

Geographical and interannual variability in biomass partitioning in grassland ecosystems: a synthesis of field data

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Summary

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- Biomass partitioning is an important variable in terrestrial ecosystem carbon modeling. However, geographical and interannual variability in f_{BNPP} , defined as the fraction of belowground net primary productivity (BNPP) to total NPP, and its relationship with climatic variables, have not been explored.
- Here we addressed these issues by synthesizing 94 site-year field biomass data at 12 grassland sites around the world from a global NPP database and from the literature.
- Results showed that f_{BNPP} varied from 0.40 to 0.86 across 12 sites. In general, savanna and humid savanna ecosystems had smaller f_{BNPP} but larger interannual variability in f_{BNPP} , and cold desert steppes had larger f_{BNPP} but smaller interannual variability. While mean f_{BNPP} at a site decreased significantly with increasing mean annual temperature and precipitation across sites, no consistent temporal response of f_{BNPP} with annual temperature and precipitation was found within sites.
- Based on these results, both geographical variability in f_{BNPP} and the divergent responses of f_{BNPP} with climatic variables at geographical and temporal scales should be considered in global C modeling.

Key words: biomass partitioning, grassland, interannual variability, meta-data synthesis, net primary productivity (NPP), precipitation, temperature.

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Introduction

An important feature of carbon cycling in terrestrial ecosystems is the partitioning of C above- and belowground (Weaver, 1958; Gilmanov *et al.*, 1997). Net primary productivity (NPP) is the primary driver of global C cycling (Field *et al.*, 1998; Scurlock *et al.*, 1999; Norby *et al.*, 2002), but the fraction of total NPP allocated belowground (f_{BNPP}) influences nutrient and water uptake, C turnover and species competition (Jackson *et al.*, 2000; Schenk & Jackson, 2002; Obrist & Arnone, 2003; Hui & Luo, 2004; Malhi *et al.*, 2004). While f_{BNPP} is an important variable in ecosystem C modeling (Cannell & Dewar, 1994; Ågren & Franklin, 2003), its value in most global terrestrial models is typically held constant (Friedlingstein *et al.*, 1999; Wullschleger *et al.*, 2001). Most NPP models do

not incorporate even moderately sophisticated submodels of C partitioning – an anticipated next step in this line of research. How much f_{BNPP} changes temporally and geographically is largely unknown (e.g. Long *et al.*, 1989). Quantifying this variable and its relationships with climate is not only necessary to model global C cycling and C sequestration in terrestrial ecosystems today and in the future, but is also important for improving our mechanistic understanding of C partitioning in terrestrial ecosystems.

Net primary productivity and biomass partitioning are strongly influenced by climate (Lieth, 1975; Melillo *et al.*, 1993; Gill & Jackson, 2000; Gower *et al.*, 2001; Schuur, 2003). Experimental studies on the relationship of NPP and climatic variables have been mostly limited to aboveground NPP (ANPP). For example, ANPP is typically positively

correlated with mean annual precipitation (MAP) in grasslands (Sala *et al.*, 1988; Lauenroth & Sala, 1992; Knapp & Smith, 2001). The ANPP modeled by CENTURY showed a significant linear relationship with moisture/radiation index across eight grasslands in the former USSR (Gilmanov *et al.*, 1997).

In contrast, only a few studies have related belowground NPP (BNPP) with climate variables (Sims *et al.*, 1978; Gill *et al.*, 2002). Ni (2004) reported a negative relationship of BNPP with mean annual temperature (MAT), but no relationship with MAP in temperate grasslands in northern China. Across large areas, the relationship between NPP and climate variables is still unclear (Potter *et al.*, 1999; Nemani *et al.*, 2003). Moreover, to our knowledge, how f_{BNPP} changes with climatic variables temporally and geographically has not been explored.

Grasslands account for approx. 25% of the land surface of the earth and 10% of global C stocks. They have a high potential sink capacity for C, and play an important role in the Earth's C cycle (Hall & Scurlock, 1991; Parton *et al.*, 1995; Schlesinger, 1997; Scurlock & Hall, 1998; Suter *et al.*, 2002). Grasslands are particularly useful for addressing questions of C partitioning, because most grassland NPP occurs belowground (Sims *et al.*, 1978; Hungate *et al.*, 1997). Compared with forests, measurements of grassland belowground biomass are also easier to obtain (Lauenroth, 2000; Gill *et al.*, 2002). Therefore more long-term below- and aboveground biomass measurements are available in grasslands than in any other ecosystem type. Strong interannual variabilities in ANPP and ecosystem gas exchanges have been reported in several grassland ecosystems (Knapp & Smith, 2001; Flanagan *et al.*, 2002; Suyker *et al.*, 2003).

The objective of this study was to determine the patterns and potential mechanisms of variation in f_{BNPP} at large geographical and temporal scales for grassland ecosystems. We

combined an online global NPP database (the Oak Ridge National Laboratory Distributed Active Archive Center) with additional data sets from the literature. Twelve sites with 3 yr or more of measurements of above- and belowground monthly biomass were selected. These sites reflected large differences in climate means and variabilities. Based on these data, we estimated ANPP and BNPP, calculated f_{BNPP} for each site-year, and explored the relationships of f_{BNPP} with climatic variables. We were particularly interested in geographical and interannual variability in f_{BNPP} and relationships with temperature and precipitation.

Materials and Methods

Data collection

The data sets used in this study were obtained primarily from an online global NPP database compiled recently at the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC; http://www.daac.ornl.gov/NPP/npp_home.html; Scurlock *et al.*, 2002). The database includes 35 intensively studied grassland sites worldwide. To analyze interannual variabilities in f_{BNPP} and NPP, we selected sites with 3 yr or more of measurements of both above- and belowground biomass at each site (10 sites altogether). We also searched recent publications and added two additional sites (Craine *et al.*, 2003; Ni, 2004). Overall, c. 840 paired monthly biomass observations in 94 site-years for 12 sites were included (Table 1). The 12 sites reflected large differences in MAT and MAP, and encompassed several major grassland types or ecoregions, including savanna, humid temperate prairie, temperate steppe, alpine meadow and cold desert steppe. Five sites were dominated by C_4 species; one site (BioCON, USA) was planted with C_3 and C_4 grasses; and the

Table 1 Characteristics of the 12 grassland sites in this study, in order of ecoregion

Site	Year	Lat	Long	Ele (m)	MAT (°C)	MAP (mm)	Dominant species	Ecoregion
Klong Hoi Khong, Thailand	1984–90	6.33 N	100.93 E	30	26.4	1540	<i>Eulalia tripicata</i> (C_4)	Humid savanna
Nairobi, Kenya	1984–94	1.33 S	36.83 E	1600	19.7	680	<i>Themeda triandra</i> (C_4)	Savanna
Jornada, USA	1970–72	32.60 N	106.85 W	1350	14.9	262	<i>Bouteloua eriopoda</i> (C_4)	Subtropical semi-desert steppe
Montecillo, Mexico	1984–94	19.46 N	98.91 W	2240	14.2	590	<i>Distichlis spicata</i> (C_4)	Forest–meadow–paramo
Osage, USA	1970–72	36.95 N	96.55 W	392	15.2	916	<i>Andropogon scoparius</i> (C_4)	Humid temperate prairie
Otradnoe, Russia	1969–73	60.83 N	30.25 E	50	8.6	543	<i>Alchemilla monticola</i> (C_3)	Humid temperate prairie
BioCON, USA	1998–02	45.40 N	93.20 W	309	7.2	751	Mixed (C_4 , C_3)	Humid temperate prairie
Haibei, China	1980–85	37.22 N	101.38 E	3300	5.7	415	<i>Kobresia humilis</i> (C_3)	Alpine meadow steppe
Matador, Canada	1968–71	50.70 N	102.72 W	676	3.0	350	<i>Agropyron</i> spp. (C_3)	Temperate dry steppe
Tumugi, China	1982–90	46.10 N	123.00 E	191	2.1	411	<i>Filifolium sibiricum</i> (C_3)	Cold desert steppe
Shortandy, Kazakhstan	1975–78	51.67 N	71.00 E	367	1.3	351	<i>Stipa zaleskyi</i> (C_3)	Cold desert steppe
Tuva, Russia	1978–80	51.83 N	94.42 E	800	–4.3	214	<i>Agropyron cristatum</i> (C_3)	Cold desert steppe

Year, measurements included in the analysis were made between these years; Lat, latitude; Long, longitude; Ele, elevation (m a.s.l.); MAT, mean annual temperature; MAP, mean annual precipitation; Ecoregion, modified from Bailey (1989).

other six were dominated by C_3 species. All measurements were made in naturally growing field conditions. We included data in burned or grazed plots if the burning or grazing occurred at least 1 yr before the biomass measurements. At the Tumugi, China site we included measurements from three plots with different plant species compositions.

Estimations of NPP and f_{BNPP}

At least six approaches are used currently to estimate NPP from biomass measurements in grasslands: (1) peak live biomass; (2) peak standing crop; (3) maximum minus minimum live biomass; (4) sum of positive increments in live biomass; (5) sum of positive increments in live and dead biomass plus litter; and (6) sum of changes in live and dead biomass with adjustment for decomposition (Long *et al.*, 1989; Scurlock *et al.*, 2002; Ni, 2004). Although method 6 is considered an accurate indicator in theory, it requires decomposition measurements which were not available for most sampling sites, so we were unable to include this approach in our analysis. Both methods 2 and 5 require standing dead biomass, and method 4 should be avoided for site comparisons because of different seasonal patterns in live biomass among sites (Scurlock *et al.*, 2002). Although method 5 appears to be an adequate predictor of NPP across all ecoregions, method 1 is still a commonly used indicator of grassland productivity (Scurlock *et al.*, 2002). In this study, following Ni (2004), we estimated ANPP and BNPP separately using method 5 when dead biomass and litter data were available (e.g. Klong Hoi Khong, Thailand and Shortandy, Kazakhstan), but method 1 was applicable at most of the sampling sites. We calculated f_{BNPP} using the equation:

$$f_{\text{BNPP}} = \text{BNPP}/(\text{ANPP} + \text{BNPP}) \quad \text{Eqn 1}$$

Relationships of f_{BNPP} with climatic variables

To investigate the relationships of f_{BNPP} with climatic variables, we collected monthly mean temperature and precipitation for these sites. Monthly minimum temperature, maximum temperature and precipitation at most of the sites were reported as accessory data at the NPP database website. If the climatic data were missing, measurements from nearby weather stations were used. At the Montecillo, Mexico site we could not find climatic data from 1991 to 1994, so we excluded those years' data in the regression analysis. Mean temperature was calculated by averaging minimum and maximum temperature. Annual temperature and precipitation were further calculated by averaging temperature and totaling precipitation, respectively, for each year at a given site.

Climatic variables showed large differences in mean values and interannual variabilities (CV) during the study years across sites (Table 2). Mean annual temperature varied from -1.73°C at Tuva, Russia to 27.68°C at Klong Hoi Khong, Thailand. The mean of annual precipitation averaged over sampling years varied from 227 mm at Tuva, Russia to 1567 mm at Klong Hoi Khong, Thailand. These values were close to the historical mean values at the sites (Table 1). Interannual variability in annual temperature was relatively smaller than variation in annual precipitation at savanna and humid savanna sites. Interannual variabilities in annual temperature and precipitation within sites were also smaller than geographical variabilities across sites.

Linear regression was conducted on f_{BNPP} with temperature and precipitation, temporally and geographically. Mean f_{BNPP} and its corresponding means of annual temperature and precipitation across years were used for the geographical analysis. The relationship of interannual variability in f_{BNPP} and interannual variabilities in climatic variables was also explored by

Table 2 Mean, median and interannual variability (CV) in the fraction of belowground net primary productivity (BNPP) to total NPP (f_{BNPP}), and mean and interannual variability in aboveground NPP (ANPP), BNPP, annual temperature (T) and annual precipitation (PPT)

Site	No. site-years	f_{BNPP}			ANPP (g DM m ⁻²)		BNPP (g DM m ⁻²)		T (°C)		PPT (mm)	
		Mean	Median	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV
Klong Hoi Khong, Thailand	6	0.50	0.49	16.22	635.73	29.10	694.52	58.48	27.68	1.37	1567.0	13.40
Nairobi, Kenya	10	0.40	0.37	19.03	236.72	27.65	162.15	43.23	19.62	3.03	675.82	36.21
Jornada, USA	6	0.74	0.72	14.23	81.62	49.08	228.08	13.50	14.58	1.75	238.53	35.96
Montecillo, Mexico	8	0.65	0.67	11.75	739.88	35.78	1246.3	42.24	13.43	25.85	557.24	33.87
Osage, USA	6	0.74	0.75	3.60	295.38	10.29	870.58	20.66	14.27	0.84	857.86	14.03
Otradnoe, Russia	7	0.74	0.74	3.04	243.13	14.31	692.10	12.08	3.92	21.72	499.04	16.98
BioCON, USA	5	0.70	0.74	8.33	408.00	23.15	944.00	17.38	7.24	9.85	751.46	15.63
Haibei, China	6	0.74	0.73	8.65	303.40	27.18	898.88	37.47	0.53	47.78	412.28	13.01
Matador, Canada	4	0.77	0.76	6.20	567.96	24.65	1957.0	8.65	2.62	27.33	345.92	30.57
Tumugi, China	30	0.87	0.86	4.37	155.18	34.49	998.51	9.61	4.30	14.24	410.94	23.70
Shortandy, Kazakhstan	3	0.86	0.85	7.28	359.67	45.19	2146.7	11.65	2.57	38.38	376.00	13.13
Tuva, Russia	3	0.84	0.88	9.24	115.80	35.29	652.67	20.94	-1.73	18.75	226.83	12.48
All sites	94	0.71	0.74	19.80	345.21	60.42	957.62	62.23	9.09	97.30	576.58	63.86

Mean and coefficient of variation for all sites are calculated from mean values at the 12 sampling sites.

regression analysis. Data analysis was carried out using SAS software (Hui & Jiang, 1996; SAS Institute Inc., Cary, NC, USA).

Results

Mean and interannual variabilities in ANPP, BNPP and f_{BNPP}

Mean ANPP varied from 81.6 to 740 g DM m⁻² yr⁻¹ across sites (Table 2). Interannual variability in ANPP within a site ranged from 10.29 to 49.08, typically *c.* 30 at most sites. Subtropical semidesert steppe, cold desert steppe, and forest–meadow–paramo sites tended to have larger interannual variabilities than other systems. Mean BNPP varied from 228 to 2147 g DM m⁻² yr⁻¹, with larger interannual variabilities again observed at savanna and humid savanna sites. For both ANPP and BNPP, geographical variability across sites was larger than interannual variability within sites.

Estimated f_{BNPP} varied substantially both from year to year and across the 12 sites (Table 2). Savanna and humid savanna sites had relatively large interannual variabilities in f_{BNPP} , but small mean values of f_{BNPP} . In contrast, cold desert steppe sites had smaller interannual variabilities in f_{BNPP} , but larger mean values. The other sites had intermediate mean values of f_{BNPP} . The lowest mean value of f_{BNPP} was 0.40 at Nairobi, Kenya (a savanna), and the highest was 0.87 at Tumugi, China (a cold

desert steppe). Across all sites, the grand mean of f_{BNPP} was 0.71 and the grand median was 0.74. Geographical variability in f_{BNPP} across the 12 sites was also larger than most interannual variabilities within the sites.

Relationships of f_{BNPP} and climatic variables

Mean f_{BNPP} across years at each site decreased linearly with means of annual temperature and precipitation (Figs 1, 2; $r^2 = 0.65$ and 0.42 , respectively, $P < 0.05$ for both). The slope of the temperature regression is -0.013 , so each 1°C increase in temperature corresponds to a 0.013 decrease in f_{BNPP} . Within sites, however, no general pattern of f_{BNPP} and annual temperature or precipitation was found. The f_{BNPP} tended to increase with increased annual temperature at some sites and decrease with temperature at others, but only at the Tumugi, China site did we find a significant positive linear relationship of f_{BNPP} and annual temperature. Similar results were found for the temporal relationship of f_{BNPP} with annual precipitation. Among the 12 sites studied, only two showed a significant negative linear relationship between f_{BNPP} and annual precipitation.

To test whether mean temperature or precipitation contributed more to the observed variation in mean f_{BNPP} , we conducted multiple regression analysis (maximum R^2 method; Hui *et al.*, 2003). Temperature was the most important variable in the regression equation ($f_{\text{BNPP}} = 0.8294 - 0.0128MT$,

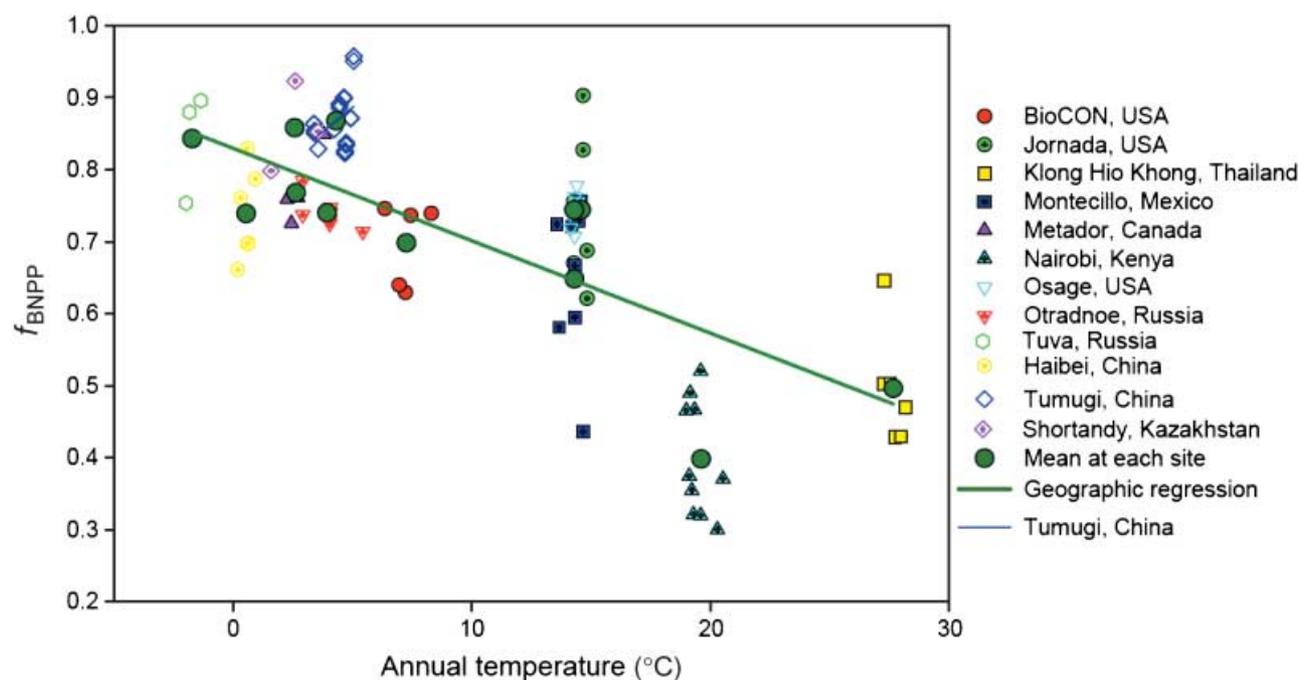


Fig. 1 Relationship of the fraction of belowground net primary productivity to total NPP (f_{BNPP}) and temperature. The overall geographical regression equation is $f_{\text{BNPP}} = 0.8290 - 0.0129MT$, $r^2 = 0.65$, $P = 0.001$, where MT is the mean of annual temperature at each site and r^2 is the coefficient of determination. The temporal relationships of f_{BNPP} and annual temperature (T) within sites show diverse trends, but mostly are not significant, except for the site at Tumugi, China ($f_{\text{BNPP}} = 0.7515 + 0.0270T$, $r^2 = 0.19$, $P = 0.02$).

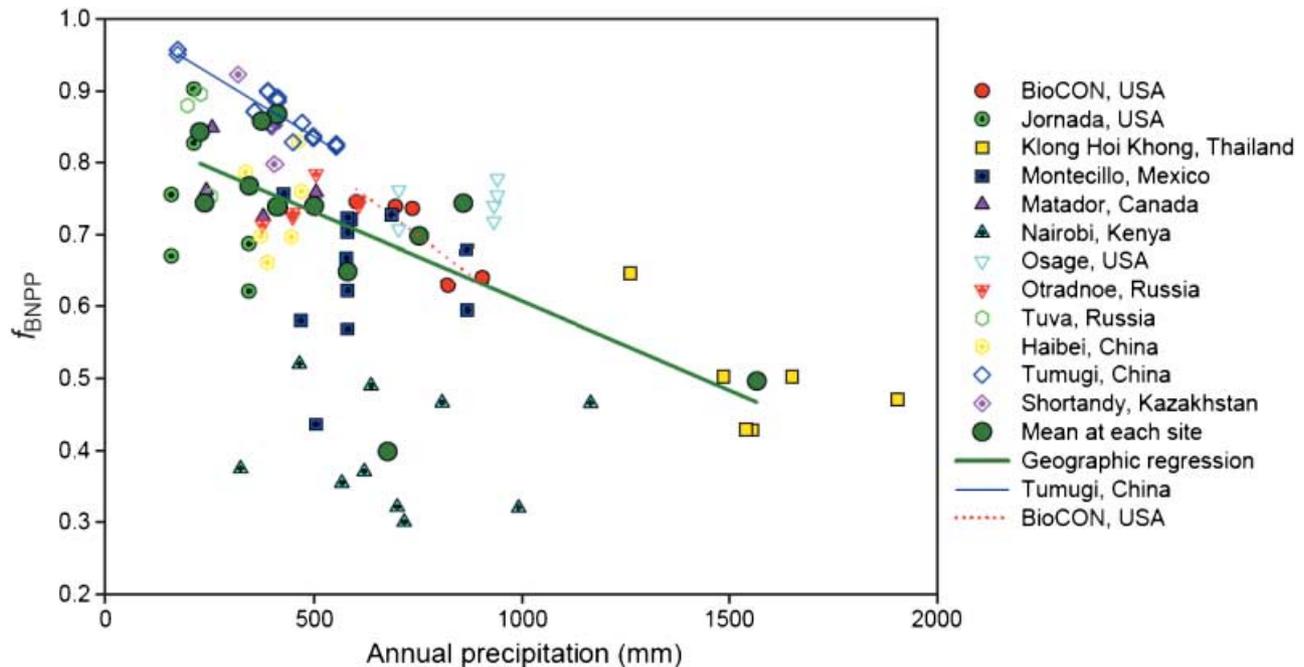


Fig. 2 Relationship of the fraction of belowground net primary productivity to total NPP (f_{BNPP}) and precipitation. The overall geographical regression equation is $f_{\text{BNPP}} = 0.8544 - 0.00025\text{MPPT}$, $r^2 = 0.42$, $P = 0.02$, where MPPT is the mean of annual precipitation at each site. The significant temporal regression equations within sites are: $f_{\text{BNPP}} = 1.0242 - 0.00043\text{PPT}$, $r^2 = 0.77$, $P = 0.05$ at BioCON, USA; $f_{\text{BNPP}} = 1.0125 - 0.00035\text{PPT}$, $r^2 = 0.82$, $P < 0.001$ at Tumugi, China, where PPT is the annual precipitation.

$r^2 = 0.653$, $P = 0.002$, where MT is the mean of annual temperature over years at a site). Adding precipitation to the temperature regression did not improve the model fit ($f_{\text{BNPP}} = 0.8349 - 0.0122\text{MT} - 0.00002\text{MPPT}$, $R^2 = 0.654$, $P = 0.008$, where MPPT is the mean of annual precipitation across years at a site), thus mean f_{BNPP} was apparently regulated mainly by mean of annual temperature geographically.

Relationships of interannual variability in f_{BNPP} with that in ANPP, BNPP and climatic variables

Simple linear regression showed a significant positive relationship of interannual variability in f_{BNPP} (CV) with that in BNPP, and tended to be positively correlated with the CVs of both ANPP and annual precipitation (Fig. 3a,b). In contrast, the relationship of the CV of f_{BNPP} with that of annual temperature was nonlinear (Fig. 3c). Multiple regression showed that the interannual variability in ANPP, BNPP and annual precipitation contributed significantly to the variation in CV of f_{BNPP} ($\text{CV}_{f_{\text{BNPP}}} = -5.8065 + 0.1495\text{CV}_{\text{ANPP}} + 0.2372\text{CV}_{\text{BNPP}} + 0.2354\text{CV}_{\text{PPT}}$, $R^2 = 0.87$, $P < 0.001$). Annual temperature did not contribute significantly to the variation in CV of f_{BNPP} , even if the quadratic function of CV in annual temperature was included. Path coefficients showed that the interannual variability in BNPP contributed most to the variation in CV of f_{BNPP} , followed by the contribution of annual precipitation (data not shown).

Discussion

By synthesizing 94 site-year field biomass measurements from a global NPP database and the literature, we investigated geographical and interannual variability in f_{BNPP} and the relationships of f_{BNPP} with climatic variables. Results showed that f_{BNPP} was negatively correlated with means of annual temperature and precipitation across sites. Temporal responses of f_{BNPP} with annual temperature and precipitation varied from site to site but were inconclusive, partly because there were relatively few data at some sites. Overall, geographical variability in f_{BNPP} across sites was typically larger than interannual variability within sites.

Relationship of f_{BNPP} and climatic variables

One interesting finding of this study was that the relationships of f_{BNPP} and climatic variables showed different patterns geographically and temporally. Strong negative relationships of mean f_{BNPP} with means of annual temperature and precipitation were found across sites. These geographical relationships could be the result of long-term plant adaptation to local climates, and reflect the contribution of vegetation to variation in f_{BNPP} . Temporal relationships of f_{BNPP} and climatic variables within sites might be more complicated and could be site-specific. We might assume that plants allocate more C to roots than to shoots during drier periods

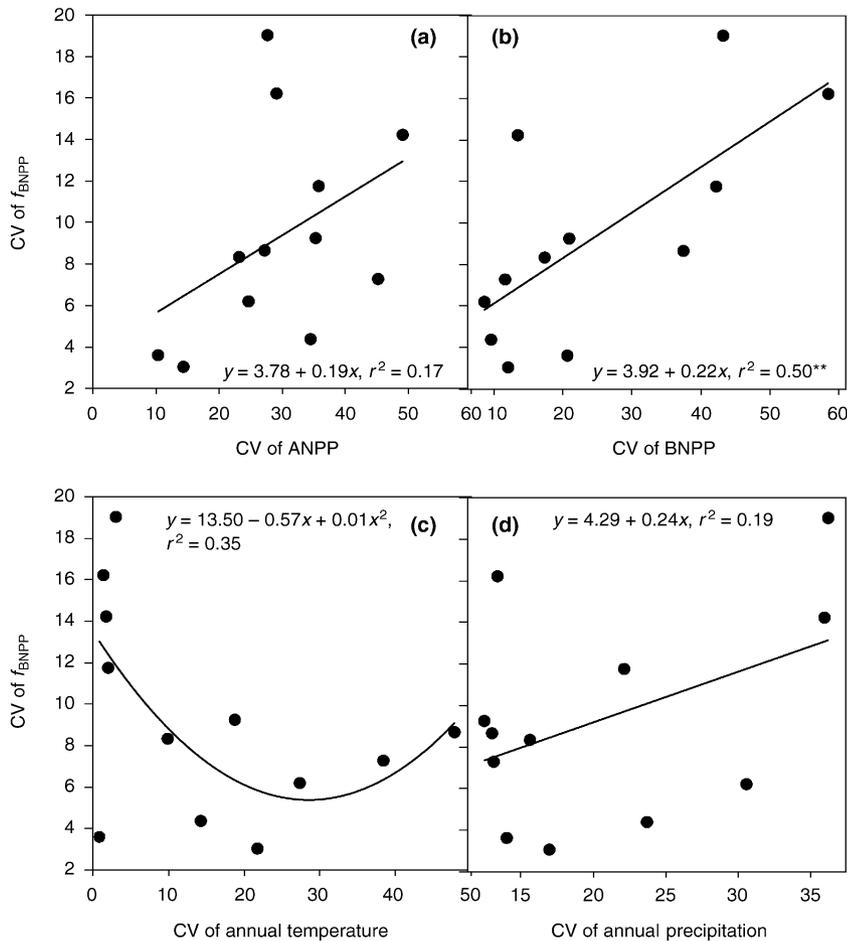


Fig. 3 Relationships of the coefficient of variation (CV) of the fraction of belowground net primary productivity to total NPP (f_{BNPP}) and CVs of ANPP (a); BNPP (b); annual temperature (c); annual precipitation (d). The regression equation is based on geographical data at 12 sites ($n = 12$; *, $P < 0.05$; **, $P < 0.01$).

(Milchunas & Lauenroth, 2001; Schenk & Jackson, 2002). Indeed, at the Tumugi, China site, temporal data showed a negative relationship of f_{BNPP} with annual precipitation, similar to that observed geographically. Milchunas & Lauenroth (2001) also found a weak relationship of biomass partitioning with precipitation using 13 yr of data from a shortgrass steppe. Different geographical and temporal responses of plants to climatic variables have been reported in the literature. For example, the relationship of ANPP and precipitation varied using geographical and temporal data (Paruelo *et al.*, 1999; Huxman *et al.*, 2004). Similarly, Gill & Jackson (2000) found that the global relationship of root turnover with climate variables did not predict the relationship with interannual variability in climate at a particular site. However, to explore temporal relationships within sites more fully, longer-term data sets may be needed.

Cluster of ecoregions based on f_{BNPP} and interannual variability in f_{BNPP}

We also found that the 12 study sites could be clustered into four groups based on their mean and interannual variability in

f_{BNPP} (Fig. 4). Savanna and humid savanna sites (Nairobi, Kenya; Klong Hoi Khong, Thailand) had small mean but large interannual variability in f_{BNPP} , while cold desert steppe sites (Tuva, Russia; Shortandy, Kazakhstan; Tumugi, China) had large mean and small interannual variability in f_{BNPP} . The other two groups, forest–meadow–paramo and semidesert steppe sites, had intermediate mean values but relatively large interannual variability in f_{BNPP} (Montecillo, Mexico; Jornada, USA), and small interannual variability in f_{BNPP} at humid temperate and alpine meadow sites (Osage, USA; Otradnoe, Russia; BioCON, USA; Matador, Canada; Haibei, China). Previous studies have shown that root : shoot ratios were larger at cooler sites (Sims *et al.*, 1978). Increased root : shoot ratios have also been correlated with drier growing conditions (Struik & Bray, 1970; Jackson *et al.*, 1996; Milchunas & Lauenroth, 2001). Together with our results, these findings indicate that plants maintain a certain correspondence of growth and biomass partitioning with annual environmental changes in each habitat (Pykh & Malkina-Pykh, 2000). Therefore the pattern of biomass partitioning may be the result of plant species adaptation and responses to both internal and environmental stimuli.

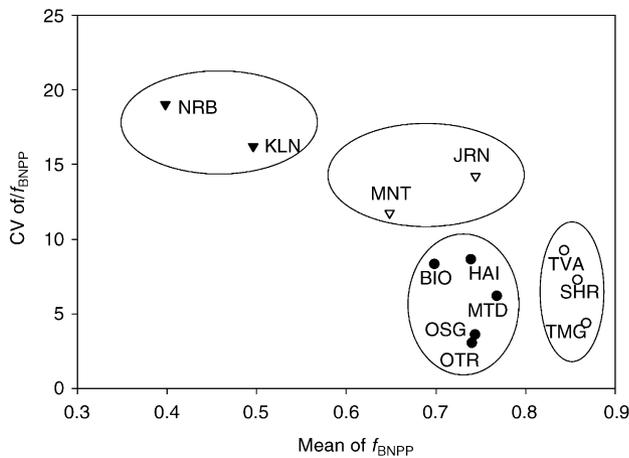


Fig. 4 Clusters of sites according to the mean and interannual variability of f_{BNPP} . KLN, Klong Hoi Khong, Thailand; NRB, Nairobi, Kenya; JRN, Jornada, USA; MNT, Montecillo, Mexico; OSG, Osage, USA; OTR, Otradnoe, Russia; BIO, BioCON, USA; HAI, Haibei, China; MTD, Matador, Canada; TMG, Tumugi, China; SHR, Shortandy, Kazakhstan; TVA, Tuva, Russia. \blacktriangledown , savanna and humid savanna; \blacktriangledown , subtropical semidesert steppe and forest-meadow-paramo; \circ , cold desert steppe; \bullet , the other ecoregions.

Comparing methods in NPP and f_{BNPP} estimations

The advantages and disadvantages of different methods for estimating NPP have been discussed extensively in the literature (Long *et al.*, 1992; Scurlock *et al.*, 2002; Ni, 2004). To examine the influence of these methods on f_{BNPP} estimation, we calculated ANPP and BNPP using the five methods described in Materials and Methods when adequate measurements were available. Similarly to Singh *et al.* (1975), we found positive linear relationships among methods for both ANPP and BNPP, with coefficients of determinations (r^2) ranging from 0.37 to 0.60 across the 12 sites. On average, methods 2 and 5 gave larger estimations for ANPP and BNPP compared with the other methods, consistent with the conclusions of Scurlock *et al.* (2002). Estimated f_{BNPP} also showed large differences among methods. While methods 3 and 4 gave similar estimates compared with method 5, method 1 produced higher values of f_{BNPP} . Significant linear correlations of f_{BNPP} were also found among these methods. Compared with f_{BNPP} estimated by method 5, method 4 showed the highest correlation with $f_4 = 0.0936 + 0.9474 \times f_5$, $r^2 = 0.77$, $P < 0.001$. While different methods yielded large differences in ANPP and BNPP estimates at some sites, the impact on f_{BNPP} is probably smaller when the same method is applied to both ANPP and BNPP.

Advantages and limitations of data synthesis

Ecological data such as NPP have accumulated greatly in recent years through many extensive field studies and large-scale integrated projects, such as the Long Term Ecological Research (LTER) network and FluxNet. Synthesis of these

long-term, broad-scale data sets is still a challenge, but has the potential to reveal general patterns and ecological rules (Knapp *et al.*, 2004). While that general goal was achieved in this study, several limitations could affect our conclusions. One was the availability of measurement data. Among 35 data sets reported in the NPP database, only 10 sites measured more than 3 yr for both above- and belowground biomass. Of 74 sites reporting biomass measurements in temperate grasslands in northern China, few studies lasted more than 3 yr, and no long-term (>3 yr) monthly belowground measurements were reported (Ni, 2004). Additional data on long-term above- and belowground biomass dynamics, as well as data for standing dead matter, litterfall, root decomposition, fine-root distribution and turnover, are needed to estimate grassland NPP and C partitioning accurately (Jackson *et al.*, 1997; Johnston *et al.*, 2004; Ni, 2004). Another limitation was the quality of measurements. For any synthesis, data quality varies widely across studies. Some sites reported only live biomass, or had many missing data points and could not be included in this synthesis. Enhancing the standard and quality of measurements would improve estimates of NPP and f_{BNPP} (Long *et al.*, 1992; Scurlock *et al.*, 2002; Ni, 2004). Finally, estimates of BNPP remain the limiting step in most NPP studies. Moreover, there are few good measures of BNPP. Fine roots are an important component of belowground biomass and nutrient uptake (Jackson *et al.*, 1997, 2000; Coomes & Grubb, 2000; Norby *et al.*, 2004), but estimating fine-root turnover and production remains a challenge (Gill & Jackson, 2000; Li *et al.*, 2003). As more and more data accumulate, these studies can yield further insights and provide directions for future research (Knapp *et al.*, 2004).

To our knowledge, this analysis provides the first synthesis of geographical and interannual variability in f_{BNPP} and its relationships with climatic variables for grasslands. We found distinct patterns of mean and interannual variability in f_{BNPP} across ecoregions, and divergent responses of f_{BNPP} with climatic variables geographically and temporally. The information provided in this study is helpful in several respects. First, it provides an estimated envelope of f_{BNPP} across large geographical and temporal scales. Instead of using a constant f_{BNPP} for grassland ecosystems, different values of f_{BNPP} at different ecoregions could be used. Second, the geographical regression equation of f_{BNPP} and climatic variables developed here could be used in global C modeling to improve model outputs in grassland ecosystems. For long-term and regional modeling studies, attention should also be given to the possible site-specific temporal responses of f_{BNPP} to climatic variables. Third, relatively larger geographical variability in f_{BNPP} could reflect fundamental controls over f_{BNPP} . Typical plant species growing in a region tend to adjust to the local environment through their biomass-partitioning strategies. For example, plants growing in deserts usually have proportionally more roots and larger f_{BNPP} . Thus we would anticipate inherent differences in the variation of f_{BNPP} at geographical vs local

scales. Finally, as global temperatures continue to increase, plants may allocate relatively less C belowground, decreasing f_{BNPP} . The shift will probably influence the storage of C belowground, as well as C turnover. How large the impact will be on terrestrial C sequestration and cycling is unclear, and additional data on geographical and interannual variability in belowground biomass components are greatly needed.

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