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

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Summary
• 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 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 $C_3$ species; one site (BioCON, USA) was planted with $C_4$ grasses; and the

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

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>Lat</th>
<th>Long</th>
<th>Ele (m)</th>
<th>MAT (°C)</th>
<th>MAP (mm)</th>
<th>Dominant species</th>
<th>Ecoregion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Klong Hoi Khong, Thailand</td>
<td>1984–90</td>
<td>6.33 N</td>
<td>100.93 E</td>
<td>30</td>
<td>26.4</td>
<td>1540</td>
<td><em>Eulalia tripicata</em> (C₄)</td>
<td>Humid savanna</td>
</tr>
<tr>
<td>Nairobi, Kenya</td>
<td>1984–94</td>
<td>1.33 S</td>
<td>36.83 E</td>
<td>1600</td>
<td>19.7</td>
<td>680</td>
<td><em>Themeda triandra</em> (C₃)</td>
<td>Savanna</td>
</tr>
<tr>
<td>Jornada, USA</td>
<td>1970–72</td>
<td>32.60 N</td>
<td>106.85 W</td>
<td>1350</td>
<td>14.9</td>
<td>262</td>
<td><em>Bouteloua eriopoda</em> (C₄)</td>
<td>Subtropical semi-desert steppe</td>
</tr>
<tr>
<td>Montecillo, Mexico</td>
<td>1984–94</td>
<td>19.46 N</td>
<td>98.91 W</td>
<td>2240</td>
<td>14.2</td>
<td>590</td>
<td><em>Distichlis spicata</em> (C₄)</td>
<td>Forest–meadow–paramo</td>
</tr>
<tr>
<td>Osage, USA</td>
<td>1970–72</td>
<td>36.95 N</td>
<td>96.55 W</td>
<td>392</td>
<td>15.2</td>
<td>916</td>
<td><em>Andropogon scoparius</em> (C₄)</td>
<td>Humid temperate prairie</td>
</tr>
<tr>
<td>Otradnode, Russia</td>
<td>1969–73</td>
<td>60.83 N</td>
<td>30.25 E</td>
<td>50</td>
<td>8.6</td>
<td>543</td>
<td><em>Alchemilla monticola</em> (C₄)</td>
<td>Humid temperate prairie</td>
</tr>
<tr>
<td>BIOCON, USA</td>
<td>1998–02</td>
<td>45.40 N</td>
<td>93.20 W</td>
<td>309</td>
<td>7.2</td>
<td>751</td>
<td><em>Mixed (C₃, C₄)</em></td>
<td>Humid temperate prairie</td>
</tr>
<tr>
<td>Haibei, China</td>
<td>1980–85</td>
<td>37.22 N</td>
<td>101.38 E</td>
<td>3300</td>
<td>5.7</td>
<td>415</td>
<td><em>Kobresia humilis</em> (C₃)</td>
<td>Alpine meadow steppe</td>
</tr>
<tr>
<td>Matador, Canada</td>
<td>1968–71</td>
<td>50.70 N</td>
<td>102.72 W</td>
<td>676</td>
<td>3.0</td>
<td>350</td>
<td><em>Agropyron spp.</em> (C₃)</td>
<td>Temperate dry steppe</td>
</tr>
<tr>
<td>Tumugi, China</td>
<td>1982–90</td>
<td>46.10 N</td>
<td>123.00 E</td>
<td>191</td>
<td>2.1</td>
<td>411</td>
<td><em>Filifolium sibiricum</em> (C₃)</td>
<td>Cold desert steppe</td>
</tr>
<tr>
<td>Shortlady, Kazakhstan</td>
<td>1975–78</td>
<td>51.67 N</td>
<td>71.00 E</td>
<td>367</td>
<td>1.3</td>
<td>351</td>
<td><em>Stipa zalesskii</em> (C₄)</td>
<td>Cold desert steppe</td>
</tr>
<tr>
<td>Tuva, Russia</td>
<td>1978–80</td>
<td>51.83 N</td>
<td>94.42 E</td>
<td>800</td>
<td>4.3</td>
<td>214</td>
<td><em>Agropyron cristatum</em> (C₄)</td>
<td>Cold desert steppe</td>
</tr>
</tbody>
</table>

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 \( \text{C}_3 \) 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:

\[
f_{BNPP} = \frac{BNPP}{(ANPP + BNPP)} \quad \text{Eqn 1}
\]

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 \( (PPT) \)

<table>
<thead>
<tr>
<th>Site</th>
<th>No. site-years</th>
<th>( f_{BNPP} )</th>
<th>ANPP (g DM m(^{-2}))</th>
<th>BNPP (g DM m(^{-2}))</th>
<th>( T ) (°C)</th>
<th>PPT (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Klong Hoi Khong, Thailand</td>
<td>6</td>
<td>0.50</td>
<td>0.49</td>
<td>16.22</td>
<td>635.73</td>
<td>29.10</td>
</tr>
<tr>
<td>Nairobi, Kenya</td>
<td>10</td>
<td>0.40</td>
<td>0.37</td>
<td>19.03</td>
<td>236.72</td>
<td>27.65</td>
</tr>
<tr>
<td>Jornada, USA</td>
<td>6</td>
<td>0.74</td>
<td>0.72</td>
<td>14.23</td>
<td>81.62</td>
<td>49.08</td>
</tr>
<tr>
<td>Montecillo, Mexico</td>
<td>8</td>
<td>0.65</td>
<td>0.67</td>
<td>11.75</td>
<td>739.88</td>
<td>35.78</td>
</tr>
<tr>
<td>Osage, USA</td>
<td>6</td>
<td>0.74</td>
<td>0.75</td>
<td>3.60</td>
<td>295.38</td>
<td>10.29</td>
</tr>
<tr>
<td>Otradnoe, Russia</td>
<td>7</td>
<td>0.74</td>
<td>0.74</td>
<td>3.04</td>
<td>243.13</td>
<td>14.31</td>
</tr>
<tr>
<td>BioCON, USA</td>
<td>5</td>
<td>0.70</td>
<td>0.74</td>
<td>8.33</td>
<td>408.00</td>
<td>23.15</td>
</tr>
<tr>
<td>Halbei, China</td>
<td>6</td>
<td>0.74</td>
<td>0.73</td>
<td>8.65</td>
<td>303.40</td>
<td>27.18</td>
</tr>
<tr>
<td>Matador, Canada</td>
<td>4</td>
<td>0.77</td>
<td>0.76</td>
<td>6.20</td>
<td>567.96</td>
<td>24.65</td>
</tr>
<tr>
<td>Tumugi, China</td>
<td>30</td>
<td>0.87</td>
<td>0.86</td>
<td>4.37</td>
<td>155.18</td>
<td>34.49</td>
</tr>
<tr>
<td>Shortandy, Kazakhstan</td>
<td>3</td>
<td>0.86</td>
<td>0.85</td>
<td>7.28</td>
<td>359.67</td>
<td>45.19</td>
</tr>
<tr>
<td>Tuva, Russia</td>
<td>3</td>
<td>0.84</td>
<td>0.88</td>
<td>9.24</td>
<td>115.80</td>
<td>35.29</td>
</tr>
<tr>
<td>All sites</td>
<td>94</td>
<td>0.71</td>
<td>0.74</td>
<td>19.80</td>
<td>345.21</td>
<td>60.42</td>
</tr>
</tbody>
</table>

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


Collections of NPP and \( f_{BNPP} \)

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). Intertannual variability in annual temperature was relatively smaller than variation in annual precipitation at savanna and humid savanna sites. Intertannual 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

\[ f_{BNPP} = \frac{BNPP}{(ANPP + BNPP)} \quad \text{Eqn 1} \]
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 ($f_{BNPP} = 0.8294 - 0.0128MT$, Fig. 1).

![Graph showing the relationship of fraction of belowground net primary productivity to total NPP ($f_{BNPP}$) and temperature.](attachment:image.png)

**Fig. 1** Relationship of the fraction of belowground net primary productivity to total NPP ($f_{BNPP}$) and temperature. The overall geographical regression equation is $f_{BNPP} = 0.8290 - 0.0129MT$, $r^2 = 0.65$, $P = 0.001$, 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 ($f_{BNPP} = 0.7515 + 0.0270T$, $r^2 = 0.19$, $P = 0.02$).
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\[ r^2 = 0.653, \ P = 0.002, \text{ where MT is the mean of annual temperature over years at a site}. \]

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 \( f_{\text{BNPP}} \) was apparently regulated mainly by mean of annual temperature geographically.

**Relationships of interannual variability in \( f_{\text{BNPP}} \) with that in ANPP, BNPP and climatic variables**

Simple linear regression showed a significant positive relationship of interannual variability in \( f_{\text{BNPP}} \) (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 \( f_{\text{BNPP}} \) 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 \( f_{\text{BNPP}} \) (\( CV_{\text{ANPP}} - 5.8065 + 0.1495\text{CV}_{\text{ANPP}} + 0.2372\text{CV}_{\text{BNPP}} + 0.2354\text{CV}_{\text{PPT}}, R^2 = 0.87, P < 0.001 \)). Annual temperature did not contribute significantly to the variation in CV of \( f_{\text{BNPP}} \), 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 \( f_{\text{BNPP}} \), 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 \( f_{\text{BNPP}} \) and the relationships of \( f_{\text{BNPP}} \) with climatic variables. Results showed that \( f_{\text{BNPP}} \) was negatively correlated with means of annual temperature and precipitation across sites. Temporal responses of \( f_{\text{BNPP}} \) 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 \( f_{\text{BNPP}} \) across sites was typically larger than interannual variability within sites.

**Relationship of \( f_{\text{BNPP}} \) and climatic variables**

One interesting finding of this study was that the relationships of \( f_{\text{BNPP}} \) and climatic variables showed different patterns geographically and temporally. Strong negative relationships of mean \( f_{\text{BNPP}} \) 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 \( f_{\text{BNPP}} \). Temporal relationships of \( f_{\text{BNPP}} \) 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.
(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.
Comparing methods in NPP and \( f_{\text{BNPP}} \) 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 \( f_{\text{BNPP}} \) 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 \( f_{\text{BNPP}} \) also showed large differences among methods. While methods 3 and 4 gave similar estimates compared with method 5, method 1 produced higher values of \( f_{\text{BNPP}} \). Significant linear correlations of \( f_{\text{BNPP}} \) were also found among these methods. Compared with \( f_{\text{BNPP}} \) estimated by method 5, method 4 showed the highest correlation with \( f_{\text{BNPP}} \) at geographical vs local scales. Instead of using a constant \( f_{\text{BNPP}} \) for grassland ecosystems, different values of \( f_{\text{BNPP}} \) at different ecoregions could be used. Second, the geographical regression equation of \( f_{\text{BNPP}} \) and climatic variables developed here could be used in global 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 \( f_{\text{BNPP}} \) to climatic variables. Third, relatively larger geographical variability in \( f_{\text{BNPP}} \) could reflect fundamental controls over \( f_{\text{BNPP}} \). 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 \( f_{\text{BNPP}} \). Thus we would anticipate inherent differences in the variation of \( f_{\text{BNPP}} \) at geographical vs local sites.

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 \( f_{\text{BNPP}} \) (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 \( f_{\text{BNPP}} \) and its relationships with climatic variables for grasslands. We found distinct patterns of mean and interannual variability in \( f_{\text{BNPP}} \) across ecoregions, and divergent responses of \( f_{\text{BNPP}} \) with climatic variables geographically and temporally. The information provided in this study is helpful in several respects. First, it provides an estimated envelope of \( f_{\text{BNPP}} \) across large geographical and temporal scales. Of 74 sites reporting biomass measurements in temperate grasslands in northern China, few studies lasted 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 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 for both above- and belowground biomass.
scales. Finally, as global temperatures continue to increase, plants may allocate relatively less C belowground, decreasing \( f_{\text{BPP}} \). This 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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References


