

## Aboveground biomass in Tibetan grasslands

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### ABSTRACT

This study investigated spatial patterns and environmental controls of aboveground biomass (AGB) in alpine grasslands on the Tibetan Plateau by integrating AGB data collected from 135 sites during 2001–2004 and concurrent enhanced vegetation index derived from MODIS data sets. The AGB was estimated at  $68.8 \text{ g m}^{-2}$ , with a larger value ( $90.8 \text{ g m}^{-2}$ ) in alpine meadow than in alpine steppe ( $50.1 \text{ g m}^{-2}$ ). It increased with growing season precipitation (GSP), but did not show a significant overall trend with growing season temperature (GST) although it was negatively correlated with GST at dry environments ( $<200 \text{ mm}$  of GSP). Soil texture also influenced AGB, but the effect was coupled with precipitation; increased silt content caused a decrease of AGB at small GSP, and generated a meaningful increase under humid conditions. The correlation between AGB and sand content indicated an opposite trend with that between AGB and silt content. An analysis of general linear model depicted that precipitation, temperature, and soil texture together explained 54.2% of total variance in AGB. Our results suggest that moisture availability is a critical control of plant production, but temperature and soil texture also affect vegetation growth in high-altitude regions.

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### 1. Introduction

Biomass is an important component of the global carbon cycle (Scurlock et al., 2002). In grassland ecosystems, the amount of aboveground biomass (AGB) determines forage availability and thus constrains herbivore carrying capacity (Jobbágy and Sala, 2000; Yahdjian and Sala, 2006). Our capability to predict the consequences of global change and design sustainable rangeland management strategies is partially dependent upon our understanding of spatial patterns and their environmental controls of AGB (Jobbágy and Sala, 2000; Nemani et al., 2003).

Biomass harvesting is a common method for estimating AGB in grasslands, but it has limitations in both temporal scale and spatial extent (Jobbágy et al., 2002). Alternatively, the relationship between satellite-based vegetation index and absorbed photosynthetic active radiation (APAR) provides a theoretical basis for estimating AGB using remote sensing data (Paruelo et al., 1997; Jobbágy et al., 2002). Remote sensing data sets have provided global coverage at relatively high temporal and spatial resolution since the early 1980s (Myneni et al., 1997; Zhou et al., 2001), and have been widely used to estimate vegetation biomass or productivity at

regional and global scales (e.g. Paruelo et al., 1997; Myneni et al., 2001; Fang et al., 2003; Zhao et al., 2005; Piao et al., 2005, 2007). In contrast with direct harvesting measurements, the satellite-based estimation approach, which combines remote sensing data with ground-based observations, can effectively extend our ability to explore regional patterns of vegetation biomass in a spatially explicit fashion (Piao et al., 2005).

A number of studies have investigated spatial patterns of AGB and their relationships with precipitation, temperature, and soil texture in grassland ecosystems (e.g. Sala et al., 1988; Epstein et al., 1997). Precipitation strongly determines AGB in grasslands, and thus has been frequently used to explain the spatial variation in production (Lauenroth, 1979; Sala et al., 1988; Burke et al., 1997; Jobbágy et al., 2002; Ni, 2004a; Fang et al., 2005). A significant relationship between AGB and temperature in grasslands has not been observed, but AGB declines with temperature after holding annual precipitation constant at 50 mm intervals (Epstein et al., 1996, 1997; Burke et al., 1997). In addition, soil texture influences AGB of grasslands through its interaction with precipitation (Sala et al., 1988; Epstein et al., 1997). The inverse texture hypothesis suggests that coarse-textured soils support greater production than fine-textured soils by reducing evaporation in arid environments, while fine-textured soils with higher water-holding capacities are more productive in humid climates (Noy-Meir, 1973). In contrast with extensive information

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about spatial patterns and environmental controls of AGB in temperate grasslands, little evidence is available for alpine grasslands (e.g. Luo et al., 2002; Piao et al., 2006).

The Tibetan Plateau is the highest and largest plateau on the earth, with a mean elevation of  $\sim 4000$  m. Mean annual temperature on the plateau is only  $1.61^\circ\text{C}$  and annual precipitation is around 413.6 mm. The natural vegetation on the plateau is dominated by alpine grasslands (alpine steppe and meadow), with  $>60\%$  of its area covered by these two vegetation types (Li and Zhou, 1998). Moreover, a large part of the plateau has not been disturbed by human activities. Hence, the uniqueness of the plateau in its climate and vegetation provides an ideal region for investigating spatial patterns and environmental controls of AGB in alpine grasslands (Luo et al., 2002; Piao et al., 2006).

In this study, we investigated AGB from 135 sites in alpine grasslands across the plateau during the summers (July and August) of 2001–2004. Using these data, we developed the relationship between site-specific AGB and the corresponding enhanced vegetation index (EVI) data derived from MODIS to estimate the magnitude and spatial distribution of AGB for alpine grasslands on the plateau. We further explored the relationships between AGB and environmental factors (precipitation, temperature, and soil texture) to understand the major controls of AGB.

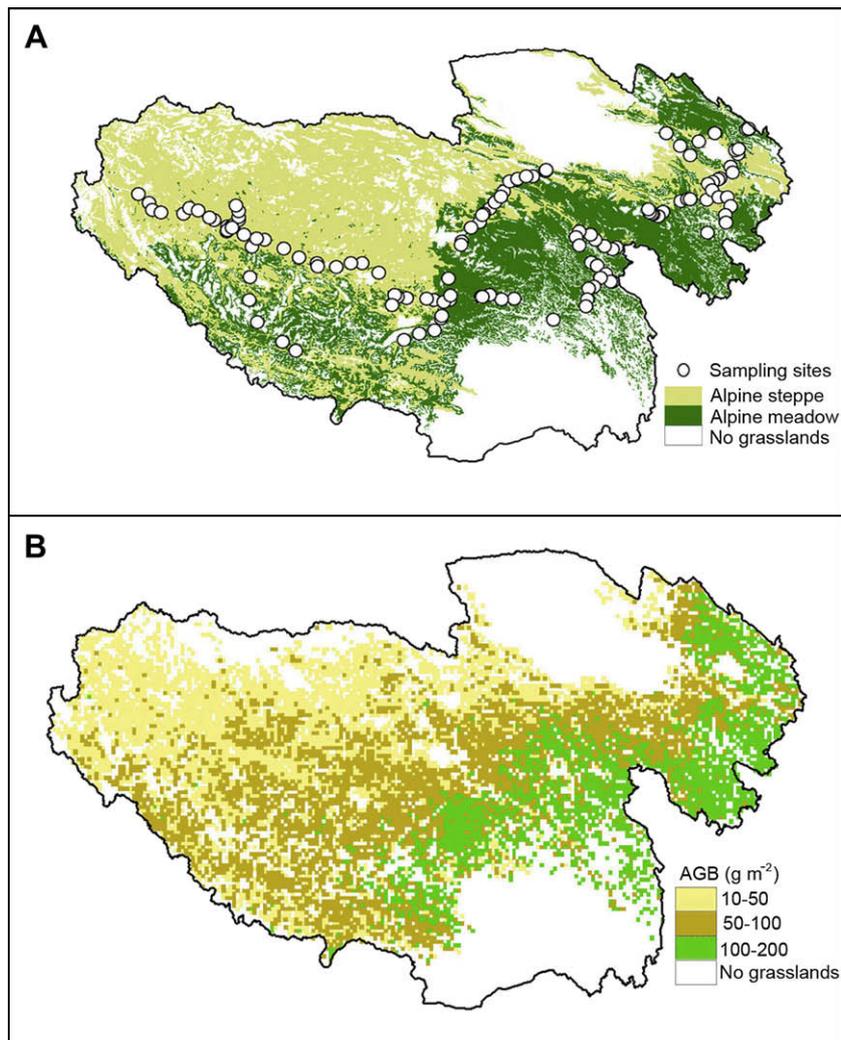
## 2. Materials and methods

### 2.1. Sampling of aboveground biomass and soil features

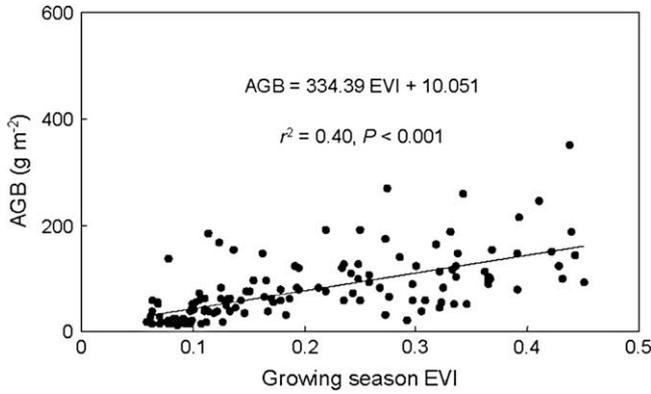
We sampled 675 plots from 135 sites (i.e. five plots from each site) on the Tibetan Plateau during the summers (July and August) of 2001–2004 (Fig. 1A). At each site ( $10 \times 10$  m), all plants in five plots ( $1 \times 1$  m) were harvested to measure aboveground biomass (AGB). Biomass samples were oven-dried at  $65^\circ\text{C}$  to constant mass, and weighed to the nearest 0.1 g. In addition, three soil profiles were selected at each site to determine soil texture. Soil was sampled at depths of 0–10, 10–20, 20–30, 30–50, 50–70, and 70–100 cm. Soil samples were air-dried, sieved (2 mm mesh), and handpicked to remove fine roots. Soil texture was determined using a particle size analyzer (Mastersizer 2000, Malvern, UK) after removal of organic matter and calcium carbonates (Yang et al., 2008).

### 2.2. MODIS-EVI, climate, and vegetation data

The moderate resolution imaging spectroradiometer (MODIS)-enhanced vegetation index (EVI) data were obtained from the United States Geological Survey (USGS), with a spatial resolution of  $500 \times 500$  m<sup>2</sup> and 16-day interval, for the period of 2001–2004



**Fig. 1.** Distributions of (A) sampling sites and (B) aboveground biomass in alpine grasslands on the Tibetan Plateau. The vegetation atlas with a scale of 1:1000 000 (Chinese Academy of Sciences, 2001) showed locations of 135 sites surveyed during 2001–2004. Spatial pattern of aboveground biomass was estimated from MODIS-EVI data at  $0.1 \times 0.1^\circ$ .



**Fig. 2.** Relationship between aboveground biomass and growing season EVI during the period of 2001–2004, which was described as  $AGB = 334.39EVI + 10.051$  ( $n = 135$ ,  $r^2 = 0.40$ ,  $P < 0.001$ ).

(<http://LPDAAC.usgs.gov>). The monthly EVI data were developed using the Maximum Value Composition (MVC) method proposed by Holben (1986). The growing season EVI data were the average of monthly EVI values from May to September, which were then aggregated to grid cells of  $0.1 \times 0.1^\circ$  (Piao et al., 2003).

Growing season temperature (mean temperature from May to September, GST) and growing season precipitation (total precipitation from May to September, GSP) used in our analysis were derived from the climate database of the Tibetan Plateau at  $0.1 \times 0.1^\circ$  resolution during 2001–2004 (Piao et al., 2003). The climate database was generated from records of 43 climatic stations located above 3000 m in elevation across the plateau. Information on distribution of grasslands was obtained from the vegetation atlas of China with a scale of 1:1 000 000 (Chinese Academy of Sciences, 2001).

**2.3. Data analysis**

We investigated spatial patterns and environmental controls of AGB in alpine grasslands by the following four steps. Firstly, we regressed site-specific AGB against corresponding EVI data (Fig. 2), then used the regression function to estimate AGB from EVI data at each pixel to produce the spatial distribution of AGB for the whole study area (Fig. 1B). We then overlapped the spatial distribution of AGB with the 1:1 000 000 vegetation atlas (Chinese Academy of Sciences, 2001) to identify AGB for alpine steppe and alpine meadow, respectively. Secondly, we performed regression analyses to evaluate the relationships between AGB and precipitation, temperature, and soil texture. Thirdly, we analyzed the effects of temperature and soil texture on AGB at five precipitation levels (100–200, 200–300, 300–400, 400–500, and 500–600 mm in GSP). At each precipitation level, we related AGB to three independent variables: GST, silt content, and sand content (Epstein et al., 1997). Finally, we conducted a general linear model (GLM) analysis to assess the proportion of variance in AGB explained by three variables (precipitation, temperature, and soil texture). GLM analysis was performed using software package R (R Development Core Team, 2005).

**3. Results and discussion**

**3.1. Size and spatial patterns of AGB**

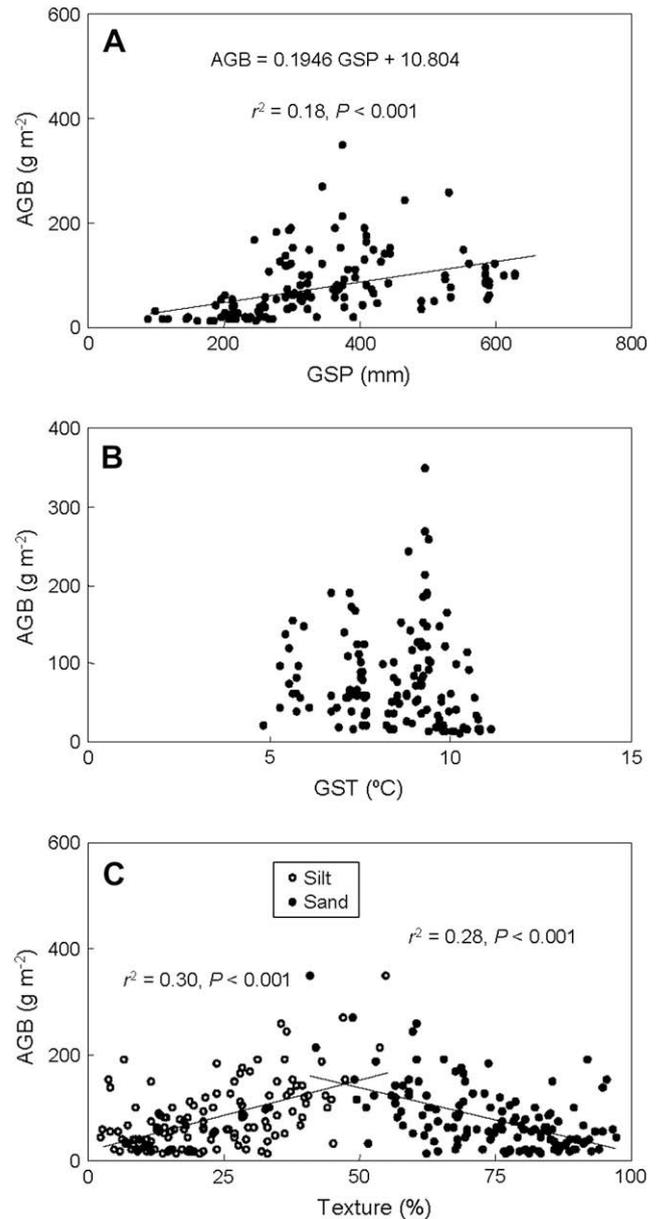
As shown in Table 1, overall mean AGB of alpine grasslands was  $68.8 \text{ g m}^{-2}$ , with greater value in alpine meadow ( $90.8 \text{ g m}^{-2}$ ) than in alpine steppe ( $50.1 \text{ g m}^{-2}$ ). Luo et al. (2002) estimated total

**Table 1**

Density and storage of aboveground biomass in alpine grasslands on the Tibetan Plateau.

Grassland type	Area ( $10^4 \text{ km}^2$ )	AGB density ( $\text{g m}^{-2}$ )			AGB storage (Tg)
		Mean	SD	Range	
Alpine steppe	61.08	50.1	18.9	10.2–190.2	30.60
Alpine meadow	51.74	90.8	38.9	10.4–215.1	46.98
Total	112.82	68.8	36.7	10.2–215.1	77.58

biomass (above- and below-ground biomass) for alpine steppe and meadow to be  $156.7$  and  $663.1 \text{ g m}^{-2}$ , respectively. To compare our estimates with their data, we partitioned AGB from total biomass for the two grassland types using their root: shoot ratios (Yang et al., in press). We found that AGB was  $25.3$  and  $85.0 \text{ g m}^{-2}$  for alpine steppe and meadow, suggesting that their estimate was significantly lower than ours ( $25.3$  vs.  $50.1 \text{ g m}^{-2}$ ) for the former and close to our measurement ( $85.0$  vs.  $90.8 \text{ g m}^{-2}$ ) for the latter. The difference for the alpine steppe was probably due to their



**Fig. 3.** Regressions of aboveground biomass to (A) growing season precipitation, (B) growing season temperature, and (C) soil texture.

limited sample size. We summed total AGB for alpine grasslands and obtained an estimate of 77.6 Tg ( $1 \text{ Tg} = 10^{12} \text{ g}$ ), about 1/4 of total AGB storage in China's grasslands (298.0–323.1 Tg) (Ni, 2004b; Piao et al., 2007). In addition, AGB showed a decrease from the southeastern ( $100\text{--}200 \text{ g m}^{-2}$ ) to northwestern part ( $10\text{--}50 \text{ g m}^{-2}$ ) (Fig. 1B), corresponding well to the precipitation gradient across the plateau (Li and Zhou, 1998).

### 3.2. Relationship between AGB and precipitation

AGB in alpine grasslands appeared to increase with GSP (Fig. 3A), consistent with that observed in temperate grasslands (e.g. Lauenroth, 1979; Sala et al., 1988; Burke et al., 1997; Jobbágy et al., 2002; Ni, 2004a; Fang et al., 2005). However, precipitation-use efficiency (the slope of the AGB-precipitation linear relationship,  $0.2 \text{ g m}^{-2} \text{ mm}^{-1}$ ) observed in alpine grasslands was lower than that in temperate grasslands ( $0.6 \text{ g m}^{-2} \text{ mm}^{-1}$ ; Sala et al., 1988). Moreover, only 18% of the variation in AGB in alpine grasslands could be explained by precipitation, much lower than that in temperate grasslands (90%; Sala et al., 1988). These differences may come from different growth-limiting factors in these two biomes (temperate and alpine grasslands). AGB in temperate grasslands was strongly influenced by the amount and seasonal distribution of precipitation (Sala et al., 1988), but it was constrained by precipitation as well as low temperature in the alpine grasslands (Fang et al., 2005; Kato et al., 2006).

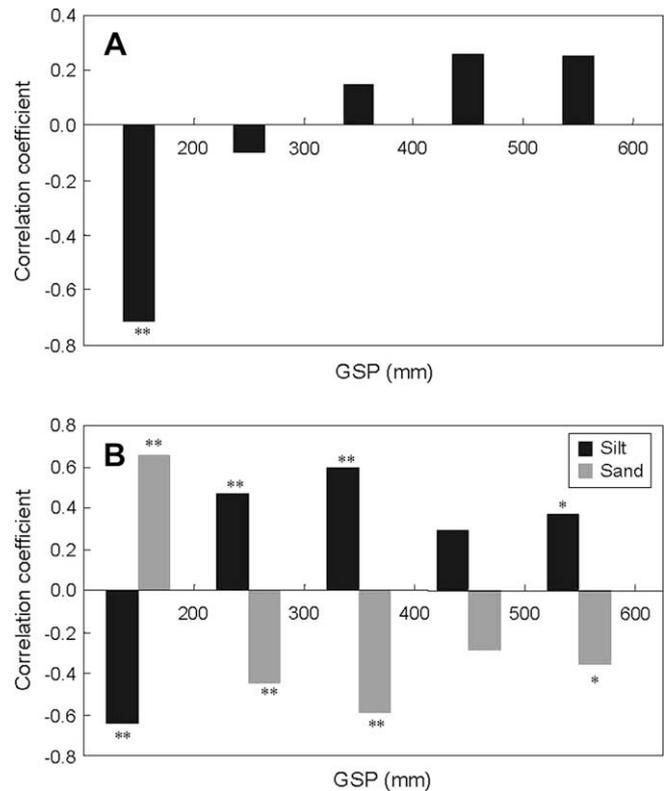
### 3.3. Relationship between AGB and temperature

Generally, AGB did not show any significant trend along the temperature gradient (Fig. 3B), indicating that temperature played a minor role in shaping spatial patterns of AGB. However, if we divided precipitation (GSP) into several 100 mm intervals, then AGB was negatively correlated with GST at low precipitation level ( $\text{GSP} < 200 \text{ mm}$ ) ( $P < 0.05$ ), but had weak positive correlations in humid environments (Fig. 4A). The negative correlation between AGB and temperature in very dry environments in alpine grasslands was consistent with that observed in temperate grasslands by Epstein et al. (1996, 1997), who claimed that higher temperature caused an increased evaporation and thus a lower plant production.

### 3.4. Relationship between AGB and soil texture

AGB increased with an increase in silt content and a decrease in sand content ( $r^2 = 0.30$ ,  $P < 0.001$  for silt content, and  $r^2 = 0.28$ ,  $P < 0.001$  for sand content) (Fig. 3C). However, this trend varied with precipitation (Fig. 4B). AGB significantly decreased with silt content when GSP was lower than 200 mm, but increased under humid conditions ( $>200 \text{ mm}$  of GSP) (Fig. 4B). The relationship between AGB and sand content exhibited an opposite pattern with the AGB vs. silt content relationship: AGB increased significantly with sand content in dry environments ( $<200 \text{ mm}$  of GSP) and decreased when GSP was higher than 200 mm (Fig. 4B).

These results supported the inverse texture hypothesis for temperate regions (Noy-Meir, 1973), which states that coarse-textured soils support higher plant production than fine-textured soils in arid environments, and vice versa in humid climates. In this study, we found larger AGB in sandy soils than in loamy soils in arid climates, but higher AGB in loamy soils than in sandy soils in humid environments, possibly due to different water-holding capacity in these two soil types (Sala et al., 1988; Epstein et al., 1997). Water accumulated in loamy soils can be easily evaporated in arid climates, while loamy soils with higher water-holding capacity could preserve available water in humid environments (Noy-Meir, 1973).



**Fig. 4.** Correlations between aboveground biomass and (A) growing season temperature and (B) soil texture along the precipitation gradient. The effects of growing season temperature and soil texture on aboveground biomass were analyzed separately at five levels of growing season precipitation (100–200, 200–300, 300–400, 400–500, and 500–600 mm). \* $P < 0.1$ , \*\* $P < 0.05$ .

### 3.5. General linear model relating AGB to environmental factors

In order to reveal the integrative effects of these environmental factors on AGB, the relationships between AGB and precipitation, temperature, and soil texture were explored using a GLM. Of the variables examined, precipitation alone explained the largest proportion (29.5%) of total variation in AGB (Table 2). The interactions of precipitation with temperature, silt content, and sand content explained 19.3% of the variance. Overall, combination of climatic variables with soil texture accounted for 54.2% of total variation. The remaining variance may be associated with other factors, such as nitrogen availability and human disturbance (Chapin et al., 2002).

## 4. Concluding remarks

Spatial patterns and environmental controls of AGB in alpine grasslands on the Tibetan Plateau were investigated using data

**Table 2**  
ANOVA of general linear model relating aboveground biomass to growing season precipitation, growing season temperature, and soil texture.

Source	df	MS	SS (%)
GST	1	0.95	5.45 <sup>a</sup>
GSP	1	5.14	29.53 <sup>a</sup>
GST × GSP	1	0.46	2.67 <sup>a</sup>
GSP × Silt	1	1.34	7.69 <sup>a</sup>
GSP × Sand	1	1.55	8.89 <sup>a</sup>
Residuals	129	0.06	45.77

Aboveground biomass data were  $\log_{10}$ -transformed before analysis. df: degree of freedom; MS: mean square; SS: proportion of variance explained by variable.

<sup>a</sup> Significant at  $P < 0.001$ .

from regional-scale field biomass sampling campaigns during 2001–2004 and concurrent EVI data sets. The regional patterns of AGB reflected the southeast-to-northwest gradient in precipitation. The linear relationship between AGB and precipitation observed in alpine grasslands was consistent with that in temperate grasslands, but precipitation-use efficiency in alpine grasslands was lower than that in temperate grasslands, probably due to the constraint of low temperature to plant production in cold regions. AGB did not show any significant trend with temperature, but a strong negative correlation with temperature at low GSP level (<200 mm). The correlations between AGB and soil texture differed in different GSP levels, supporting the inverse texture hypothesis which suggested that sandy soils with lower water-holding capacity led to greater plant production than loamy soils with higher water-holding capacity in arid climates. Overall, about 54.2% of total variation of AGB in alpine grasslands could be explained by climatic variables and soil texture. Our findings revealed that, as in temperate grasslands, moisture availability, which interacted with other environmental factors (such as temperature and soil texture), was a determinant of AGB in alpine grasslands.

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### References

- Burke, I.C., Lauenroth, W.K., Parton, W.J., 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. *Ecology* 78, 1330–1340.
- Chapin, F.S., Matson, P.A., Mooney, H.A., 2002. *Principles of Terrestrial Ecosystem Ecology*. Springer-Verlag, New York.
- Chinese Academy of Sciences, 2001. *Vegetation Atlas of China*. Science Press, Beijing.
- Epstein, H.E., Lauenroth, W.K., Burke, I.C., Coffin, D.P., 1996. Ecological responses of dominant grasses along two climatic gradients in the Great Plains of the United States. *Journal of Vegetation Science* 7, 777–788.
- Epstein, H.E., Lauenroth, W.K., Burke, I.C., 1997. Effects of temperature and soil texture on ANPP in the U.S. Great Plains. *Ecology* 78, 2628–2631.
- Fang, J.Y., Piao, S.L., Field, C.B., Guo, Q.H., Zhou, L.M., Peng, C.H., Tao, S., 2003. Increasing net primary production in China from 1982 to 1999. *Frontiers in Ecology and the Environment* 1, 293–297.
- Fang, J.Y., Piao, S.L., Zhou, L.M., He, J.S., Wei, F.Y., Myneni, R.B., Tucker, C.J., Tan, K., 2005. Precipitation patterns alter growth of temperate vegetation. *Geophysical Research Letters* 32, doi:10.1029/2005GL024231.
- Holben, B.N., 1986. Characteristics of maximum-value composite images for temporal AVHRR data. *International Journal of Remote Sensing* 7, 1435–1445.
- Jobbágy, E.G., Sala, O.E., 2000. Controls of grass and shrub aboveground production in the Patagonian steppe. *Ecological Applications* 10, 541–549.
- Jobbágy, E.G., Sala, O.E., Paruelo, J.M., 2002. Patterns and controls of primary production in the Patagonian steppe: a remote sensing approach. *Ecology* 83, 307–319.
- Kato, T., Tang, Y.H., Gu, S., Hirota, M., Du, M.Y., Li, Y.N., Zhao, X.Q., 2006. Temperature and biomass influences on interannual changes in CO<sub>2</sub> exchange in an alpine meadow on the Qinghai-Tibetan Plateau. *Global Change Biology* 12, 1285–1298.
- Lauenroth, W.K., 1979. Grassland primary production: North American grasslands in perspective. In: French, N.R. (Ed.), *Perspectives in Grassland Ecology*. Springer-Verlag, New York, pp. 3–24.
- Li, W.H., Zhou, X.M., 1998. *Ecosystems of Qinghai-Xizang (Tibetan) Plateau and Approach for Their Sustainable Management*. Guangdong Science and Technology Press, Guangzhou.
- Luo, T.X., Li, W.H., Zhu, H.Z., 2002. Estimated biomass and productivity of natural vegetation on the Tibetan Plateau. *Ecological Applications* 12, 980–997.
- Myneni, R.B., Dong, J., Tucker, C.J., Kaufmann, R.K., Kauppi, P.E., Liskim, J., Zhou, L., Alexeyev, V., Hughes, M.K., 2001. A large carbon sink in the woody biomass of northern forests. *Proceedings of the National Academic Sciences of the United States of America* 98, 14784–14789.
- Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G., Nemani, R.R., 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386, 698–702.
- Nemani, R.R., Keeling, C.D., Hashimoto, H., Jolly, W.M., Piper, S.C., Tucker, C.J., Myneni, R.B., Running, S.W., 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* 300, 1560–1563.
- Ni, J., 2004a. Estimating net primary productivity of grasslands from field biomass measurements in temperate northern China. *Plant Ecology* 174, 217–234.
- Ni, J., 2004b. Forage yield-based carbon storage in grasslands of China. *Climatic Change* 67, 237–246.
- Noy-Meir, I., 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4, 23–51.
- Paruelo, J.M., Epstein, H.E., Lauenroth, W.K., Burke, I.C., 1997. ANPP estimates from NDVI for the central grassland region of the United States. *Ecology* 78, 953–958.
- Piao, S.L., Fang, J.Y., He, J.S., 2006. Variations in vegetation net primary production in the Qinghai-Xizang Plateau, China from 1982 to 1999. *Climatic Change* 74, 253–267.
- Piao, S.L., Fang, J.Y., Zhou, L.M., Guo, Q.H., Henderson, M., Ji, W., Li, Y., Tao, S., 2003. Interannual variations of monthly and seasonal normalized difference vegetation index (NDVI) in China from 1982 to 1999. *Journal of Geophysical Research* 108, doi:10.1029/2002JD002848.
- Piao, S.L., Fang, J.Y., Zhou, L.M., Zhu, B., Tan, K., Tao, S., 2005. Changes in vegetation net primary productivity from 1982 to 1999 in China. *Global Biogeochemical Cycles* 19, doi:10.1029/2004GB002274.
- Piao, S.L., Fang, J.Y., Zhou, L.M., Tan, K., Tao, S., 2007. Changes in biomass carbon stocks in China's grasslands between 1982 and 1999. *Global Biogeochemical Cycles* 21, doi:10.1029/2005GB002634.
- R Development Core Team, 2005. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Sala, O.E., Parton, W.J., Joyce, L.A., Lauenroth, W.K., 1988. Primary production of the central grassland region of the United States. *Ecology* 69, 40–45.
- Scurlock, J.M.O., Johnson, K., Olson, R.J., 2002. Estimating net primary productivity from grassland biomass dynamics measurements. *Global Change Biology* 8, 736–753.
- Yang, Y.H., Fang, J.Y., Tang, Y.H., Ji, C.J., Zheng, C.Y., Zhu, B., 2008. Storage, patterns and controls of soil organic carbon in the Tibetan grasslands. *Global Change Biology* 14, 1592–1599.
- Yang, Y.H., Fang, J.Y., Ji, C.J., Han, W.X. Above- and belowground biomass allocation in Tibetan grasslands. *Journal of Vegetation Science*, in press.
- Yahdjian, L., Sala, O.E., 2006. Vegetation structure constraints primary production response to water availability in the Patagonian steppe. *Ecology* 87, 952–962.
- Zhao, M.S., Heinsch, F.A., Nemani, R.R., Running, S.W., 2005. Improvements of the MODIS terrestrial gross and net primary production global data set. *Remote Sensing of Environment* 95, 164–176.
- Zhou, L.M., Tucker, C.J., Kaufmann, R.K., Slayback, D., Shabanov, N.V., Myneni, R.B., 2001. Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. *Journal of Geophysical Research* 106, 20069–20083.