

Rainfall variability in ecosystem CO₂ flux studies

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ABSTRACT: The structure and function of ecosystems are strongly affected by rainfall variability in grasslands worldwide. We used a diversity index (Shannon index [I]) and 3 non-diversity indices (coefficient of variation [CV], standard deviation [SD], and dry days [U_d]) to analyze rainfall variability and the relationship of rainfall variability with 1982–2008 above-ground net primary productivity (ANPP) and 2003–2008 growing season (May–September) net ecosystem CO₂ exchange (NEE). A series of bivariate regressions were performed with precipitation (P) and 1 measure of its temporal variability (CV, I , SD, or U_d) as an independent variable. The regression models were evaluated with regard to their ability to predict ANPP. Only the model with P and I as the predictors was statistically significant at $p < 0.01$, and had the highest coefficient of determination ($R^2 = 0.50$). ANPP increased with increasing I ($r = 0.45$, $p = 0.05$), but no consistent relationship with the total amount of annual rainfall was observed ($r = -0.17$, $p = 0.46$). Using all data from a 6 yr study period, the Shannon index explained 50% of the change in NEE. In general, the Shannon index had the best spread and sensitivity under different rainfall regimes and was the most appropriate index for carbon flux studies.

KEY WORDS: Rainfall variability · Shannon index · Coefficient of variation · Standard deviation · Dry day

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1. INTRODUCTION

Altered precipitation patterns resulting from increasing atmospheric concentrations of carbon dioxide (CO₂) and other greenhouse gases are receiving increasing attention from scientists (Trenberth 1999, Harper et al. 2005). These changes include the increasing frequency of seasonal droughts and extreme rainfall events (Easterling et al. 2000). Such changes in the growing season are also likely to have larger per-event precipitation inputs separated by longer dry intervals, and may have important ecological consequences for ecosystem production (Knapp & Seastedt 1985, Fay et al. 2003).

Recently, many studies on the relationship between precipitation and carbon flux have focused on grassland ecosystems. Grasslands exhibit strong and rapid structural and functional responses to this variability in seasonal rainfall (Weltzin et al. 2003). These studies have investigated how productivity, carbon fluxes, and physiology respond to altered rainfall patterns using both observational and manipulation studies in grasslands (Knapp et al. 2002, Fay et al. 2003, Huxman

et al. 2004, Reynolds et al. 2004, Harper et al. 2005). Although these studies have provided us with a better understanding of the responses of terrestrial ecosystems to potential changes in precipitation, few studies have recognized the importance of quantifying the degree of rainfall variability in grassland ecosystems in different environments. Although difficult to quantify, an index of rainfall changes that quantitatively describes the relationship between rainfall variability and carbon fluxes would be beneficial. To achieve this goal, it is necessary to explore various metrics of interannual and seasonal rainfall change in order to identify the most appropriate measures for carbon flux studies.

The metrics analyzed herein include annual and monthly measures of rainfall evenness (the spread of rainfall across the months of a given year), the monthly coefficient of variation across days, the standard deviation (SD) of mean monthly rainfall, and the number of dry days during 6 growing seasons (2003–2008). Our objective was to identify the most appropriate index for describing the rainfall variability used in ecosystem CO₂ flux studies.

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2. MATERIALS AND METHODS

2.1. Site description

The experimental site is located within the Inner Mongolia Grassland Ecosystem Research Station in the Xilin River Watershed of the Inner Mongolia Autonomous Region (43° 32' N, 116° 40' E, 1200 m above sea level [a.s.l.]). The study site, of 400 × 600 m dimensions, has been fenced off since 1979 and is located on a smooth wide plain containing low hills. The tops of the low hills are 20 to 30 m above the surrounding plain, and the hills have slopes of <5°. The climate of the area is a semi-arid continental temperate steppe climate with a dry spring and humid summer. The average annual temperature is -0.4°C, with a growing season of 150 to 180 d. The annual precipitation range is 320 to 400 mm, and rainfall is concentrated within the June to August period.

The soil at the experimental site is a dark chestnut (Mollisol), and the soil depth is usually >125 to 150 cm (Wang & Cai 1988). The A-horizon extends to a depth of 20 to 30 cm, and there is no obvious CaCO₃ layer in the soil profile. The soil consists of 21% clay, 60% sand, and 19% silt. Of the 86 species of flowering plants that belong to 28 families and 67 genera at the site, 11 of them are grass species (Jiang 1985). The xeric rhizomatous grass *Leymus chinensis* is the constructive species, and *Agropyron cristatum*, *Cleistogenes squarrosa*, and *Carex duriuscula* are the dominant species. The heights of grass clusters are 50 to 60 cm; the coverage averages 30 to 40%, but can reach as high as 60 to 70% during rainy years. Litter is able to accumulate within the enclosure by preventing sheep from grazing in the area.

2.2. Vegetation sampling

Field sampling began in early May and ended in mid-October, at intervals of about 2 wk since 1982. Five 1 m² quadrats were randomly placed on each sampling date. Cover, density, growth height, and phenological phases of each species were recorded. The above-ground parts of the vegetation were clipped to ground level and immediately returned to the laboratory for dry-matter measurements. The clipped plant material was separated into live and standing dead parts, which were weighed as the fresh weight of live biomass and standing dead, respectively. Plant materials were oven-dried at 65°C, and dry weights of live biomass and standing dead were recorded (Xiao et al. 1995). Litter from the sampled quadrats was also collected. Between 1987 and 1989, only measurements of above-ground live biomass were taken; therefore, data

on standing dead are unavailable for that period. The summation of peak live above-ground biomass of individual species was used to calculate annual above-ground net primary productivity (ANPP) during the growing season (Xiao et al. 1995).

2.3. Net ecosystem exchange and rainfall measurements

An eddy covariance system (EC) was utilized to measure continuous CO₂ flux over the grassland. The footprint area calculated using the footprint model (Kljun et al. 2004) from the predominant wind directions is about 200 m. CO₂ flux was measured at 2.2 m above the ground using an open-path infrared CO₂/H₂O gas analyzer (LI-7500, LI-COR). The EC measurements were taken at a frequency of 10 Hz, and turbulent fluxes were recorded on a datalogger (CR5000, Campbell Scientific) as half-hour averages. A tipping bucket rain gauge positioned at 1.5 m above the ground (TE525MM, Campbell Scientific) was used to measure precipitation, which was recorded with a digital datalogger (CR23X, Campbell Scientific; for details, see Hao et al. 2007).

2.4. Data analysis

A 3-dimensional coordinate rotation was applied to the 3-dimensional wind components, which aligned the horizontal velocity measurement normal to the mean wind streamlines and brought the averaged lateral and vertical velocity components to zero. To investigate the effects of various coordinate rotations, we also applied a planar-fit rotation (Wilczak et al. 2001). The difference between any 2 corrections, however, was only minor. A density correction was also applied to the flux calculations (Webb et al. 1980). Approximately 20% of the data obtained from our EC system was discarded due to precipitation and power failure leading to data gaps. To fill in missing data resulting from data-screening criteria (Lee & Fuentes 1999) and instrument malfunction, we used the MDV (mean diurnal variation) (Falge et al. 2001) and interpolation methods (Xu & Baldocchi 2004).

Since we were interested in how to quantify rainfall variability in a meaningful manner, we analyzed rainfall and ANPP between 1982 and 2008, and NEE (net ecosystem exchange, with negative values indicating that CO₂ was absorbed by the grassland) for the 2003–2008 growing seasons. At the same time, we also quantitatively analyzed the relationship between rainfall variability and ANPP by regression analysis.

2.5. Evenness of rainfall

For rainfall evenness, a modified Shannon index, which reflects both the number of species and their relative abundance, was applied from species diversity literature (Magurran 1988, Bronikowski & Webb 1996), with the formula as follows:

$$I = \frac{-\sum p_i \ln(p_i)}{\ln(N)}$$

where p_i is the proportion of rainfall per month or day and N is number of months (12) or days (30 or 31). In diversity indices used in the simulation study, the number of species is analogous to the number of months in a year or days in a month, and the proportion of the total sample in each species is analogous to the proportion of rainfall in each event to total annual rainfall in each year or monthly rainfall in each month. A diversity index equal to 1 implies complete evenness (i.e. equivalent amounts of rain in each month or day), and an index equal to 0 implies complete unevenness (i.e. all rain in 1 mo or 1 d) (Bronikowski & Webb 1996).

There is no *a priori* choice for using the Shannon index as a more accurate reflection of the variability of rainfall across days than other variability indices, although some indices may be more appropriate for certain study objectives. For this reason, we also considered other variability indices, including (1) the coefficient of variation (CV), (2) the SD of mean annual rainfall or monthly rainfall during the growing season (May–September), and (3) the number of months (U_m) with $<20 \text{ mm mo}^{-1}$ of rainfall per year or the number of days (U_d) with $<3 \text{ mm d}^{-1}$ of rainfall per month ($<20 \text{ mm mo}^{-1}$ rainfall or $>3 \text{ mm d}^{-1}$ rainfall may be more effective to stimulate ecosystem carbon uptake than $<3 \text{ mm d}^{-1}$ for this grassland; Hao et al. 2010) (Table 1).

3. RESULTS

3.1. Precipitation and ANPP in 1982–2008

Total annual precipitation and ANPP from 1982 to 2008 are shown in Fig. 1. Total annual precipitation varied from 127 mm in 2005 to 507 mm in 1998, with a mean of 333 mm. On average, 89% of the annual rainfall occurs in the period from April to September. ANPP varied considerably, from 107.2 g m^{-2} in 1982 to 254.2 g m^{-2} in 1990, with an average ANPP of 186.3 g m^{-2} . The variability in ANPP was associated with low annual precipitation

and large interannual variation in rainfall on this steppe. Peak above-ground live biomass of the *L. chinense* steppe generally was observed in the period between late July and late August.

Table 1. Shannon diversity (I), coefficient of variation (CV), standard deviation (SD), and dry months $<20 \text{ mm}$ rainfall (U_m), 1982–2008, at a *Leymus chinense*-dominated steppe in the Inner Mongolia Plateau, China. Note: the data from 1999 to 2002 are default

Year	I	CV	SD	U_m
1982	0.40	120.89	28.53	6
1983	0.77	111.68	26.98	7
1984	0.74	126.00	33.36	7
1985	0.76	129.71	34.37	7
1986	0.74	116.29	41.58	7
1987	0.48	120.51	33.03	7
1988	0.72	133.61	34.63	7
1989	0.81	103.31	24.89	7
1990	0.57	200.55	75.92	9
1991	0.71	141.67	44.18	8
1992	0.79	108.79	41.25	6
1993	0.75	127.06	38.46	8
1994	0.74	133.78	34.63	7
1995	0.77	108.02	26.12	7
1996	0.71	137.61	40.58	8
1997	0.79	103.30	25.70	7
1998	0.70	152.27	64.33	7
2003	0.76	116.27	37.91	7
2004	0.70	126.79	39.26	7
2005	0.56	160.93	16.96	9
2006	0.64	153.46	38.18	8
2007	0.50	135.01	20.15	8
2008	0.60	130.93	26.25	8

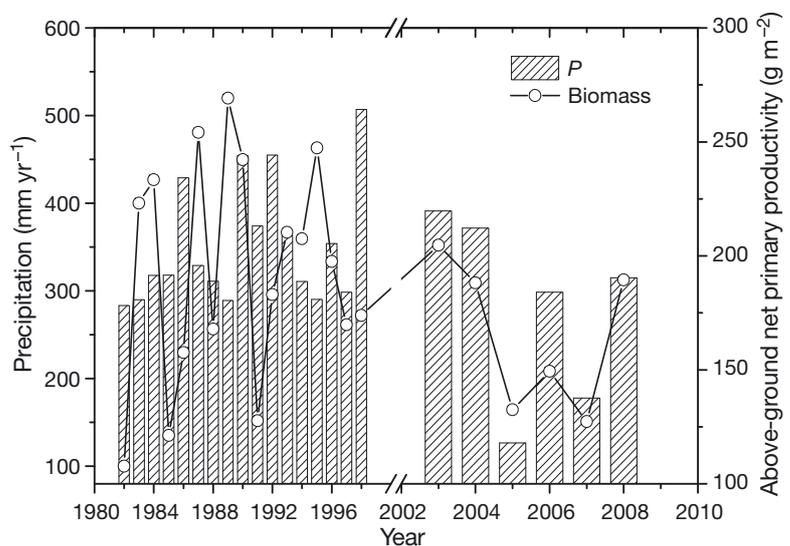


Fig. 1. Annual precipitation (P) and above-ground net primary productivity (Biomass) from 1982 to 2008, over a *Leymus chinense*-dominated steppe in Mongolia Plateau, China

Table 2. Regression analysis of rainfall variability measures and above-ground net primary productivity (ANPP) in 1982–2008 over a *Leymus chinense*-dominated steppe in Inner Mongolia, China. P_T : total precipitation; I : Shannon diversity; CV: coefficient of variation; SD: standard deviation; U_m : dry months <20 mm rainfall

	Analysis	R^2	F (df)	p
Rain and Shannon	$ANPP = -3.98 + 0.01(P_T) + 275.82(I)$	0.50	10.3 (2, 20)	<0.01
Rain and CV	$ANPP = 192.30 + 0.13(P_T) - 0.39(CV)$	0.11	0.92 (2, 20)	0.42
Rain and SD	$ANPP = 141.36 + 0.19(P_T) - 0.54(SD)$	0.10	0.61 (2, 20)	0.55
Rain and dry days	$ANPP = 136.37 + 0.13(P_T) + 1.11(U_m)$	0.12	0.54 (2, 20)	0.59

Table 3. Shannon diversity (I), coefficient of variation (CV), standard deviation (SD), dry days (U_d), and net ecosystem exchange (NEE, mol CO₂ m⁻² mo⁻¹) during the 2003–2008 growing seasons. P_g : growing season precipitation

	P_g (mm)	I	CV	SD	U_d	NEE
2003						
May	67	0.52	45	4.58	25	0.46
Jun	61	0.64	47	12.56	24	-3.08
Jul	115	0.68	63	20.58	23	-1.79
Aug	80	0.60	48	15.02	26	-1.05
Sep	61	0.57	42	4.93	26	-0.87
2004						
May	30	0.48	39	2.47	27	1.72
Jun	74	0.53	42	5.78	26	-0.04
Jul	62	0.59	47	4.18	24	-3.44
Aug	121	0.57	42	9.15	23	-5.76
Sep	59	0.46	37	5.27	25	-1.91
2005						
May	13	0.47	38	1.06	29	0.61
Jun	39	0.46	36	3.57	27	0.23
Jul	47	0.74	59	2.53	28	1.11
Aug	25	0.42	33	2.40	28	0.01
Sep	3	0.32	29	0.30	30	1.26
2006						
May	2	0.24	26	0.29	31	2.69
Jun	76	0.53	36	7.33	25	-0.03
Jul	123	0.67	10	6.84	22	-0.80
Aug	20	0.26	71	1.86	29	1.36
Sep	40	0.45	36	3.65	27	-0.22
2007						
May	31	0.30	48	2.06	27	1.58
Jun	22	0.60	36	1.97	28	-2.57
Jul	66	0.30	23	4.63	26	2.66
Aug	33	0.51	16	2.66	28	-1.42
Sep	12	0.46	38	1.07	28	1.59
2008						
May	42	0.40	42	3.21	29	0.70
Jun	66	0.60	40	5.72	24	-2.51
Jul	76	0.31	32	9.44	29	-0.49
Aug	93	0.68	5.0	6.06	23	-6.02
Sep	10	0.56	47	0.71	30	-2.86

3.2. Relationship between the 4 indices and ANPP

Using data from all years in the study period, the 4 indices (I , SD, CV, and U_m) and total annual precipitation (P_T) were applied in a series of multiple regressions to analyze and predict ANPP for this typical grassland in the Inner Mongolia Plateau. The multiple re-

gressions indicated that between ANPP and I , P_T had a higher coefficient of determination, $R^2 = 0.50$ ($p < 0.01$), while that between other indices and P_T was $R^2 = 0.10$ ($p > 0.1$) (Table 2). The Shannon index and P_T explained 50% of ANPP variability. The coefficients for I and U_m were positive, whereas the coefficients for CV and SD were negative and essentially zero.

The ANPP increased with increasing I ($r = 0.45$, $p = 0.05$; Fig. 2b), but no consistent relationship with the total amount of annual rainfall was observed for ANPP ($r = -0.17$, $p = 0.46$; Fig. 2a). The CV and SD were weakly and negatively correlated with ANPP ($r = -0.40$, $p = 0.05$ for CV and $r = -0.31$, $p = 0.19$ for SD; Fig. 2c,d).

3.3. Precipitation, NEE, and the 4 indices in the 2003–2008 growing seasons

To evaluate the relationship between 4 indices and NEE, it is necessary to understand the variation in precipitation, NEE, and 4 indices during the growing season (May–September; Table 3). They exhibited both intra- and interannual change during the 6 study years. The maximum values for monthly precipitation occurred in July or August of each year, ranging from 47 mm in July of 2005 to 123 mm in July of 2006. The monthly I , CV, and SD values during the growing season were different among the 6 years. However, the U_d values during the study period were similar. Integrated monthly values of NEE for the 6 yr study period reached large values (-6.02 to -0.02 mol CO₂ m⁻² mo⁻¹) from June to August of each year, except 2005, with negative values indicating that CO₂ was absorbed by the grassland.

3.4. Relationship between the 4 indices and NEE

The 4 indices and total growing season precipitation (P_g) during the 6 growing seasons were employed to determine the relationship between NEE and the 4 indices in this grassland ecosystem (Table 4). For the 2003 growing season, P_g and I explained 99% of the total

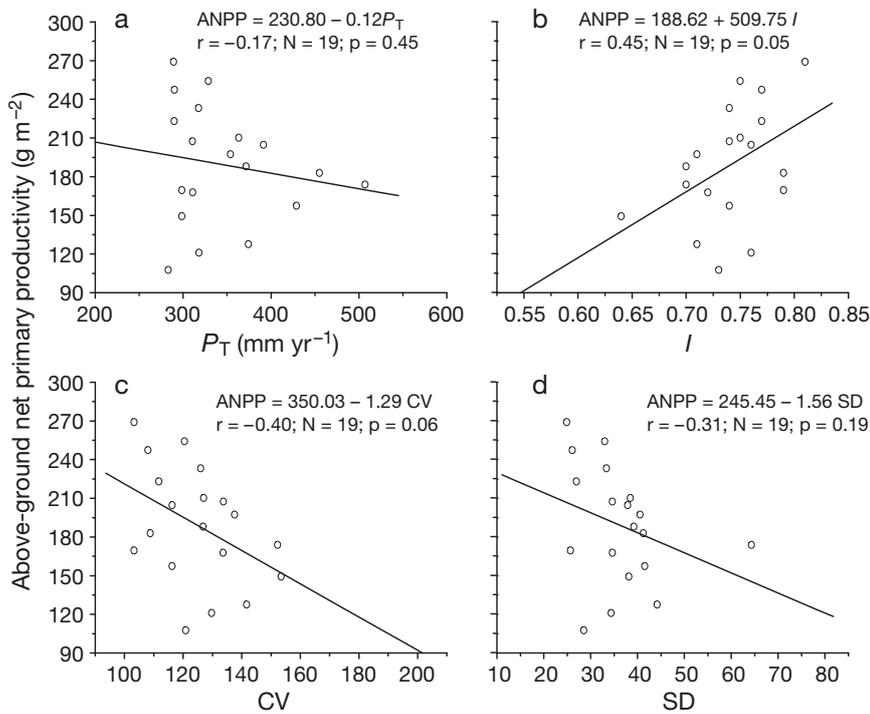


Fig. 2. Relationship between above-ground net primary productivity (ANPP) and (a) total annual precipitation (P_T), (b) Shannon diversity index (I), and (c,d) 2 non-diversity indices (coefficient of variation [CV], standard deviation [SD])

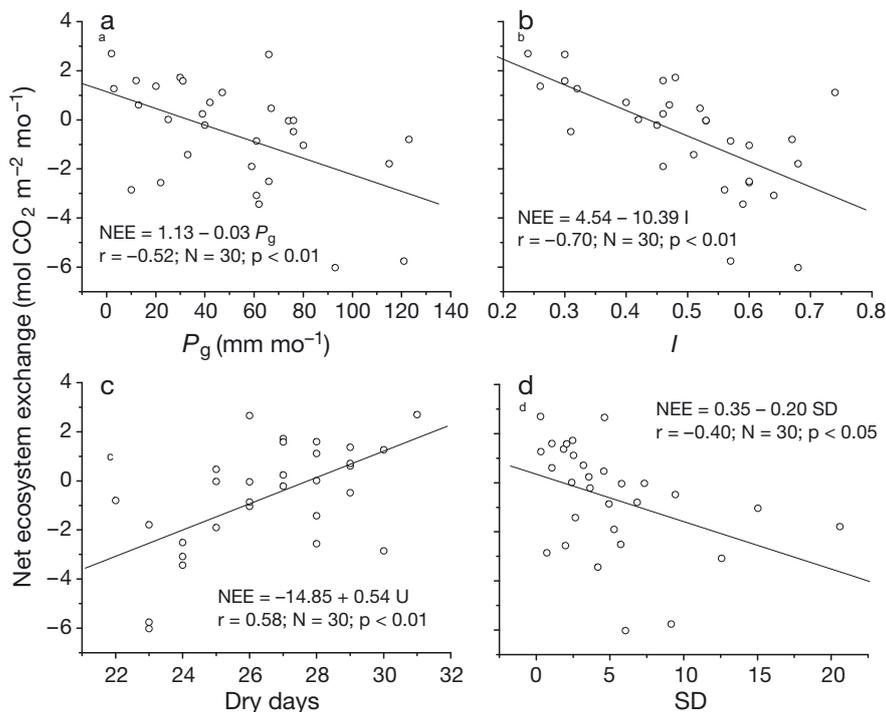


Fig. 3. Relationship between net ecosystem CO₂ exchange (NEE) at the ecosystem level and (a) growing season precipitation (P_g , May–September), (b) Shannon diversity index (I), and (c,d) 2 non-diversity indices (dry days [U_d] and standard deviation [SD], respectively)

variance in NEE with a linear model ($p < 0.01$). In other years, P_g and I were also the most prominent predictors of NEE, with the exception of 2005, when P_g and U_d explained a greater percentage of total variance in NEE ($R^2 = 0.87$, $p = 0.13$). When data from the entire 6 yr period were analyzed together, the R^2 value for I was 0.45 ($p < 0.01$). The other 3 indices (CV, SD, and U_d) were 0.27, 0.27, and 0.34 ($p < 0.05$), respectively.

Data from the entire 6 yr period were analyzed together in order to determine the relationships between NEE and P_g , I , CV, SD, and U_d . NEE and the variability indexes I , P_g , and SD were negatively correlated, while NEE and U_d were positively correlated (Fig. 3). The Shannon index correlated most strongly with monthly NEE and explained about 50 % of the variation in NEE ($R^2 = 0.49$, $p = 0.02$). The CV exhibited no significant relationship with NEE (data not shown).

4. DISCUSSION

Alterations in precipitation patterns, such as variation in the amount and timing of rainfall, have attracted many ecologists to research the effects of changing rainfall on ecosystem processes (Fay et al. 2002, 2003, Knapp et al. 2002, Weltzin et al. 2003, Harper et al. 2005). The CV and SD have frequently been used to describe the degree of change in rainfall (Xiao et al. 1995, Fay et al. 2003). For example, Fay et al. (2002) have utilized the length of dry periods to depict rainfall regimes. Bronikowski & Webb (1996) used the Shannon index (I) to critically examine rainfall variability measures for behavioral ecology studies.

Our objective in the present study was to identify the index of rainfall variability that best represents variability in carbon flux studies. According to our analysis, the diversity index—the Shannon index (I)—exhibited the best spread and sensitivity under different rainfall regimes. This diversity measure was analyzed, not only using the Shannon index (I), but by the Simpson, McIntosh, Berger-Parker, and Brillouin indices, which were also used by Bronikowski & Webb (1996). These in-

Table 4. Regression analysis of rainfall variability and carbon flux (NEE, net ecosystem exchange, mol CO₂ m⁻² mo⁻¹) for 6 growing seasons in 2003–2008 over a *Leymus chinense*-dominated steppe grassland in Inner Mongolia, China. P_g : growing season precipitation; I : Shannon diversity; CV: coefficient of variation; SD: standard deviation; U_d : dry days

Analysis	Regression Equation	R ²	F (df)	p
2003				
Rain and Shannon	NEE = -12.16 - 0.04(P_g) + 27.74(I)	0.99	128 (2, 4)	<0.01
Rain and CV	NEE = -9.23 - 0.15(P_g) + 0.44(CV)	0.57	1.32 (2, 4)	0.43
Rain and SD	NEE = 2.86 - 0.06(P_g) + 0.28(SD)	0.72	2.6 (2, 4)	0.28
Rain and dry days	NEE = 20.11 - 0.018(P_g) - 0.70(U_d)	0.32	0.48 (2, 4)	0.68
2004				
Rain and Shannon	NEE = -9.26 - 0.06(P_g) + 13.29(I)	0.80	2.85 (2, 4)	0.26
Rain and CV	NEE = -9.58 + 0.07(P_g) + 0.16(CV)	0.73	2.83 (2, 4)	0.26
Rain and SD	NEE = -2.79 + 0.15(P_g) - 1.10(SD)	0.73	2.7 (2, 4)	0.27
Rain and dry days	NEE = 44.65 + 0.006(P_g) - 1.73(U_d)	0.53	2.56 (2, 4)	0.35
2005				
Rain and Shannon	NEE = 0.35 + 0.32(P_g) - 3.76(I)	0.46	0.84 (2, 4)	0.54
Rain and CV	NEE = 0.57 + 0.03(P_g) - 0.05(CV)	0.58	1.41 (2, 4)	0.43
Rain and SD	NEE = 7.11 - 0.04(P_g) + 0.76(SD)	0.78	3.58 (2, 4)	0.22
Rain and dry days	NEE = 24.05 - 0.04(P_g) - 0.84(U_d)	0.87	0.44 (2, 4)	0.13
2006				
Rain and Shannon	NEE = 4.56 + 0.02(P_g) - 11.31(I)	0.85	5.77 (2, 4)	0.14
Rain and CV	NEE = 2.64 - 0.03(P_g) - 0.01(CV)	0.77	3.41 (2, 4)	0.23
Rain and SD	NEE = 2.16 - 0.01(P_g) - 0.26(SD)	0.78	3.62 (2, 4)	0.21
Rain and dry days	NEE = 43.25 + 0.008(P_g) + 1.47(U_d)	0.90	230.36 (2, 4)	<0.05
2007				
Rain and Shannon	NEE = 8.30 - 0.02(P_g) - 16.90(I)	0.82	4.60 (2, 4)	0.18
Rain and CV	NEE = -5.22 + 0.08(P_g) + 0.10(CV)	0.41	0.71 (2, 4)	0.58
Rain and SD	NEE = 1.67 + 0.57(P_g) - 8.09(SD)	0.71	2.49 (2, 4)	0.28
Rain and dry days	NEE = 112.05 - 0.11(P_g) - 3.95(U_d)	0.72	2.57 (2, 4)	0.28
2008				
Rain and Shannon	NEE = 6.29 - 0.02(P_g) - 14.4(I)	0.84	5.28 (2, 4)	0.15
Rain and CV	NEE = -11.32 + 0.05(P_g) + 0.18(CV)	0.62	1.64 (2, 4)	0.37
Rain and SD	NEE = -0.68 - 0.11(P_g) + 0.91(SD)	0.52	1.08 (2, 4)	0.48
Rain and dry days	NEE = -23.66 + 0.02(P_g) + 0.74(U_d)	0.54	1.18 (2, 4)	0.45
2003–2008				
Rain and Shannon	NEE = 4.29 - 0.02(P_g) - 8.22(I)	0.45	10.95 (2, 4)	<0.01
Rain and CV	NEE = 0.67 - 0.03(P_g) + 0.11(CV)	0.27	5.09 (2, 27)	<0.05
Rain and SD	NEE = 1.13 - 0.03(P_g) - 0.01(SD)	0.27	4.96 (2, 27)	<0.05
Rain and dry days	NEE = -13.32 - 0.004(P_g) + 0.49(U_d)	0.34	3.95 (2, 27)	<0.05

indices could be appropriate for different purposes. Ideally, for carbon flux studies, one would choose an index based on how well it correlated with carbon exchange. Bronikowski & Webb (1996) tested these diversity indices under varying rainfall regimes and suggested that the Shannon index exhibited the best properties. Of the non-diversity indices analyzed, the index for the number of dry days was the most ambiguous. For the 2003 and 2004 growing seasons, the corresponding regression coefficients had the smallest values when compared with other indices. However, the number of dry days had the maximum regression coefficient in the 2005 growing season (Table 4). These findings are probably due to the extreme drought status in 2005 (only 126 mm precipitation from May to September). Although the Shannon index and 2 other non-diversity indices were consistently

informative in regression models between 2003 and 2008, we should not ignore the importance of the number of dry days as a rainfall variability index.

Carbon flux is affected by differences in the distribution of rain. Furthermore, diurnal changes in rainfall may be significant to the process of carbon cycling (Austin et al. 2004, Huxman et al. 2004). For example, the size of a precipitation pulse may affect the duration and magnitude of subsequent carbon fluxes (Huxman et al. 2004). If carbon fluxes are truly affected by the interannual difference in the monthly distribution of rainfall, the relationship between carbon flux and variability in rainfall should be a factor when choosing between apparently reasonable variability measurements (Bronikowski & Webb 1996). As Fig. 3 clearly illustrates, NEE is most strongly negatively correlated with I ($r = -0.70$, $p = 0.05$) and most positively correlated with U_d ($r = 0.58$, $p = 0.05$). The negative correlation between NEE and I indicates that the ecosystem absorbs more CO₂ as rainfall distribution becomes more even. The positive correlation with U_d indicates that more CO₂ is released from the ecosystem to the atmosphere as rainfall distribution becomes more uneven.

Previous studies suggested that grassland ANPP was influenced by precipitation quantity and intra-annual rainfall variability (Briggs & Knapp 1995, 2001, Nippert et al. 2006). However, the relationship between ANPP and precipitation was not significant ($r = -0.17$, $p = 0.45$; Fig. 2a) in our study. We should note that ANPP and the Shannon index were positively correlated ($r = 0.45$, $p = 0.05$; Fig. 2b), whereas the correlation with the CV was highly negatively correlated ($r = -0.40$, $p = 0.05$; Fig. 2c). The Shannon index was more informative in the regression model than the other 3 non-diversity measures of variability. The relationship between CO₂ fluxes and variability in precipitation should be robust to the choice among apparently reasonable variability measures.

Currently, the CV has been widely used to describe rainfall variability (Nicholls & Wong 1990, Xiao et al. 1995, Fang et al. 2001, Bonebrake & Mastrandrea

2010). CV and *I* showed a high negative correlation ($r = -0.90$, $p < 0.001$). The higher CV indicated a more uneven distribution of precipitation, and higher rainfall variability. SD and CV had no significantly positive correlation ($r = 0.17$, $p = 0.60$). Similarly, *I* and SD also had a (non-significant) negative correlation ($r = -0.30$, $p = 0.17$). Considering the discussion above, the Shannon index appears to be the most appropriate index to describe rainfall variability when analyzing carbon flux.

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LITERATURE CITED

- Bronikowski A, Webb C (1996) Appendix: a critical examination of rainfall variability measures used in behavioral ecology studies. In: Bronikowski AM & Altman J (1996) Foraging in a variable environment: weather patterns and the behavioral ecology of Baboons. *Behav Ecol Sociobiol* 39:27–30
- Austin AT, Yahdjian ML, Stark JM, Belnap J, Porporato A (2004) Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141:221–235
- Briggs JM, Knapp AK (1995) Interannual variability in primary production in tallgrass prairie, climate, soil moisture, topographic position and fire as determinants of above-ground biomass. *Am J Bot* 82:1024–1030
- Briggs JM, Knapp AK (2001) Determinants of C₃ forb growth and production in a C₄ dominated grassland. *Plant Ecol* 152:93–100
- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. *Science* 289:2068–2074
- Falge E, Baldocchi DD, Richard O (2001) Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agric For Meteorol* 107:43–69
- Fang J, Piao S, Tang Z, Peng C, Ji W (2001) Interannual variability in net primary production and precipitation. *Science* 293:1723
- Fay PA, Jonathan DC, Brett TD, Michelle SL (2002) Altered rainfall patterns, gas exchange, and growth in grasses and forbs. *Int J Plant Sci* 163:549–557
- Fay PA, Carlisle JD, Knapp AK (2003) Productivity response to altered rainfall patterns in a C₄-dominated grassland. *Oecologia* 137:245–251
- Hao YB, Wang YF, Huang XZ (2007) Seasonal and interannual variation in water vapor and energy exchange over a typical steppe in Inner Mongolia, China. *Agric For Meteorol* 146:57–69
- Hao YB, Wang YF, Cui XY (2010) The response of ecosystem CO₂ exchange to small precipitation pulses over a temperate steppe. *Plant Ecol* 209:335–347
- Harper CW, John MB, Philip AF, Alank K, Jonathan DC (2005) Increased rainfall variability and reduced rainfall amount decreases soil CO₂ flux in a grassland ecosystem. *Glob Change Biol* 11:322–334
- Huxman TE, Snyder KA, Tissue D (2004) Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141:254–268
- Jiang S (1985) An introduction to the Inner Mongolia Grassland Ecosystem Research Station, Academia Sinica. In: Inner Mongolia Grassland Ecosystem Research Station (ed) Research on grassland ecosystem. Science Press, Beijing, p 1–11
- Kljun N, Calanca P, Rotach MW (2004) A simple parameterization for flux footprint predictions. *Boundary-Layer Meteorol* 112:503–523
- Knapp AK, Seastedt TR (1985) Grassland, Konza Prairie, and long-term ecological research. In: Knapp AK, Briggs JM, Hartnett DC, Collins SL (eds) Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, p 3–15
- Knapp AK, Fay PA, Blair JM, Collins SL (2002) Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298:2202–2204
- Lee X, Fuentes D (1999) Long-term observation of the atmospheric exchange of CO₂ with a temperate deciduous forest in southern Ontario, Canada. *J Geophys Res* 104: 15975–15984
- Magurran AE (1988) Ecological diversity and its measurement. Princeton University Press, Princeton, NJ
- Nicholls N, Wong KK (1990) Dependence of rainfall variability on mean rainfall, latitude, and the Southern Oscillation. *J Clim* 3:163–170
- Nippert JB, Knapp AK, Briggs JM (2006) Intra-annual rainfall variability and grassland productivity: Can the past predict the future? *Plant Ecol* 184:65–74
- Reynolds JF, Kemp PR, Ogle K, Fernandez RJ (2004) Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water and plant responses. *Oecologia* 141:194–210
- Bonebrake TC, Mastrandrea MD (2010) Tolerance adaptation and precipitation changes complicate latitudinal patterns of climate change impacts. *Proc Natl Acad Sci USA* 107: 12581–12586
- Trenberth KE (1999) Conceptual framework for changes of extremes of the hydrological cycle with climate change. *Clim Change* 42:327–339
- Wang J, Cai Y (1988) Studies of genesis, types and characteristics of the soils of the Xilin River basin. In: Inner Mongolia Grassland Ecosystem Research Station (ed) Research on grassland ecosystem. Science Press, Beijing, p 23–83
- Webb EK, Pearman GI, Leuning R (1980) Correction of flux measurements for density effects due to heat and water vapor transfer. *Q J R Meteorol Soc* 106:85–100
- Weltzin JF, Loik ME, Schwinning S (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience* 53:941–952
- Wilczak JM, Oncley SP, Stage SA (2001) Sonic anemometer tilt correction algorithms. *Boundary-Layer Meteorol* 99: 127–150
- Xiao XM, Wang YF, Jiang S, Ojima D (1995) Interannual variation in the climate and above-ground biomass of *Leymus chinensis* steppe and *Stipa grandis* steppe in Xilin River basin, Inner Mongolia, China. *J Arid Environ* 31:283–299
- Xu L, Baldocchi DD (2004) Seasonal variation in carbon dioxide exchange over Mediterranean annual grassland in California. *Agric For Meteorol* 123:79–96

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