rest of the day was characterized by weak CO₂ emission. Note that although all times
317 in China are reported as the Beijing time, the study site was not sufficiently far east of
318 Beijing for this to affect the physiological meaning of these times. The average diurnal
319 GPP was also characterized by a single peak from around 05:00 to around 19:30, and
320 the diurnal R_{ec} was characterized by an approximately horizontal line at about 0.75
321 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

322 In summer, the sandy grassland was a CO₂ sink in all years, with NEE, GPP, and R_{ec}
323 averaging -0.66 ± 0.08 , 2.45 ± 0.09 , and 1.79 ± 0.04 g C m⁻² d⁻¹, respectively (Fig. 4b).
324 The diurnal cycles of NEE and GPP were also characterized by a single peak, and the
325 ecosystem CO₂ uptake reached its peak from around 10:30 to 12:00 (Fig. 5b). The
326 diurnal R_{ec} pattern was similar to the spring, but at a higher level (about 1.79 $\mu\text{mol m}^{-2}$
327 s^{-1}).

328 In autumn, the sandy grassland was a net source of atmospheric CO₂ in all years,
329 with NEE, GPP, and R_{ec} averaging 0.50 ± 0.03 , 0.26 ± 0.03 , and 0.76 ± 0.04 g C m⁻²
330 d⁻¹, respectively (Fig. 4c). The diurnal dynamics of NEE, GPP, and R_{ec} in autumn (Fig.
331 5c) were similar to those in spring (Fig. 5a), but the magnitudes of NEE and GPP in
332 autumn were lower than in the spring. The diurnal R_{ec} was similar to the value in the
333 spring, at about 0.73 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

334 In winter, the grassland ecosystem functioned as a net CO₂ source in all years, with
335 an average seasonal NEE of 0.59 ± 0.02 g C m⁻² d⁻¹ (Fig. 4d). It should also be noted

336 that since the investigation started on 14 September 2014 and ended on 31 December
337 2018, the 2017 to 2018 winter was only about one-third of the usual length (i.e., it did
338 not include data from January and February 2019). The diurnal dynamics of the winter
339 NEE differed from the other seasons (Fig. 5d), with a minimum release value of 0.36
340 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and with two emission peaks: at $0.78 \mu\text{mol m}^{-2} \text{s}^{-1}$ (08:00) and $0.85 \mu\text{mol}$
341 $\text{m}^{-2} \text{s}^{-1}$ (16:30).

342 **3.3 Response of NEE, GPP and R_{ec} to changes in environmental factors**

343 At an annual scale, the major environment difference among the years with a
344 complete dataset (2015, 2016, and 2018) was the amount of precipitation (Fig. S4). We
345 analyzed the relationship between precipitation and the annual NEE, GPP, and R_{ec} in
346 2015, 2016, and 2018 (Fig. 6). We found that GPP and R_{ec} increased significantly with
347 increasing annual precipitation, whereas NEE decreased significantly with increasing
348 annual precipitation, indicating that the ecosystem's carbon sequestration capacity
349 increased with increasing precipitation. Taken together, these results indicated different
350 magnitudes and directions of response of the three parameters to annual precipitation.

351 At a monthly scale, the temperature, precipitation, and CO_2 fluxes (NEE, GPP, and
352 R_{ec}) were relatively stable in winter (Fig. S4 and Fig. 4d). We have therefore focused
353 on the relationships between NEE, its components, and the associated environmental
354 factors in the other three seasons (Fig. 7-8). In the spring, the total monthly precipitation
355 was significantly negatively correlated with NEE, but significantly positively correlated
356 with GPP and R_{ec} , and GPP responded more strongly than R_{ec} to precipitation: $\text{slope}_{\text{GPP}}$
357 $(0.88) > \text{slope}_{\text{Rec}}(0.43)$. In summer, the total monthly precipitation was not significantly
358 correlated with NEE, GPP, and R_{ec} . In autumn, the total monthly precipitation was
359 significantly positively correlated with GPP and R_{ec} , with a similar strength of the
360 response to precipitation: $\text{slope}_{\text{Rec}}(0.75)$ and $\text{slope}_{\text{GPP}}(0.72)$, therefore, NEE was not
361 significantly correlated with total monthly precipitation.

362 At a daily scale, we calculated the correlations between the three CO_2 fluxes (NEE,
363 R_{ec} , and GPP) and T_{soil} and performed regression analysis to understand their
364 relationship with SWC at depths of 10, 20, 30, 40, and 50 cm in the spring, summer,

365 and autumn periods (Table S1, Fig. 8). In spring, NEE was significantly negatively
366 correlated with T_{soil} from 0 to 50 cm, with SWC from 10 to 50 cm, and with SWC from
367 0 to 10 cm. GPP and R_{ec} were significantly positively correlated with these
368 environmental factors. In summer, NEE was significantly negatively correlated with
369 T_{soil} from 0 to 50 cm and with SWC from 40 to 50 cm, but was not significantly
370 correlated with SWC from 0 to 10 cm. GPP and R_{ec} were significantly positively
371 correlated with T_{soil} from 0 to 50 cm, SWC from 10 to 50 cm, and SWC from 0 to 10
372 cm. T_{soil} from 0 to 50 cm had a smaller impact on NEE, GPP, and R_{ec} in summer than
373 in spring. In autumn, NEE was significantly positively correlated with T_{soil} from 0 to
374 50 cm and with SWC from 0 to 10 cm, but significantly negatively correlated with SWC
375 from 10 to 30 cm. GPP and R_{ec} were significantly positively correlated with T_{soil} from
376 0 to 50 cm, SWC from 10 to 50 cm, and SWC from 0 to 10 cm.

377 **4 Discussion**

378 **4.1 Annual and seasonal mean and diurnal variability**

379 *As we hypothesized*, the sandy grassland ecosystem in the present study was a net
380 CO_2 source at an annual scale, with an annual mean NEE of $49 \pm 8 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the
381 years for which a complete dataset was available (2015, 2016, and 2018). *This result*
382 *was consistent with results for other ecosystems with similar climate and geographical*
383 *conditions. For example, a grassland in New Mexico, United States, was a net source*
384 *of $31 \text{ g C m}^{-2} \text{ yr}^{-1}$ during dry study periods (Petrie et al., 2015). A savanna in southern*
385 *Arizona, United States, was also a net source of CO_2 to the atmosphere, with emission*
386 *ranging from 14 to $95 \text{ g C m}^{-2} \text{ yr}^{-1}$ and the strength of the source increasing with*
387 *decreasing precipitation (Scott et al., 2014). A woodland in central Australia was*
388 *carbon-neutral during a dry year (Cleverly et al., 2013). In contrast, many other arid*
389 *and semiarid dry ecosystems were a significant net sink for CO_2 . For example, a desert*
390 *ecosystem in the United States had net C sequestration of 102 to $110 \text{ g C m}^{-2} \text{ yr}^{-1}$*
391 *(Wohlfahrt et al., 2008); an artificial sand-binding vegetation system in China's Tengger*
392 *Desert had net sequestration of 14 and $23 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Gao et al., 2012); a phreatophyte-*
393 *dominated desert ecosystem in China's Gurbantonggut Desert had net sequestration of*

394 5 to 40 g C m⁻² yr⁻¹ (Liu et al., 2016a); and a shrubland in China's Mu Us desert had net
395 sequestration of 77 g C m⁻² yr⁻¹ (Jia et al., 2014). There are several possible reasons for
396 these differences among studies: (1) Our observations in 2015 and 2016 were in dry
397 years with precipitation considerably below the long-term average, and because NEE
398 was negatively related to precipitation (Fig. 6), this would have decreased carbon
399 sequestration by the ecosystem. Previous studies showed that annual species such as
400 the vegetation in our study area can be extremely vulnerable to drought (Jongen et al.,
401 2011; Sun et al., 2015; Liu et al., 2016a). Drought was the main source of inter-annual
402 variation in terrestrial carbon sequestration, as it decreases GPP and increases NEE
403 (Webb et al., 1978; Sala et al., 1988; Ciais et al., 2005). (2) Our study site is still
404 recovering from severe degradation, and has relatively low vegetation productivity, and
405 the restoration of degraded sandy grassland ecosystems is a long process (Li et al.,
406 2019). Therefore, the ecosystem has not yet reached the threshold at which it will
407 change into a CO₂ sink, and it will be necessary to study NEE for a longer period to
408 reveal when that change occurs and the ecosystem's long-term response to
409 environmental and biological factors (Su et al., 2003; Niu et al., 2018).

410 In spring, the sandy grassland was a net CO₂ source in all years (Fig. 4a). Before the
411 growing season, both GPP and R_{ec} increased with increasing temperature and
412 precipitation (Niu et al., 2011; Rey et al., 2011). However, plants are just beginning to
413 germinate in the spring, so the carbon sequestration capacity of the ecosystem is less
414 than the carbon release capacity (Delpierre et al., 2010; Liu et al., 2016a; Zhang et al.,
415 2016). Therefore, the ecosystem was a net CO₂ source.

416 In summer, the sandy grassland was a CO₂ sink in all years (Fig. 4b). Our results
417 agree with previous results for the study area (Li et al., 2015), as well as with results
418 for a semiarid savanna in Australia (Hutley et al., 2005) and a grassland in California
419 (Ma et al., 2007). GPP and R_{ec} increased because of the favorable temperature and
420 moisture conditions. However, because photosynthesis is greater than respiration
421 during the peak of the growing season (Kemp, 1983; Liu et al., 2016a; Niu et al., 2018),
422 the ecosystem became a net CO₂ sink.

423 In the autumn and winter, the sandy grassland was a net CO₂ source in all years (Fig.
424 4c, d). At the end of the growing season (in autumn), annual plants began to die and
425 photosynthesis weakened (Fang et al., 2014). As a result, the ecosystem gradually
426 transformed from a carbon sink to a carbon source (Keenan et al., 2009; Kiely et al.,
427 2009). In winter, plants are either dead or dormant, so there is no C uptake.

428 At the diurnal scale, NEE in the spring and summer showed CO₂ uptake during the
429 day (06:00-18:00), and CO₂ emission during the night (Fig. 5a, b). NEE decreased with
430 increasing light intensity during the day, reached its peak value around noon, then
431 increased until sunset, when the ecosystem changed from net carbon absorption to net
432 carbon release (Wagle and Kakani, 2014; Jia et al., 2014).

433 In autumn and winter, the sandy grassland ecosystem showed CO₂ emission
434 throughout the day (Fig. 5c, d). At a diurnal scale, the ecosystem showed carbon
435 “uptake” in winter, but at a level too small to display in Figure 5d. This phenomenon
436 may have resulted from heating effects in the open-path infrared gas analyzer (Burba et
437 al., 2008). We recently created a Li-Cor LI-8150 gas analyzer system with six long-
438 term monitoring chambers in the footprint area for the eddy covariance measurements,
439 which we will use to test whether that hypothesis is correct.

440 **4.2 Impacts of the environment on NEE, GPP, and R_{ec}**

441 Understanding the relationships between precipitation patterns and inter-annual
442 variations of carbon flux is an important step towards predicting how future climate
443 change will affect carbon cycles in arid and semiarid ecosystems (Poulter et al., 2014;
444 Scott et al., 2014; Liu et al., 2016a). Our results demonstrated the important roles of the
445 environmental factors in regulating the direction and amount of NEE between the
446 atmosphere and the ecosystem in a sandy grassland in the Horqin Sandy Land. The
447 dominant environmental factors differed among seasons at the different scales (Nakano
448 et al., 2008; Ueyama et al., 2010).

449 At an annual scale, the amount of precipitation was the dominant factor in regulating
450 the annual carbon exchange of this sandy grassland. NEE was negatively linearly
451 related to precipitation on an annual basis (Fig. 6). This result is consistent with data

452 from a northern temperate grassland in Canada (Flanagan et al., 2002) and a tallgrass
453 prairie in the United States (Suyker et al., 2003). Annual herbaceous plants are
454 vulnerable to decreased precipitation, which decreases their productivity by reducing
455 stomatal conductance and leaf area, while simultaneously increasing the soil water
456 deficit (Ford et al., 2008). Soil water deficits and decreased substrate availability for
457 soil microbes can also decrease R_{ec} (Shi et al., 2014). In addition, GPP generally
458 responds more strongly than R_{ec} to drought in arid and semiarid areas (Schwalm et al.,
459 2010; Litvak et al., 2015; Delgado-Balbuena et al., 2019). Our result was consistent
460 with these studies, as the slope of the regression line that relates precipitation to GPP
461 (0.98) was much higher than that for R_{ec} (0.51) (Fig. 6). However, we must improve
462 our understanding of the responses of the ecosystem to precipitation and the underlying
463 mechanisms that control whether it will be a carbon source or sink. To accomplish this,
464 it will be necessary to observe the ecosystem continuously for a longer period of time.

465 The dominant factors varied seasonally. In the spring, NEE was most strongly
466 affected by T_{soil} (Fig. 8), SWC (Fig. 8), and the amount of precipitation (Fig. 7). After
467 experiencing the winter cold and drought, GPP and R_{ec} increased with increasing
468 temperature and precipitation during the spring (Chu et al., 2013; Wolf et al., 2016). In
469 the present study, NEE was negatively related to the amount of precipitation (Fig. 7),
470 which suggests that spring precipitation leads to increased ecosystem carbon uptake in
471 sandy grassland, likely because the water replenishes the soil water storage in time to
472 facilitate the emergence and growth of shallow-rooted annual plants (Scott et al., 2000;
473 Liu et al., 2016a). In turn, this increases ecosystem CO_2 uptake. Therefore, spring
474 precipitation results in greater emergence and growth of annuals, which leads to a
475 higher contribution of this season to the ecosystem productivity (Huang et al., 2015).

476 In semiarid ecosystems such as our study site, summer precipitation supplies the
477 majority of the annual precipitation and soil moisture for most of the annual plant
478 growth (Emmerich and Verdugo, 2008; Sun et al., 2015). Our results showed that NEE
479 was significantly negatively correlated with SWC from 40 to 50 cm. This is likely to
480 be related to the size and frequency of each precipitation event. For example, events

481 with high precipitation (>20 mm) occurred five times in 2018, versus not at all in 2015
482 and once in 2016 (Table 1), and the carbon uptake in 2018 was higher than that in 2015
483 and 2016 (Fig. 4b). Effective precipitation may penetrate deeper into the soil, thereby
484 recharging soil water in deeper layers, which stimulates plant growth and carbon
485 absorption (Harper et al., 2005; Bell et al., 2012); on the other hand, the water can
486 potentially move below the rooting zone and become unavailable to plants. However,
487 our results indicated that the relationship between SWC from 0 to 10 cm and NEE was
488 not significant. The near-surface SWC would be closely linked to small precipitation
489 amounts (<5 mm) (Fig. 2). Studies suggest that small precipitation amounts may be
490 intercepted by the plant canopy or may replenish only the near-surface soil, where water
491 may evaporate before plants can take advantage of it, thereby reducing its impact on
492 NEE (Schwinning and Sala, 2004; Hao et al., 2010). Therefore, the effective
493 precipitation events appear to be more efficient than small precipitation events for
494 regulating NEE in sandy grassland in the summer.

495 In the autumn, NEE increased with increasing T_{soil} and SWC from 0 to 10 cm (Fig.
496 8). As was the case in the summer, the near-surface SWC was closely related to small
497 precipitation events (<5 mm). However, unlike in the summer, autumn is cooler and
498 moisture evaporates more slowly from the near-surface soil, and microbial respiration
499 is sensitive to precipitation when the temperature is suitable for microbial activity in
500 semiarid regions (Huxman et al., 2004; Sponseller, 2006; Roby et al., 2019). Thus,
501 small rainfall events can stimulate ecosystem CO_2 loss chiefly through their effect on
502 microbial respiration (Reynolds et al., 2004; Hao et al., 2010). However, the
503 relationship between NEE and SWC in deeper soil layers was negative (Fig. 8c), which
504 was similar to the relationship in summer.

505 In winter, the annual plants had withered, so there was no GPP and the entire
506 ecosystem was characterized by carbon emission (Morgner et al., 2010; Gao et al.,
507 2012). Our results showed that NEE increased with decreasing SWC and temperature
508 (Table S1). Previous studies found that when SWC decreases sufficiently to create
509 water stress, it may replace temperature as the main factor that controls soil respiration

510 in arid and semiarid areas in winter (Wu et al., 2010; Escolar et al., 2015), and as a
511 result, soil respiration decreased with decreasing SWC (Manzoni et al., 2011; Oikawa
512 et al., 2011). Our results were inconsistent with these previous studies. This may be due
513 to the effects of drought, since precipitation during the winter amounted to between 1
514 and 6 % of the annual precipitation, and this drought would be exacerbated by strong
515 winter winds in the Horqin Sandy Land (Fig. S5; Wang et al., 2005; Liu et al., 2016b).
516 The soil organic matter and nutrients would also be lost faster when SWC decreases
517 and the wind strengthens, resulting in increased carbon emission (Lal, 2004;
518 Munodawafa, 2011).

519 **5 Conclusions**

520 Our field data indicated that the sandy grassland has functioned as a net CO₂ source
521 at an annual scale, with a mean annual NEE of 49 ± 8 g C m⁻² yr⁻¹. At the seasonal scale,
522 the sandy grassland showed net CO₂ absorption during the summer, but net CO₂ release
523 in the other seasons. At the diurnal scale, the ecosystem showed a strong single daytime
524 absorption peak in the spring and summer, but strong CO₂ emission at night. In autumn
525 and winter, the ecosystem was characterized by CO₂ emission throughout the day.

526 Annual precipitation was significantly negatively correlated with NEE. Seasonally,
527 NEE was mainly affected by T_{soil} and the amount of precipitation in the spring, by the
528 frequency and amount of effective precipitation events in summer, by T_{soil} and SWC at
529 all depths in autumn, and by T_{soil} at all depths and SWC from 30 to 50 in winter. Our
530 findings demonstrated the importance of long-term, high-frequency field monitoring in
531 sandy land to improve our understanding of CO₂ cycling and its likely responses to a
532 changing climate. However, it will be necessary to study the NEE for a longer period
533 to reveal its long-term response to environmental and biological factors and learn when
534 the ecosystem will recover sufficiently to become a net carbon sink on an annual basis.

535 *Data availability.* In agreement with the FAIR Data standards, the data used in this
536 article are archived, published, and available in a dedicated repository:
537 <http://doi.org/10.4121/uuid:35deeb02-8165-49b7-af8d-160d537ae15a>.

538 *Competing interests.* The authors declare that they have no conflict of interest.

539 *Author contributions.* YQL, YYN, HBY, XYW, and YLD designed the study; YYN,
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549 **References**

550 Asner, G. P., Archer, S., Hughes, R. F., Ansley, R. J., and Wessman, C. A.: Net changes
551 in regional woody vegetation cover and carbon storage in Texas Drylands, 1937–
552 1999, *Glob. Change Biol.*, 9, 316–335, [https://doi.org/10.1046/j.1365-](https://doi.org/10.1046/j.1365-2486.2003.00594.x)
553 [2486.2003.00594.x](https://doi.org/10.1046/j.1365-2486.2003.00594.x), 2003.

554 Bagan, H., Takeuchi, W., Kinoshita, T., and Bao, Y. H.: Land cover classification and
555 change analysis in the Horqin Sandy Land from 1975 to 2007, *IEEE J. Sel. Topics*
556 *in Applied Earth Observations and Remote Sensing*, 3, 168-177.
557 <https://doi.org/10.1109/jstars.2010.2046627>, 2010.

558 Baldocchi, D., Falage, E., Gu, L. H., Olson, R., Hollinger, D., Running, S., Anthoni, P.,
559 Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law,
560 B., Lee, X. H., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw, U. K. T.,
561 Pilegaard, K., Schmid, H. P., Valentini, R., Verma, S., Vesala, T., Wilson, K., and
562 Wofsy, S.: Fluxnet: a new tool to study the temporal and spatial variability of
563 ecosystem-scale carbon dioxide, water vapor, and energy flux densities, *Bulletin*
564 *of the American Meteorological Society.*, 82, 2415–2434.
565 [https://doi.org/10.1175/1520-0477\(2001\)082<2415:FANTTS>2.3.CO;2](https://doi.org/10.1175/1520-0477(2001)082<2415:FANTTS>2.3.CO;2), 2001.

566 Barrett, G. W.: The effects of an acute insecticide stress on a semi-enclosed grassland
567 ecosystem, *Ecology*, 49, 1019, <https://doi.org/10.2307/1934487>, 1968.

568 **Bell, T. W., Menzer, O., Troyo-Diequez, E., and Oechel, W. C.: Carbon dioxide**
569 **exchange over multiple temporal scales in an arid shrub ecosystem near La Paz,**

570 Baja California Sur, Mexico. *Glob. Change Biol.*, 18, 2570–2582.
571 <https://doi.org/10.1111/j.1365-2486.2012.02720.x>, 2012.

572 Biederman, J. A., Scott, R. L., Bell, T. W., Bowling, D. R., Dore, S., Garatuza-Payan,
573 J., Kolb, T. E., Krishnan, P., Krofchec, D. J., Litv, M. E., Maurer, G. E., Meyers,
574 T. P., Oechel, W. C., Papuga, S. A., Ponce-Campos, G. E., Rodriguez, J. C., Smith,
575 W. K., Vargas, R., Watts, C. J., Yepez, E. A., and Goulden, M. L.: CO₂ exchange
576 and evapotranspiration across dryland ecosystems of southwestern North
577 America. *Glob. Change Biol.*, 23, 4204–4221. <https://doi.org/10.1111/gcb.13686>,
578 2017.

579 Biederman, J. A., Scott, R. L., Goulden, M. L., Vargas, R., Litvak, M. E., Kolb, T. E.,
580 Yepez, E. A., Oechel, W. C., Blanken, P. D., Bell, T. W., Garatuza-Payan, J.,
581 Maurer, G. E., Dore, S., and Burns, S. P.: Terrestrial carbon balance in a drier
582 world: the effects of water availability in southwestern North America. *Glob.*
583 *Change Biol.*, 22, 1867-1879. <https://doi.org/10.1111/gcb.13222>, 2016.

584 Burba, G. G., McDermitt, D. K., Grelle, A., and Daniel, J. A.: Addressing the influence
585 of instrument surface heat exchange on the measurements of CO₂ flux from open-
586 path gas analyzers, *Glob. Change Biol.*, 14, 1854-1876,
587 <https://doi.org/10.1111/j.1365-2486.2008.01606.x>, 2008.

588 Chu, J. M., Wang, Q., Fan, Z. P., and Li, F. Y.: Effects of soil moisture condition and
589 freeze-thaw cycle on soil respiration of different land-use types in Horqin Sandy
590 Land, *Chinese J. Ecol.*, (in Chinese), 32, 1399-1404, <http://www.cje.net.cn/EN/>,
591 2013.

592 Ciais, P. H., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., Aubinet, M.,
593 Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., Noblet, N. D., Friend,
594 A. D., Friedlingstein, P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A.,
595 Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J. M.,
596 Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J. F., Sanz, M. J.,
597 Schulze, E. D., Vesala, T., and Valentini, R.: Europe-wide reduction in primary
598 productivity caused by the heat and drought in 2003, *Nature*, 437, 529-533,
599 <https://doi.org/10.1038/nature03972>, 2005.

600 Cleverly, J., Boulain, N., Villalobos-Vega, R., Grant, N., Faux, R., Wood, C., Cook, P.

601 G., Yu, Q., Leigh, A., and Eamus, D.: Dynamics of component carbon fluxes in
602 a semi-arid Acacia woodland, central Australia, *JGR Biogeosciences.*, 118,
603 1168–1185, <http://dx.doi.org/10.1002/jgrg.20101>, 2013.

604 Cleverly, J., Eamus, D., Gorsel, E. V., Chen, C., Rumman, R., Luo, Q. Y., Coupe, N. R.,
605 Li, L. H., Kljun, N., Faux, R., Yu, Q., and Huete, A.: Productivity and
606 evapotranspiration of two contrasting semiarid ecosystems following the 2011
607 global carbon land sink anomaly, *Agric. For. Meteorol.*, 220, 151-159.
608 <https://doi.org/10.1016/j.agrformet.2016.01.086>, 2016.

609 Czobel, S., Szirmai, O., Nemeth, Z., Gyuricza, C., H ázi, J., T óth, A., Schellenberger, J.,
610 Vasa, L., and Penksza, K.: Short-term effects of grazing exclusion on net
611 ecosystem CO₂ exchange and net primary production in a Pannonian sandy
612 grassland, *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, 40, 67-72,
613 <https://doi.org/10.15835/nbha4028300>, 2012.

614 Delgado-Balbuena, J., Arredondo, J. T., Loescher, H. W., Pineda-Mart ínez, L. F.,
615 Carbajal, J. N., and Vargas, R.: Seasonal precipitation legacy effects determine
616 the carbon balance of a semiarid grassland, *JGR Biogeosciences*, 124, 987-1000,
617 <https://doi.org/10.1029/2018JG004799>, 2019.

618 Delpierre, N., Soudani, K., Francois, C., Pontailier, J. Y., Nikinmaa, E., Misson, L.,
619 Aubinet, M., Bernhofer, C., Granier, A., Grünwald, T., Heinesch, B., Longdoz,
620 B., Ourcival, J. M., Rambal, S., Vesala, T., and Dufrene, E.: Exceptional carbon
621 uptake in European forests during the 2007 warm spring: a data- model analysis,
622 *Glob. Change Biol.*, 15, 1455-1474. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2486.2008.01835.x)
623 [2486.2008.01835.x](https://doi.org/10.1111/j.1365-2486.2008.01835.x), 2010.

624 Emmerich, W. E.: Carbon dioxide fluxes in a semiarid environment with high carbonate
625 soils, *Agric. For. Meteorol.*, 116, 91–102, [https://doi.org/10.1016/s0168-](https://doi.org/10.1016/s0168-1923(02)00231-9)
626 [1923\(02\)00231-9](https://doi.org/10.1016/s0168-1923(02)00231-9), 2003.

627 Emmerich, W. E., and Verdugo, C. L.: Precipitation thresholds for CO₂ uptake in grass
628 and shrub plant communities on Walnut Gulch Experimental Watershed, *Water*
629 *Resour. Res.*, 44, 435-443. <https://doi.org/10.1029/2006wr005690>, 2008.

630 Escolar, C., Maestre, F. T , and Rey. A.: Biocrusts modulate warming and rainfall
631 exclusion effects on soil respiration in a semi-arid grassland, *Soil Biol. Biochem.*,
632 80, 9-17, <https://doi.org/10.1016/j.soilbio.2014.09.019>, 2015.

633 Falge, E., Baldocchi, D., Olson, R., Anthoni, P., and Dolman, H.: Gap filling strategies
634 for defensible annual sums of net ecosystem exchange, *Agric. For. Meteorol.*,
635 107, 43-69, [https://doi.org/10.1016/S0168-1923\(00\)00225-2](https://doi.org/10.1016/S0168-1923(00)00225-2), 2001.

636 Fang, S. X., Zhou, L. X., Tans, P. P., Ciais, P., Steinbacher, M., Xu, L., and Luan, T.: *In*
637 *situ* measurement of atmospheric CO₂ at the four WMO/GAW stations in China,
638 *Atmos. Chem. Phys.*, 14, 27287-27326. [https://doi.org/10.5194/acp-14-2541-](https://doi.org/10.5194/acp-14-2541-2014)
639 2014, 2014.

640 Flanagan, L. B., Wever, L. A., Carlson, P. J., Seasonal and interannual variation in
641 carbon dioxide exchange and carbon balance in a northern temperate grassland,
642 *Glob. Change Biol.*, 8, 599–615. [http://dx.doi.org/10.1046/j.1365-](http://dx.doi.org/10.1046/j.1365-2486.2002.00491.x)
643 2486.2002.00491.x, 2002.

644 Ford, C. R., Mitchell, R. J., and Teskey, R. O.: Water table depth affects productivity,
645 water use, and the response to nitrogen addition in a savanna system. *Can. J. For.*
646 *Res.*, 38, 2118-2127. <https://doi.org/10.1139/X08-061>, 2008.

647 Gang, C. C., Zhang, J., and Li, J. L.: The advances in the carbon source/sink researches
648 of typical grassland ecosystem in China, *Procedia Environ. Sci.*, 10, 1646-1653.
649 <https://doi.org/10.1016/j.proenv.2011.09.259>, 2011.

650 Gao, Y. H., Li, X. R., Liu, L. C., Jia, R. L., Yang, H. T., Li, G., and Wei, Y. P.: Seasonal
651 variation of carbon exchange from a revegetation area in a Chinese desert, *Agric.*
652 *For. Meteorol.*, 156, 134-142, <https://doi.org/10.1016/j.agrformet.2012.01.007>,
653 2012.

654 Hair, J. F., Black, B., Babin, B., Anderson, R. E., and Tatham, R. L.: *Multivariate data*
655 *analysis*, 6th Ed. New Jersey: Prentice Hall, 2005.

656 Hao, Y. B., Wang, Y. F., Mei, X., and Cui, X. R.: The response of ecosystem CO₂
657 exchange to small precipitation pulses over a temperate steppe. *Plant Ecol.*, 209,
658 335-347. <https://doi.org/10.1007/s11258-010-9766-1>, 2010.

659 Harper, C. W., Blair, J. M., Fay, P. A., Knapp, A. K., and Carlisle, J. D.: Increased
660 rainfall variability and reduced rainfall amount decreases soil CO₂ flux in a
661 grassland ecosystem. *Glob. Change Biol.*, 11, 322–334.
662 <https://doi.org/10.1111/j.1365-2486.2005.00899.x>, 2005.

663 Hastings, S. J., Oechel, W. C., and Muhliamelo, A.: Diurnal, seasonal and annual
664 variation in the net ecosystem CO₂ exchange of a desert shrub community

665 (sarcocaulis) in Baja California, Mexico. *Glob. Change Biol.*, 11, 927-939,
666 <https://doi.org/10.1111/j.1365-2486.2005.00951.x>, 2010.

667 **Huang, G., Li, Y., and Collins, B.: Phenological transition dictates the seasonal**
668 **dynamics of ecosystem carbon exchange in a desert steppe, *J. Veg. Sci.*, 26, 337-**
669 **347. <http://dx.doi.org/10.1111/jvs.12236>, 2015.**

670 Huenneke, L. F., Anderson, J. P., Remmenga, M., and Schlesinger, W. H.:
671 Desertification alters patterns of aboveground net primary production in
672 Chihuahuan ecosystems, *Glob. Change Biol.*, 8, 247-
673 264. <https://doi.org/10.1046/j.1365-2486.2002.00473.x>, 2002.

674 Hutley, L. B., Leuning, R., Beringer, J., and Cleugh, H. A.: The utility of the eddy
675 covariance techniques as a tool in carbon accounting: tropical savanna as a case
676 study, *Austral. J. Bot.*, 53, 663. <https://doi.org/10.1071/Bt04147>, 2005.

677 **Huxman, T. E., Snyder, K. A., Tissue, D., Leffler, A. J., Ogle, K., Pockman, W. T.,**
678 **Sandquist, D. R., Potts, D. L., and Schwinning, S.: Precipitation pulses and**
679 **carbon fluxes in semiarid and arid ecosystems, *Oecologia*, 141, 254–268,**
680 **<https://doi.org/10.1007/s00442-004-1682-4>, 2004.**

681 Jia, X., Zha, T. S., Wu, B., Zhang, Y. Q., Gong, J. N., Qin, S. G., Chen, G. P., Kellomäki,
682 S., and Peltola, H.: Biophysical controls on net ecosystem CO₂ exchange over a
683 semiarid shrubland in northwest China, *Biogeosciences*, 11, 4679-4693.
684 <https://doi.org/10.5194/bg-11-4679-2014>, 2014.

685 Jongen, M., Pereira, J. S., Aires, L. M. I., and Pio, C. A.: The effects of drought and
686 timing of precipitation on the inter-annual variation in ecosystem-atmosphere
687 exchange in a mediterranean grassland. *Agric. For. Meteorol.*, 151, 595-606,
688 <https://doi.org/10.1016/j.agrformet.2011.01.008>, 2011.

689 **Joseph Turk, F., Pasadena, J. P. L., Li, L., and Haddad, Z. S.: Physical modeling of**
690 **microwave surface emissivity from passive microwave satellite observations**
691 **room 256 (New Orleans Convention Center), 2012.**

692 Kang, W. P., Wang, T., and Liu, S. L.: The response of vegetation phenology and
693 productivity to drought in semi-arid regions of Northern China, *Remote Sensing.*,
694 10, 727. <https://doi.org/10.3390/rs10050727>, 2018.

695 Keenan, T., García, R., Friend, A. D., Zaehle, S., Sabate, S.: Improved understanding
696 of drought controls on seasonal variation in Mediterranean forest canopy CO₂

697 and water fluxes through combined *in situ* measurements and ecosystem
698 modelling, *Biogeosci. Discuss.*, 6, 2285-2329, <https://doi.org/10.5194/bgd-6-2285-2009>, 2009.

700 Kemp, P. R.: Phenological patterns of Chihuahuan desert plants in relation to the timing
701 of water availability, *J. Ecol.*, 71, 427-436. <https://doi.org/10.2307/2259725>,
702 1983.

703 Kiely, G., Leahy, P., Sottocornola, M., Laine, A., Mishurov, M., Albertson, J., and
704 Carton, O.: Celticflux: measurement and modelling of greenhouse gas fluxes
705 from grasslands and a peatland in Ireland. Irish Environmental Protection
706 Agency, STRIVE Report 24,
707 <http://www.epa.ie/pubs/reports/research/climate/strivereport24.html>, 2009.

708 Knorr, W., Prentice, I. C., House, J. I., and Holland, E. A.: Long-term sensitivity of soil
709 carbon turnover to warming, *Nature*, 433, 298–301.
710 <https://doi.org/10.1038/nature03226>, 2005.

711 Lal, R.: Potential of desertification control to sequester carbon and mitigate the
712 greenhouse effect, *Clim. Change*, 51, 35–72.
713 <https://doi.org/110.1023/a:1017529816140>, 2001.

714 Lal, R.: Carbon sequestration in dryland ecosystems, *Environ. Manage.*, 33, 528–544.
715 <https://doi.org/10.1007/s00267-003-9110-9>, 2004.

716 Lee, X. H., Massman, W. J., and Law, B. E.: Handbook of micrometeorology, Springer,
717 Berlin. Vol. 29 of the Atmospheric and Oceanographic Sciences Library,
718 <https://doi.org/10.1007/1-4020-2265-4>, 2004.

719 Li, L., Wang, Y. P., Beringer, J., Shi, H., Cleverly, J., Cheng, L., Eamus, D., Huete, A.,
720 Hutley, L., Lu, X. J., Piao, S. L., and Zhang, L.: Responses of LAI to rainfall
721 explain contrasting sensitivities to carbon uptake between forest and non-forest
722 ecosystems in Australia, *Scientific Reports*, 7, 11720.
723 <https://doi.org/10.1038/s41598-017-11063-w>, 2017.

724 Li, R. P., and Zhou, G. S.: A temperature-precipitation based leafing model and its
725 application in Northeast China, *Plos One.*, 7, e33192.
726 <https://doi.org/10.1371/journal.pone.0033192>, 2012.

727 Li, Y. Q., Wang X. Y., Chen, Y. P., Luo, Y. Q., Lian, J., Niu, Y. Y., Gong, X. W., Yang,
728 H., and Yu, P. D.: Changes in surface soil organic carbon in semiarid degraded

729 Horqin Grassland of northeastern China between the 1980s and the 2010s,
730 *Catena*, 174, 217–226, <https://doi.org/10.1016/j.catena.2018.11.021>, 2019.

731 Li, Y. Q., Zhang, J. P., Zhao, X. Y., Zhang, T. H., Li, Y. L., Liu, X. P., and Chen, Y. P.:
732 Comparison of soil physico-chemical properties under different land-use and
733 cover types in northeastern China's Horqin Sandy Land, *Sciences in Cold and*
734 *Arid Regions.*, 8, 495-506. <https://doi.org/10.3724/SP.J.1226.2016.00495>, 2016.

735 Li, Y. Q., Zhao, X. Y., Chen, Y. P., Luo, Y. Q., and Wang, S. K.: Effects of grazing
736 exclusion on carbon sequestration and the associated vegetation and soil
737 characteristics at a semi-arid desertified sandy site in Inner Mongolia, northern
738 China, *Can. J. Soil Sci.*, 92, 807-819, <https://doi.org/10.4141/cjss2012-030>, 2012.

739 Li, Y. Q., Zhao, X. Y., Wang, S. K., Zhang, F. X., Lian, J., Huang, W. D., and Qu, H.:
740 Carbon accumulation in the bulk soil and different soil fractions during the
741 rehabilitation of desertified grassland in Horqin Sandy Land (northern China),
742 *Pol. J. Ecol.*, 63, 88-101, <https://doi.org/10.3161/15052249PJE2015.63.1.008>,
743 2015.

744 Litvak, M. E., Krofcheck, D. J., and Maurer, G.: Quantifying the resilience of carbon
745 dynamics in semi-arid biomes in the Southwestern U.S. to drought, *Am. Geophys.*
746 *Union Fall. Meeting. Abstract*, 2015.

747 Liu, R., Cieraad, E., Li, Y., and Ma, J. J. E.: Precipitation pattern determines the inter-
748 annual variation of herbaceous layer and carbon fluxes in a phreatophyte-
749 dominated desert ecosystem, *Ecosystems*, 19, 601-614,
750 <https://doi.org/10.1007/s10021-015-9954-x>, 2016a.

751 Liu, S. L., Kang, W. P., and Wang, T.: Drought variability in Inner Mongolia of northern
752 China during 1960–2013 based on standardized precipitation evapotranspiration
753 index, *Environ. Earth Sci.*, 75, 145. <https://doi.org/10.1007/s12665-015-4996-0>,
754 2016b.

755 Lloyd, J., and Taylor, J. A.: On the temperature dependence of soil respiration,
756 *Functional Ecology*, 8, 315-323, <https://doi.org/10.2307/2389824>, 1994.

757 Ma, S. Y., Baldocchi, D. D., Xu, L. K., and Hehn, T.: Inter-annual variability in carbon
758 dioxide exchange of an oak/grass savanna and open grassland in California.
759 *Agric. For. Meteorol.*, 147, 157-171,
760 <https://doi.org/10.1016/j.agrformet.2007.07.008>, 2007.

761 Manzoni, S., Schimel, J. P., and Porporato, A.: Physical vs. physiological controls on

762 water-stress in soil microbial communities, 96th ESA Annual Convention 2011.
763 <https://doi.org/10.1890/11-0026.1>, 2011.

764 Morgner, E., Elberling, B., Strebel, D., and Cooper, E. J.: The importance of winter in
765 annual ecosystem respiration in the high arctic: effects of snow depth in two
766 vegetation types, *Polar Research*, 29, 58-74. [https://doi.org/10.1111/j.1751-](https://doi.org/10.1111/j.1751-8369.2010.00151.x)
767 [8369.2010.00151.x](https://doi.org/10.1111/j.1751-8369.2010.00151.x), 2010.

768 Munkhdalai, Z. A., Feng, Z. W., Wang, X. K., and Sun, H. W.: Sandy grassland
769 blowouts in Hulunbuir, northeast China: geomorphology, distribution, and causes,
770 *Progress in Natural Science: Materials International*, 17, 68-73.
771 <https://doi.org/10.1080/10020070612331343227>, 2007.

772 Munodawafa, A.: Maize grain yield as affected by the severity of soil erosion under
773 semi-arid conditions and granitic sandy soils of Zimbabwe, *Physics and*
774 *Chemistry of the Earth Parts A/B/C*, 36, 963-967,
775 <https://doi.org/10.1016/j.pce.2011.07.068>, 2011.

776 Mureithi, S. M., Verdoodt, A., and Rans, E. V.: Effects and implications of enclosures
777 for rehabilitating degraded semi-arid rangelands: critical lessons from Lake
778 Baringo Basin, Kenya, *Land Degradation and Desertification: Assessment,*
779 *Mitigation and Remediation*, https://doi.org/10.1007/978-90-481-8657-0_9,
780 2010.

781 Nakano, T., Nemoto, M., and Shinoda, M.: Environmental controls on photosynthetic
782 production and ecosystem respiration in semi-arid grasslands of Mongolia, *Agric.*
783 *For. Meteorol.*, 148, 1456-1466, <https://doi.org/10.1016/j.agrformet.2008.04.011>,
784 2008.

785 Niu, S. L., Luo, Y. Q., Fei, S. F., and Montagnani, L.: Seasonal hysteresis of net
786 ecosystem exchange in response to temperature change: patterns and causes,
787 *Glob. Change Biol.*, 17, 3102-3114, [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2486.2011.02459.x)
788 [2486.2011.02459.x](https://doi.org/10.1111/j.1365-2486.2011.02459.x), 2011.

789 Niu, Y. Y., Li, Y. Q., Wang, X. Y., Gong, X. W., Luo, Y. Q., and Tian, D.Y.:
790 Characteristics of annual variation in net carbon dioxide flux in a sandy grassland
791 ecosystem during dry years. *Acta Prataculturae Sinica (in Chinese)*, 27, 215-221,
792 <https://doi.org/10.11686/cyxb2017231>, 2018.

793 Noretto, M. D., Jobb gy, E. G., and Paruelo, J. M.: Carbon sequestration in semi-arid
794 rangelands: comparison of *Pinus ponderosa* plantations and grazing exclusion in
795 NW Patagonia, *J. Arid Environ.*, 67, 142-156,

796 <https://doi.org/10.1016/j.jaridenv.2005.12.008>, 2006.

797 Oikawa, P., Grantz, D. A., and Jenerette, D.: Variation in the temperature sensitivity of
798 heterotrophic soil respiration in response to pulse water events and substrate
799 limitation. Am. Geophys. Union Fall. Meeting. Abstract, 2011.

800 Petrie, M. D., Collins, S. L., Swann, A. M., Ford, P. L., and Litvak, M. E.: Grassland to
801 shrubland state transitions enhance carbon sequestration in the northern
802 Chihuahuan desert, Glob. Change Biol., 21, 1226-1235.
803 <http://dx.doi.org/10.1111/gcb.12743>, 2015.

804 Ponce Campos, G. E., Moran, M. S., Huete, A., Zhang, Y., Bresloff, C., Huxman, T. E.,
805 Eamus, D., Bosch, D. D., Buda, A. R., Gunter, S. A., Scalley, T. H., Kitchen, S.
806 G., McClaran, M. P., McNab, W. H., Montoya, D. S., Morgan, J. A., Peters, D. P.
807 C., Sadler, E. J., Seyfried, M. S., and Starks, P. J.: Ecosystem resilience despite
808 large-scale altered hydroclimate conditions, Nature, 494, 349–352,
809 <http://dx.doi.org/10.1038/nature11836>, 2013.

810 Poulter, B., Frank, D., Ciais, P., Myneni, R. B., Andela, N., Bi, J., Broquet, G., Canadell,
811 J. G., Chevallier, F., and Liu, Y. Y.: Contribution of semi-arid ecosystems to
812 interannual variability of the global carbon cycle, Nature, 509, 600–603,
813 <https://doi.org/10.1038/nature13376>, 2014.

814 Prev éy, J. S., Seastedt, T. R., and Wilson, S.: Seasonality of precipitation interacts with
815 exotic species to alter composition and phenology of a semi-arid grassland. J.
816 Ecol., 102, 1549-1561. <https://doi.org/10.1111/1365-2745.12320>, 2014.

817 Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P.,
818 Bernhofer, C., Buchmann, N., Gilmanov, T., and Granier, A.: On the separation
819 of net ecosystem exchange into assimilation and ecosystem respiration: review
820 and improved algorithm. Glob. Change Biol., 11, 1424-1439.
821 <https://doi.org/10.1111/j.1365-2486.2005.001002.x>, 2005.

822 Rey, A., Pegoraro, E., Oyonarte, C., Were, A., Escribano, P., and Raimundo, J.: Impact
823 of land degradation on soil respiration in a steppe (*Stipa tenacissima* L.) semi-
824 arid ecosystem in the SE of Spain, Soil Biol. Biochem., 43, 393-403.
825 <https://doi.org/10.1016/j.soilbio.2010.11.007>, 2011.

826 Reynolds, J. F., Kemp, P. R., Ogle, K., and Fernandez, R. J.: Modifying the “pulse-

827 reserve” paradigm for deserts of North America: precipitation pulses, soil water
828 and plant responses, *Oecologia*, 141, 194–210. <https://doi.org/10.2307/40005681>,
829 2004.

830 Roby, M. C., Scott, R. L., Barron-Gafford, G. A., Hamerlynck, E. P., and Moore, D. J.
831 P.: Environmental and vegetative controls on soil CO₂ efflux in three semiarid
832 ecosystems, *Soil Systems*, 3, 6. <https://doi.org/10.3390/soilsystems3010006>,
833 2019.

834 Ruiz-Jaen, M, C., and Aide, T. M.: Restoration success: how is it being measured?
835 *Restor. Ecol.*, 13, 569-577, <https://doi.org/10.1111/j.1526-100X.2005.00072.x>,
836 2005.

837 Sala, O. E., Parton, W. J., Joyce, L. A., and Lauenroth, W.K.: Primary production of the
838 central grassland region of the United States, *Ecology*, 69, 40–45.
839 <https://doi.org/10.2307/1943158>, 1988.

840 Schmid, H. P.: Experimental design for flux measurements: matching scales of
841 observations and fluxes. *Agric. For. Meteorol.*, 87, 179-200.
842 [http://dx.doi.org/10.1016/S0168-1923\(97\)00011-7](http://dx.doi.org/10.1016/S0168-1923(97)00011-7), 1997.

843 Schwalm, C. R., Williams, C. A., Schaefer, K., Arneeth, A., Bonal, D., Buchmann, N.,
844 Chen, J., Law, B. E., Lindroth, A., Luysaert, S., Reichstein, M., and Richardson,
845 A. D.: Assimilation exceeds respiration sensitivity to drought: a FLUXNET
846 synthesis, *Glob. Change Biol.*, 16, 657–670, [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2486.2009.01991.x)
847 [2486.2009.01991.x](https://doi.org/10.1111/j.1365-2486.2009.01991.x), 2010.

848 Schwinning, S., and Sala, O. E., Hierarchy of responses to resource pulses in arid and
849 semi-arid ecosystems, *Oecologia.*, 141, 211–220.
850 <https://doi.org/10.2307/40005682>, 2004.

851 Scott, R. L., Biederman, J. A., Hamerlynck, E. P., and Barron-Gafford, G. A.: The
852 carbon balance pivot point of southwestern U.S. semiarid ecosystems: insights
853 from the 21st century drought, *JGR Biogeosciences*, 120, 2612-2624.
854 <https://doi.org/110.1002/2015JG003181>, 2015.

855 Scott, R. L., Jenerette, G. D., Potts, D. L., and Huxman, T. E.: Effects of seasonal
856 drought on net carbon dioxide exchange from a woody-plant-encroached
857 semiarid grassland, *JGR Biogeosciences*, 114, G04004.

858 <https://doi.org/10.1029/2008jg000900>, 2009.

859 Scott, R. L., Shuttleworth, W. J., Goodrich, D. C., and Maddock, T.: The water use of
860 two dominant vegetation communities in a semiarid riparian ecosystem, *Agric.*
861 *For. Meteorol.*, 105, 241–256. [http://dx.doi.org/10.1016/s0168-1923\(00\)00181-](http://dx.doi.org/10.1016/s0168-1923(00)00181-7)
862 [7](http://dx.doi.org/10.1016/s0168-1923(00)00181-7), 2000.

863 Scott R. L., Huxman, T. E., Barron-Gafford, G. A., Jenerette, G. D., Young, J. M., and
864 Hamerlynck, E. P.: When vegetation change alters ecosystem water availability,
865 *Glob. Change Biol.*, 20, 2198–2210. <http://dx.doi.org/10.1111/gcb.12511>, 2014.

866 Shachak, M., Sachs, M., and Moshe, I.: Ecosystem management of desertified
867 shrublands in Israel, *Ecosystems*, 1, 475-483.
868 <https://doi.org/10.1007/s100219900043>, 1998.

869 Shen, M. G., Piao, S. L., Cong, N., Zhang, G.X., and Jassens, I. A.: Precipitation
870 impacts on vegetation spring phenology on the Tibetan Plateau. *Glob. Change*
871 *Biol.*, 21, 3647-3656. <https://doi.org/10.1111/gcb.12961>, 2015.

872 Shi, Z., Thomey, M. L., Mowll, W., and Litvak, M.: Differential effects of extreme
873 drought on production and respiration: synthesis and modeling analysis,
874 *Biogeosciences*, 11, 621-633. <https://doi.org/10.5194/bg-11-621-2014>, 2014.

875 Sousa, F. P., Ferreira, T. O., Mendonça, E. S., Romero, R. E., and Oliveira, J. G. B.:
876 Carbon and nitrogen in degraded Brazilian semi-arid soils undergoing
877 desertification, *Agric. Ecosyst. Environ.*, 148, 11-21.
878 <https://doi.org/10.1016/j.agee.2011.11.009>, 2012.

879 Sponseller, R. A.: Precipitation pulses and soil CO₂ flux in a Sonoran Desert ecosystem,
880 *Glob. Change Biol.*, 13, 426–436. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2486.2006.01307.x)
881 [2486.2006.01307.x](https://doi.org/10.1111/j.1365-2486.2006.01307.x), 2006.

882 Su, Y. Z., Zhao, H. L., and Zhang, T. H.: Influence of grazing and enclosure on carbon
883 sequestration in degraded sandy grassland, Inner Mongolia, North China. *J.*
884 *Environ. Sci.*, (In Chinese), 46, 321-328.
885 <https://doi.org/10.1080/00288233.2003.9513560>, 2003.

886 Sun, D. C., Li, Y. L., Zhao, X. Y., Zuo, X. A., and Mao, W.: Effects of enclosure and
887 grazing on carbon and water fluxes of sandy grassland, *Chinese Journal of Plant*
888 *Ecology* (in Chinese), 39, 565-576. <https://doi.org/10.17521/cjpe.2015.0054>,
889 2015.

890 Suyker, E. A., Verma, S. B., Burba, G. G.: Inter-annual variability in net CO₂ fluxes
891 exchange of a native tallgrass prairie, *Glob. Change Biol.*, 9, 255–265.
892 <http://dx.doi.org/10.1046/j.1365-2486.2003.00567.x>, 2003.

893 Ueyama, M., Ichii, K., Hirata, R., Takagi, K., Asanuma, J., Machimura, T., Nakai, Y.,
894 Ohta, T., Saigusa, N., Takahashi, Y., and Hirano, T.: Simulating carbon and water
895 cycles of larch forests in East Asia by the BIOME-BGC model with AsiaFlux
896 data, *Biogeosciences*, 7, 959-977. <https://doi.org/10.5194/bg-7-959-2010>, 2010.

897 Vest, K. R., Elmore, A. J., Kaste, J. M., and Okin, G. S.: Functional connectivity as a
898 possible indicator of desertification in degraded grasslands, Am. Geophys. Union
899 Fall. Meeting. Abstract B51A-0383, 2011.

900 Wagle, P., and Kakani, V. G.: Environmental control of daytime net ecosystem
901 exchange of carbon dioxide in switchgrass, *Agric. Ecosyst. Environ.*, 186, 170-
902 177, <https://doi.org/10.1016/j.agee.2014.01.028>, 2014.

903 Wang, X. M., Dong, Z. B., Yan, P., Zhang, J. Z., and Qian, G. Q.: Wind energy
904 environments and dunefield activity in the Chinese deserts, *Geomorphology*, 65,
905 33-48, <https://doi.org/10.1016/j.geomorph.2004.06.009>, 2005.

906 Webb, E. K., Pearman, G. I., and Leuning, R.: Correction of flux measurements for
907 density effects due to heat and water vapor transfer, *Q. J. Roy. Meteorol. Soc.*,
908 106, 85-100, <https://doi.org/10.1002/qj.49710644707>, 1980,

909 Webb, W., Szarek, S., Lauenroth, W., Kinerson, R., and Smith, M.: Primary productivity
910 and water use in native forest, grassland, and desert ecosystem, *Ecology*, 59,
911 1239–1247, <https://doi.org/10.2307/1938237>, 1978.

912 Wohlfahrt, G., Fenstermaker, L. F., and Arnone, J.A. III: Large annual net ecosystem
913 CO₂ uptake of a Mojave Desert ecosystem, *Global Change Biol.*, 14, 1475-1487.
914 <https://doi.org/10.1111/j.1365-2486.2008.01593.x>, 2008.

915 Wolf, S., Keenan, T. F., Fisher, J. B., Baldocchi, D. D., Desai, A. R., Richardson, A.D.,
916 Scott, R. L., Law, B. E., Litvak, M. E., Brunsell, N. A., Peters, W., and Laan-
917 Luijkx, I. T.: Warm spring reduced carbon cycle impact of the 2012 US summer
918 drought. *PNAS*, 113, 5880-5885. <https://doi.org/10.1073/pnas.1519620113>,
919 2016.

920 Wu, C. Y., Chen, J. M., Pumpanen, J., Cescatti, A., Marcolla, B., Blanken, P. D., Ardö,
921 J., Tang, Y. H., Magliulo, V., Georgiadis, T., Soegaard, H., Cook, D. R., and
922 Harding, R. J.: An underestimated role of precipitation frequency in regulating

923 summer soil moisture. *Environ. Res. Lett.*, 7, 024011.
924 <http://dx.doi.org/10.1088/1748-9326/7/2/024011>, 2012.

925 Wu, X., Yao, Z. N., Brüggemann, N., and Shen, Z. Y.: Effects of soil moisture and
926 temperature on CO₂ and CH₄ soil atmosphere exchange of various land use/cover
927 types in a semi-arid grassland in Inner Mongolia, China. *Soil Biol. Biochem.*, 42,
928 773-787, <https://doi.org/10.1016/j.soilbio.2010.01.013>, 2010.

929 Xu, L. K., and Baldocchi, D. D.: Seasonal variation in carbon dioxide exchange over a
930 Mediterranean annual grassland in California, *Agric. For. Meteorol.*, 123, 79-96,
931 <https://doi.org/10.1016/j.agrformet.2003.10.004>, 2004.

932 Yan, C. Z., Wang, Y. M., Feng, Y. S., and Wang, J. H.: Macro-scale survey and dynamic
933 studies of sandy land in Ningxia by remote sensing, *Journal of Desert Research*
934 (in Chinese), 23, 34-37. [https://doi.org/1000-694X\(2003\)02-0132-04](https://doi.org/1000-694X(2003)02-0132-04), 2003.

935 Yun, H. B., Wu, Q. B., Zhuang, Q. L., Chen, A. P., Yu, T., Lyu, Z., Yang, Y. Z., Jin, H.
936 J., Liu, G. J., Qu, Y., and Liu, L. C.: Consumption of atmospheric methane by the
937 Qinghai–Tibet Plateau alpine steppe ecosystem, *Cryosphere*, 9, 2803-2819.
938 <https://doi.org/10.5194/tc-12-2803-2018>, 2018.

939 Zhang, B. W., Li, S., Chen, S. P., Ren, T. T., Yang, Z. Q., Zhao, H. L., Liang, Y., and
940 Han, X. G.: Arbuscular mycorrhizal fungi regulate soil respiration and its
941 response to precipitation change in a semiarid steppe, *Sci. Rep.*, 6, 19990,
942 <https://doi.org/10.1038/srep19990>, 2016.

943 Zhao, H. L., Li, Y. Q., and Zhou, R. L.: Effects of desertification on C and N storages
944 in grassland ecosystem on Horqin sandy land, *Chinese Journal of Applied*
945 *Ecology (in Chinese)*, 18, 2412. <https://doi.org/10.1360/yc-007-1324>, 2007.

946 Zhao, W. Z., and Liu, B.: The response of sap flow in shrubs to rainfall pulses in the
947 desert region of China. *Agric. For. Meteorol.*, 150, 1297–1306.
948 <https://doi.org/10.1016/j.agrformet.2010.05.012>, 2010.

949 Zhao, W. Z., and Liu, H.: Precipitation pulses and ecosystem responses in arid and
950 semiarid regions: a review, *Chinese Journal of Applied Ecology (in Chinese)*, 22,
951 243-249. <https://doi.org/10.3724/SP.J.1011.2011.00197>, 2011.

952 Zhao, X. Y., Wang, S. K., Luo, Y. Y., Huang, W. D., Qu, H., and Lian, J.: Toward
953 sustainable desertification reversion: a case study in Horqin Sandy Land of
954 northern China. *Sciences in Cold and Arid Regions*, 1, 23-28.

955 <https://doi.org/10.3724/SP.J.1226.2015.00023>, 2015.

956 Zhao, Y. L., Song, Z. L., Xu, X. T., Li, Z. M., Guo, F. S., and Pan, W. J.: Nitrogen
957 application increases phytolith carbon sequestration in degraded grasslands of
958 North China, *Ecol. Res.*, 31, 117-123, [https://doi.org/10.1007/s11284-015-1320-](https://doi.org/10.1007/s11284-015-1320-0)
959 [0](https://doi.org/10.1007/s11284-015-1320-0), 2016.

960 Zhou, Y. Y., Li, X. R., Gao, Y. H., He, M. Z., Wang, M. M., Wang, Y. L., Zhao, L. N.,
961 and Li, Y. F.: Carbon fluxes response of an artificial sand-binding vegetation
962 system to ainfall variation during the growing season in the Tengger Desert, *J.*
963 *Environ. Manage.*, 266, 110556, <https://doi.org/10.1016/j.jenvman.2020.110556>,
964 2020.

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966 **Figure captions**

967 **Fig. 1.** (a) Locations of the Horqin Sandy Land and the Naiman station. (b) and (c) are
968 photos of the eddy covariance site at the Naiman station during the growing and
969 dormant seasons, respectively.

970 **Fig. 2.** Changes in soil water content (SWC) at depths of 10, 20, 30, 40, and 50 cm that
971 resulted from precipitation events in spring, summer, and autumn. Precipitation ≥ 5 mm
972 represents effective precipitation.

973 **Fig. 3.** Seasonal and inter-annual variation in the daily average net ecosystem CO₂
974 exchange (NEE), gross primary productivity (GPP), and ecosystem respiration (R_{ec})
975 from (a-e) 2014 to 2018. (f) Annual cumulative NEE, GPP and R_{ec} from 2014 to 2018.
976 Positive NEE values indicate net CO₂ release, whereas negative values indicate net CO₂
977 uptake by the ecosystem. Note that the initial measurements were from 15 September
978 to 23 December 2014, so no data are available for the first part of 2014.

979 **Fig. 4.** Seasonal mean net ecosystem CO₂ exchange (NEE), gross primary productivity
980 (GPP), and ecosystem respiration (R_{ec}) from 2014 to 2018: (a) spring (March, April,
981 and May), (b) summer (June, July, and August), (c) autumn (September, October, and
982 November), and (d) winter (December, January, and February). Note that the initial
983 measurements were from 15 September to 23 December 2014, so no data are available
984 for the first part of 2014.

985 **Fig. 5.** Diurnal changes in mean net ecosystem CO₂ exchange (NEE), gross primary
986 productivity (GPP), and ecosystem respiration (R_{ec}) from 2014 to 2018: (a) spring
987 (March, April, and May), (b) summer (June, July, and August), (c) autumn (September,
988 October, and November), and (d) winter (December, January, and February). Note that
989 the initial measurements were from 15 September to 23 December 2014, so the spring
990 and summer data do not include the period before 15 September. The final
991 measurements were obtained on 31 December 2018, so the winter period from 2017 to
992 2018 was only about one-third of the usual length (i.e., it did not include data from
993 January and February 2019).

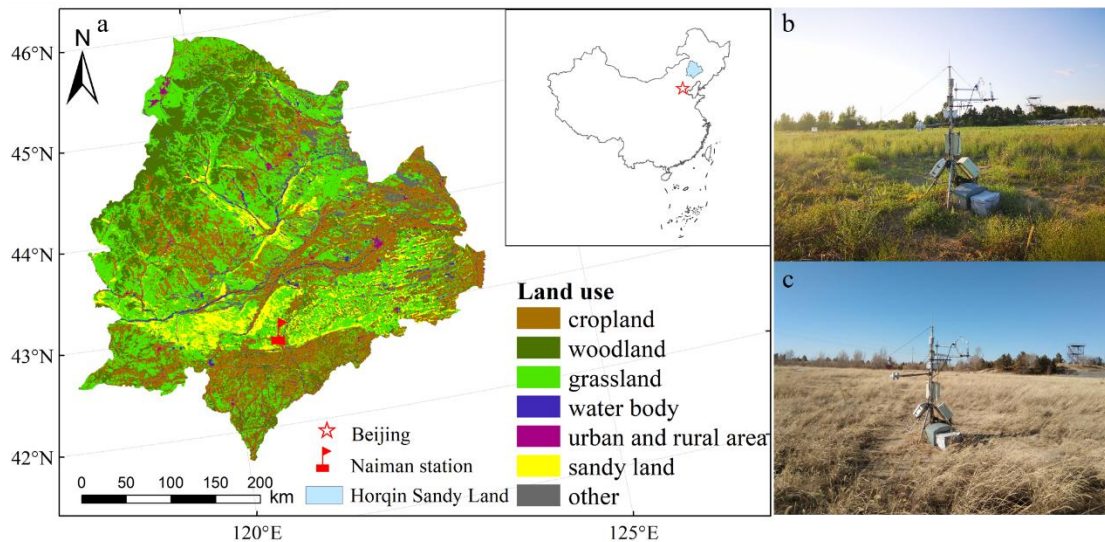
994 **Fig. 6.** Relationship between annual precipitation and net ecosystem carbon exchange

995 (NEE), gross primary productivity (GPP), and ecosystem respiration (R_{ec}) for the years
996 with a complete dataset (2015, 2016, and 2018).

997 **Fig. 7.** Relationship between monthly net ecosystem carbon exchange (NEE), gross
998 primary productivity (GPP), and ecosystem respiration (R_{ec}) and the corresponding
999 monthly precipitation in spring (March, April, and May), summer (June, July, and
1000 August), and autumn (September, October, and November).

1001 **Fig. 8.** Relationships between daily net ecosystem carbon exchange (NEE), gross
1002 primary productivity (GPP), and ecosystem respiration (R_{ec}) and the average soil
1003 temperature (T_{soil}) and soil water content (SWC). Before the regression analysis, SWC
1004 was divided into two depth ranges: the near-surface soil (0 to 10 cm) and deeper soil
1005 (10 to 50 cm). However, NEE was only correlated with SWC at depths of 40 to 50 cm
1006 in the summer and 20 to 30 cm in the autumn based on the results of a collinearity test
1007 for the three seasons. T_{soil} was divided into a single range (0 to 50 cm) based on the
1008 results of a collinearity test for the three seasons: Spring (March, April, and May),
1009 summer (June, July, and August), autumn (September, October, and November).

1010 **Fig. 1.**

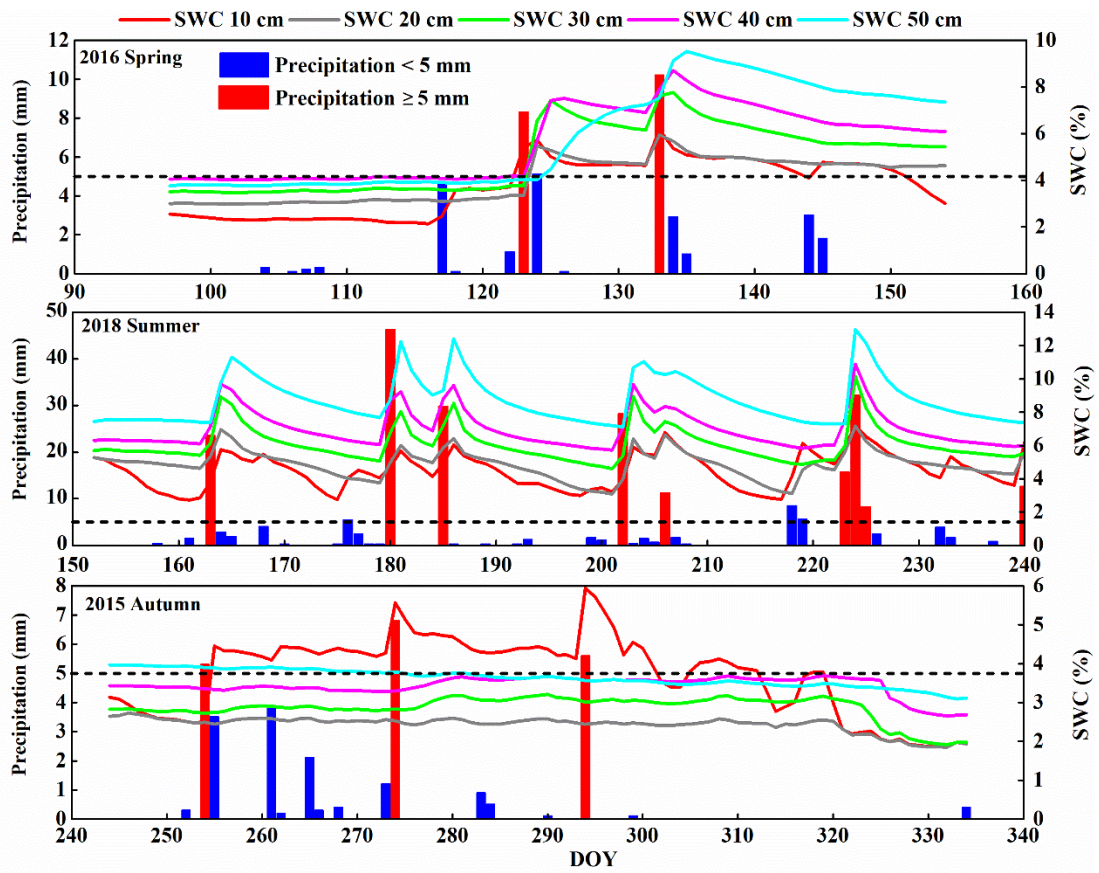


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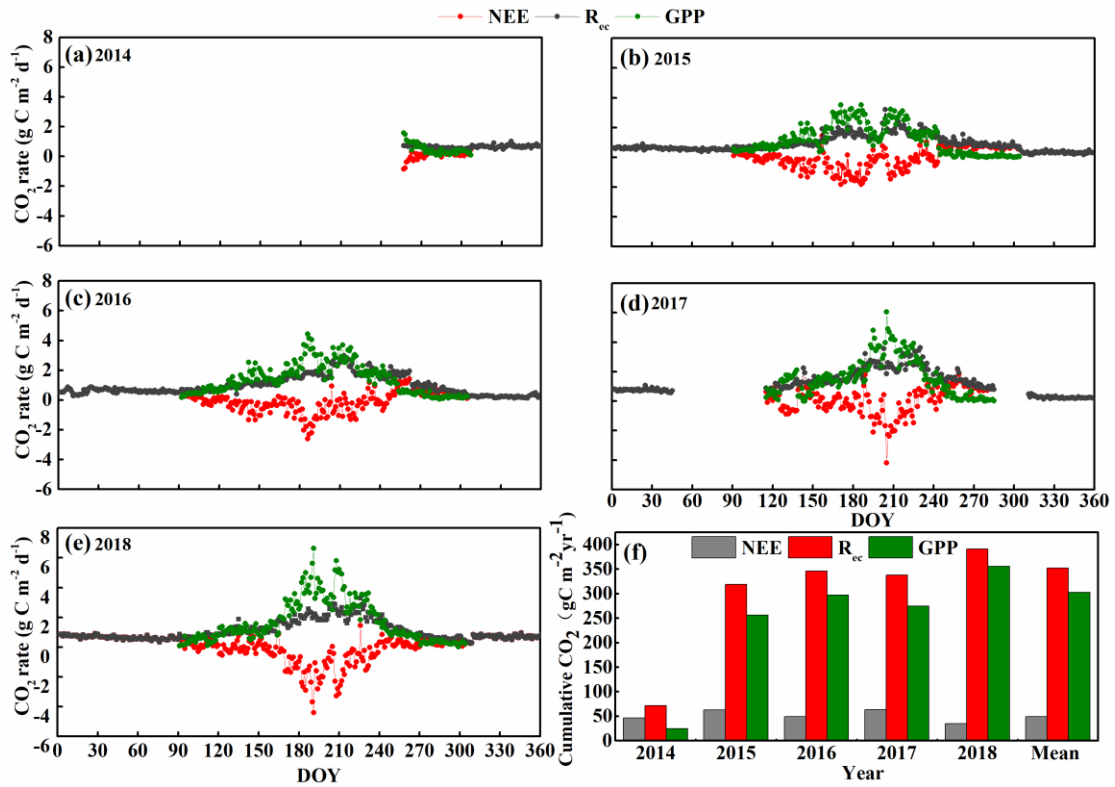
Fig. 2.



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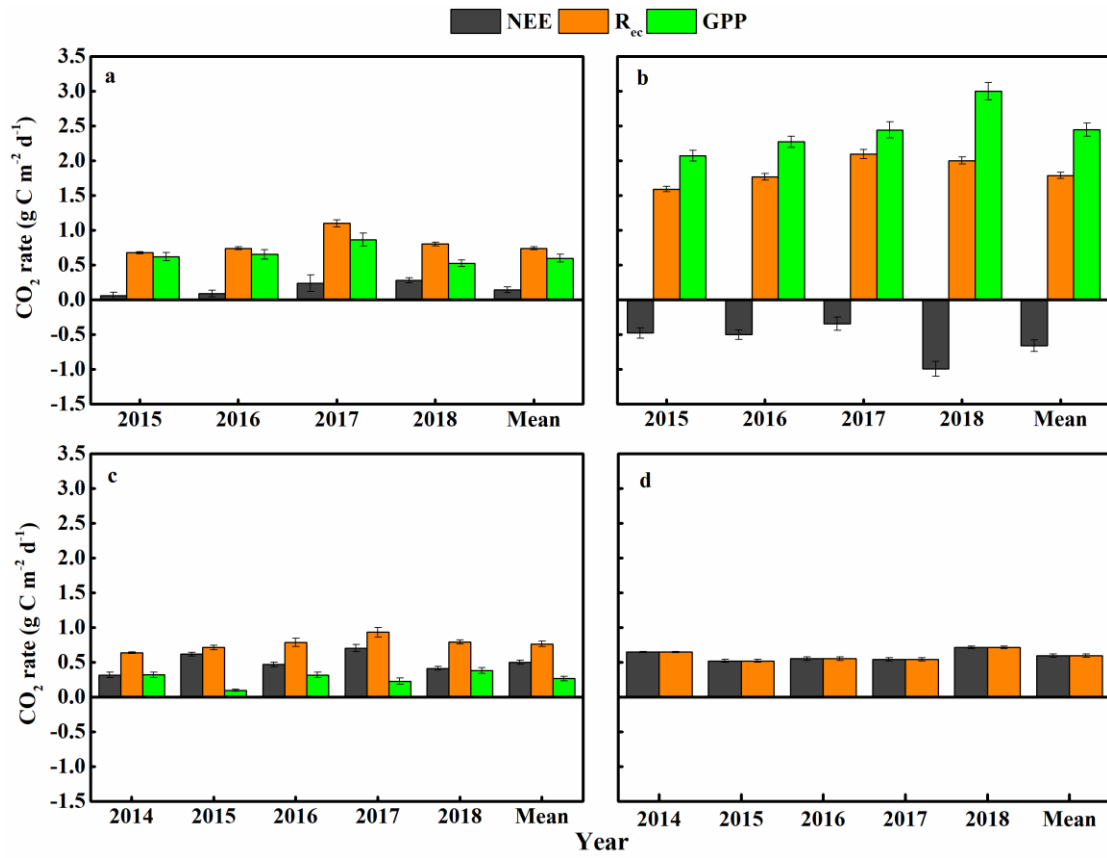
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Fig. 3.



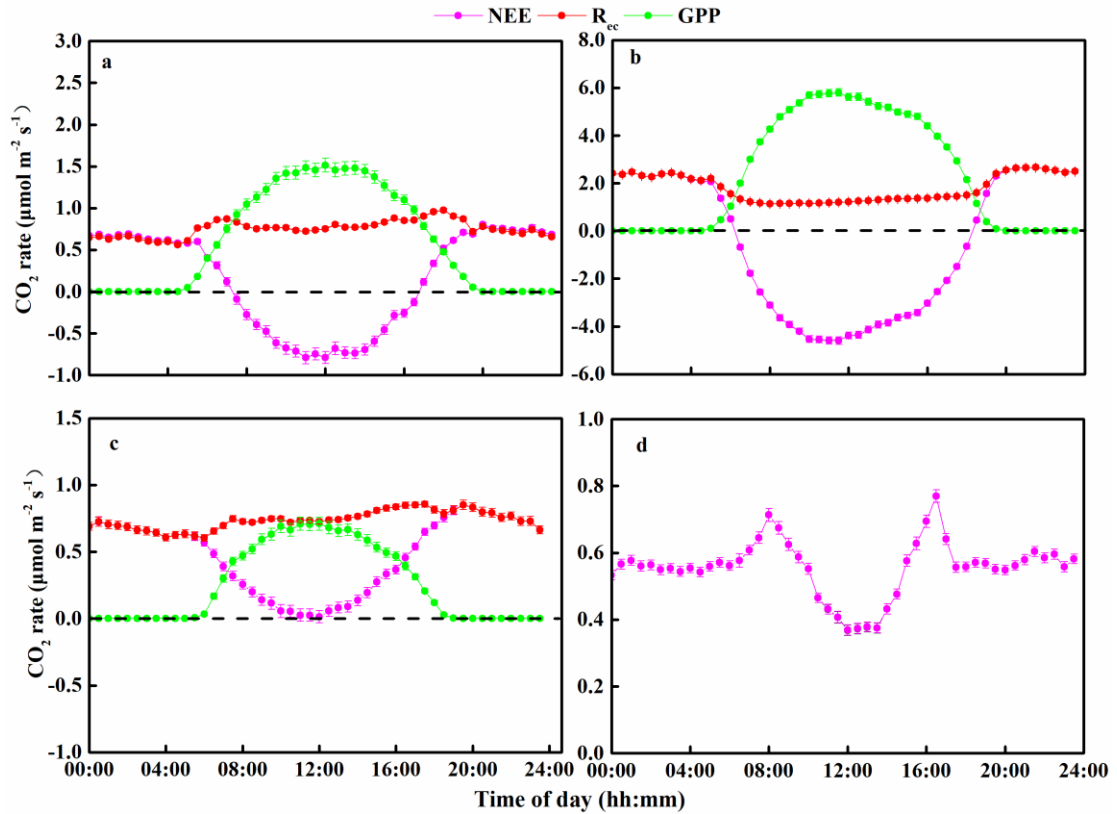
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1017 **Fig. 4.**



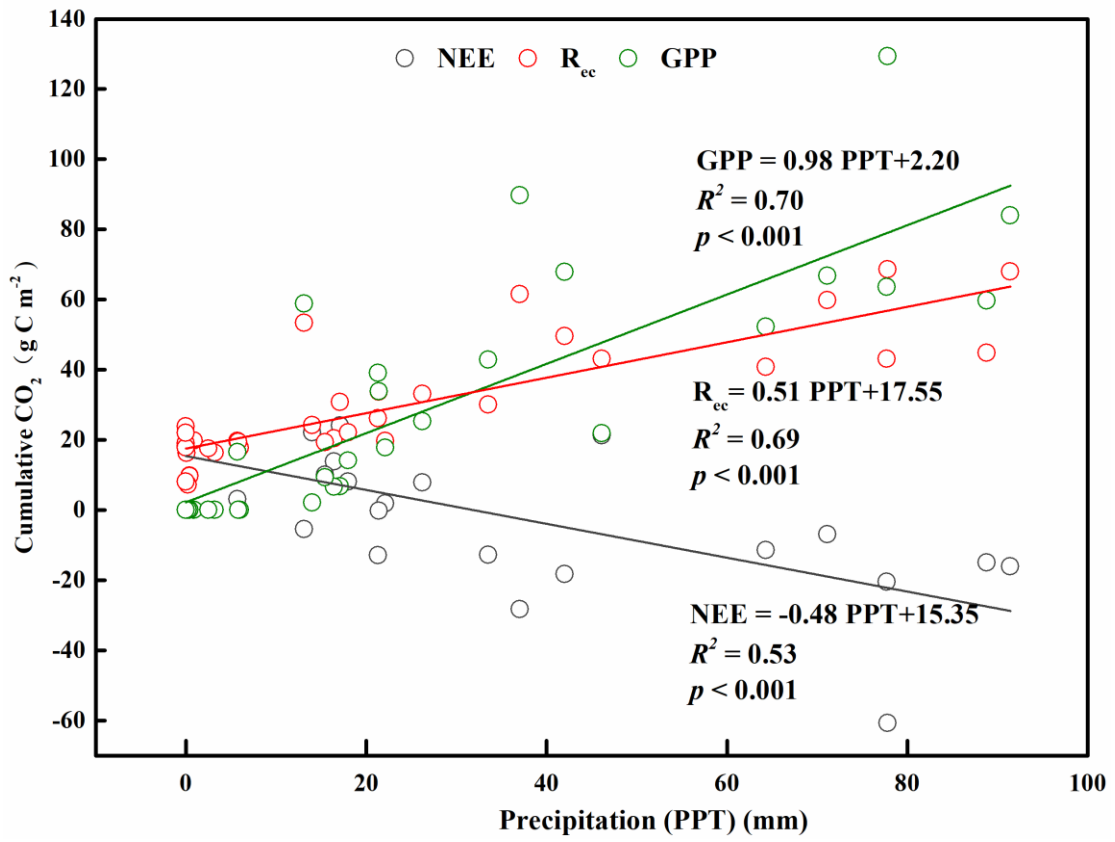
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1019 **Fig. 5.**



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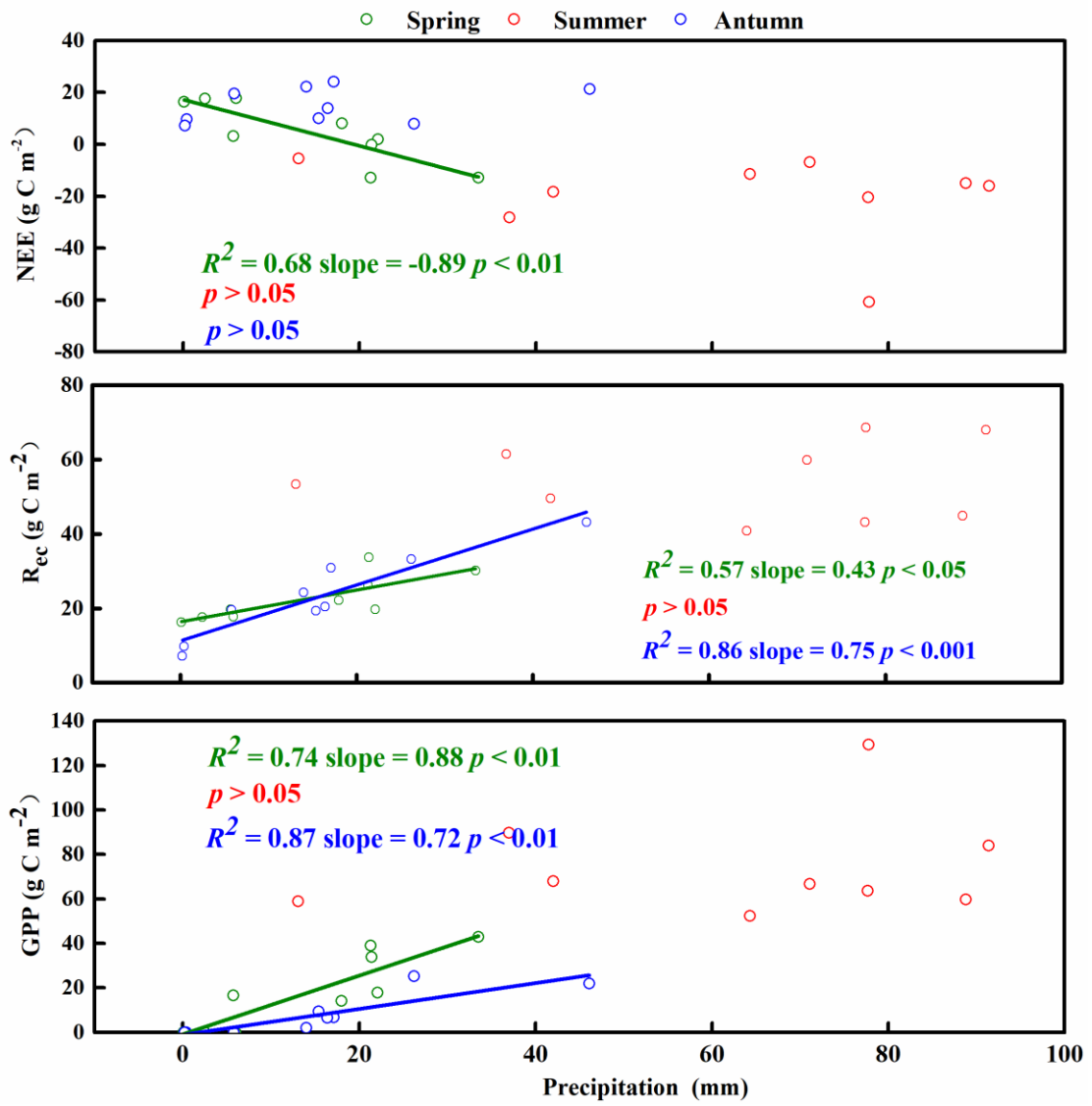
1021 **Fig. 6**



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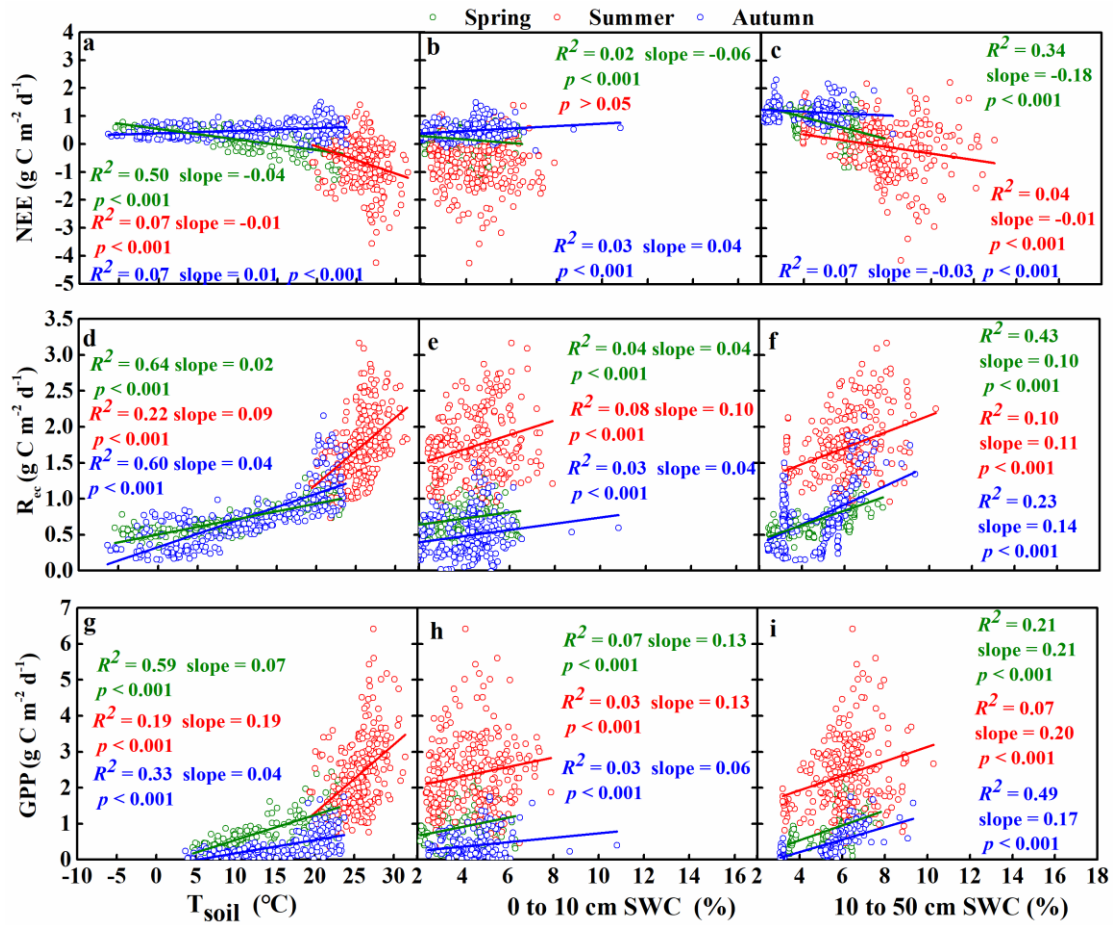
1024 **Fig. 7**



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1027 **Fig. 8**



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1029 **Table 1** Seasonal number of precipitation events for all years, grouped by size class and
 1030 season, and the total precipitation.

Season	Year	Magnitude of precipitation event (mm)					Total Precipitation (mm)
		0-5	5-10	10-15	15-20	> 20	
Spring	2015	10	2	2	0	0	43.5
	2016	15	2	1	0	0	41.7
	2018	10	2	1	0	0	45.4
Summer	2015	22	7	3	0	0	132.8
	2016	39	5	3	2	1	172.4
	2018	26	4	2	1	5	258.0
Autumn	2015	13	3	0	0	0	31.5
	2016	12	2	1	0	1	62.7
	2018	9	1	2	0	0	47.4

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