

DIVERSITY AND PRODUCTIVITY OF SEMI-ARID GRASSLAND OF INNER MONGOLIA: INFLUENCE OF PLANT FUNCTIONAL TYPE AND PRECIPITATION

Jyoti Bhandari¹, Xuebiao Pan^{1,*}, Lizhen Zhang¹, Pei Wei¹, Changxiu Shao¹, Dhruba Bijaya G.C.²,
Que Yue Li¹ and Imran Mehmood¹

¹College of Resources and Environmental Sciences, China Agricultural University, Beijing, China; ²Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 10010, China.

*Corresponding author's e-mail: panxb@cau.edu.cn

Studies of the relationship between diversity and biomass are essential for the sustainable management and restoration of grasslands. The objective of this study was to examine the influence of C3 and C4 plants on species diversity and productivity relationship in the grassland of Inner Mongolia. Above ground dry matter, species richness and diversity were measured in semi-arid grassland at 20 sites in Inner Mongolia during the summers of 2007, 2008 and 2012. In this study, a total of 60 quadrates were located and study sites were divided into three categories (sites dominated by C3 plants, sites with a mixture of C3 and C4 plants and sites dominated by C4 plants) on the basis of above ground dry matter ratio of C3 and C4 plants. Above ground dry matter was the highest in sites dominated by C4 plants. At sites dominated by C3 and at C3 and C4 mixed sites a significant positive linear relationship between above ground dry matter with both species richness index and Simpson's diversity index was recorded. However, in sites dominated by C4 plants, above ground dry matter is not significantly related to species richness and diversity. The results suggest that the sites dominated by C3 plants and the C3 and C4 mixed sites are important for diversity conservation in semi-arid grassland of Inner Mongolia.

Keywords: C3 and C4 plants, dominant sites, species richness index, Simpson's diversity index, dry matter

INTRODUCTION

About 30% of the world's terrestrial land area is covered primarily by arid and semi-arid ecosystems that provide important and effective ecosystem services (Jing *et al.*, 2013). The grasslands of China are important components of Eastern Eurasian steppes, extending 4500 Km from northeast China to the loess plateau, and then continuing to the Tibetan Plateau, with natural grasslands accounting for 40% of the total land area of the China (Ma *et al.*, 2008). As the grasslands of Inner Mongolia are situated in a temperate continental arid region, there is east to west diversity in climate, soil, vegetation, and biogeochemical cycling (Xia, 1995; Liu *et al.*, 2012; Ni *et al.*, 2007) providing an opportunity to explore the relationships between productivity and environmental factors (Hastings *et al.*, 2007; Zhang and Dong, 2010).

Estimation and measurements of vegetation biomass not only plays an important role in the study of production, carbon cycles, and allocation of nutrients in terrestrial ecosystems but also supports natural resource management. Most of the previous studies of grasslands in Inner Mongolia focused on establishing relationships between above ground dry matter and environmental factors (Ma *et al.*, 2008; Fan *et al.*, 2008; Dan *et al.*, 2013; Grace *et al.* (1999) suggested that species diversity is just one of several factors determining productivity of grasslands and that disturbance,

spatial heterogeneity and gradients in the species pool may also be important. Bai *et al.* (2007) showed that there is positive linear relationship between plant productivity and diversity at multiple organizational levels across local, landscape and regional scales. However, we have limited knowledge on how biodiversity affects plant productivity in semi-arid area and no previous studies have analyzed the relationship between biodiversity and above ground dry matter in response to plant functional type (C3 and C4 plant) in the semi-arid grassland of Inner Mongolia.

Ecologically, the C4 paths productivity is more in environments characterized by high light intensities, high temperatures, and perhaps limited soil moisture (Doliner and Jolliffe, 1979) where as C3 grasses are superior at low temperatures and shade conditions (Ehleringer, 1978). Barrens *et al.* (1982) suggested that both productivity and species diversity are related to topographic features and not necessarily determined by the relative proportion or contribution of C4 taxa. Competition for the resources is one of the important biotic factors regulating plant growth (Aarssen, 1989; Aguiar *et al.*, 2001). The competition between C3 and C4 plant types could eventually result in altered species composition at the ecosystem scale (Still *et al.*, 2003). Therefore, understanding C3 and C4 plants response to productivity is important to improve our knowledge of productivity-diversity relationship mechanisms.

In semi-arid grassland ecosystems precipitation is one of the most limiting environmental factors influencing plant productivity (Noy-Meir, 1973; Le Houérou, 1984; Oosterheld *et al.*, 2001; O'Connor *et al.*, 2001) and survival (Snyman, 2004). Rain use efficiency (RUE), the amount of biomass produced per unit precipitation, is an important measure for assessing the response of plant productivity to changes in precipitation gradient (Le Houérou, 1984; Huxman *et al.*, 2004; Bai *et al.*, 2008). However, there is insufficient knowledge about the mechanisms of productivity and diversity of plant communities in the semi-arid zone (Cheng *et al.*, 2008) despite the importance of these mechanisms for grassland management. For understanding the mechanism of the relationship between plant productivity and diversity it is important to know how functional types of dominant species influence the plant productivity. Therefore, we hypothesized that there would be positive relationship between species diversity and productivity and it would be largely influenced by plant functional type i.e. the ratio of C3 and C4 species expressed by above ground dry matter and precipitation. The objective of this study was to test our hypotheses to explore the mechanisms by which the relationship between productivity and diversity is affected.

MATERIALS AND METHODS

Study area: The field investigations were conducted in the

semi-arid grassland of Inner Mongolia in northern China at 20 sites in 2007, 2008 and 2012. Inner Mongolia is dominated by arid and semi-arid temperate continental to continental monsoon climate. In the study sites, mean annual temperature (MAT) varied from -2.4°C to 6.5°C , and mean annual precipitation (MAP) ranged from 176 to 416 mm. According to the China Vegetation Classification System, the grasslands of Inner Mongolia are classified mainly into three divisions: desert steppe, typical steppe, and meadow steppe.

Data collection: Field sampling was conducted during the grass growing season from 2 to 16 August in 2007, from 14 to 25 August in 2008 and from 13 to 20 August in 2012. Selected sampling area (Fig. 1) had not been cut or grazed. A line transect of 100 m was measured and within this line, three (1 m^2 quadrat) sample plots were established at distance of 30m. The geographical location and altitude of each site were recorded by a Global Positioning System (Garmin eTrex GPS). A total of 60 quadrates each year were surveyed, in each of which grass species were identified, and the number of plants per species, canopy cover and height were measured. Plants were separated by species and harvested in each sampling quadrat to measure above ground dry matter. In each quadrat, plants were clipped at the ground surface and the vegetation was collected by hand. The clipped above ground plant materials were oven dried at 80°C for 24 hours to obtain above ground dry matter (g m^{-2}). On the basis of ratio of above ground dry matter of C3 and

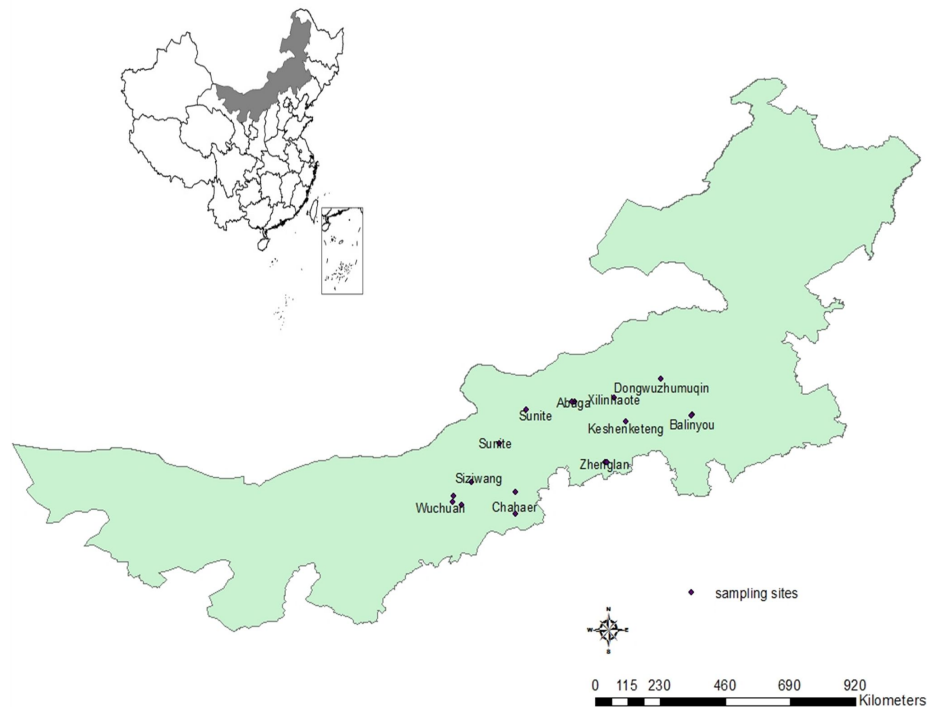


Figure 1. Study area and sampling sites in grasslands of Inner Mongolia.

Table 1. ADM (g m⁻²) and ADM (g m⁻²) ratio of C3 and C4 plant in grasslands of Inner Mongolia

Name of sites	Above ground dry matter (g m ⁻²)			
	2007	2008	2012	Mean
Sites dominated by C3 plants	104.18±95.59	150.02 ±14.72	158.70 ±20.33	138.45 ±09.78
C3 and C4 mixed site	70.68 ± 4.40	133.31 ±14.29	123.08 ±03.06	123.08 ±03.06
Sites dominated by C4 plants	78.35±13.08	132.30 ±10.46	219.79 ±33.01	143.48 ±23.25
Above ground dry matter ratio of C3 and C4 plant				
Sites dominated by C3 plants	4.28 ±0.90	4.33 ±0.71	-	4.31 ±0.57
C3 and C4 mixed site	1.39 ±0.30	2.99 ±0.75	-	2.19 ±0.42
Sites dominated by C4 plants	0.58 ±0.12	0.60 ±0.17	-	0.59 ±0.10

C4 plants, study sites were classified into those dominated by C3 plants (C3:C4 > 2.5), C3 and C4 mixed plant sites (C3:C4=0.7 to 2.5) and sites dominated by C4 plants (C3:C4<0.7) (Table 1). The MAT and MAP in the investigation years were obtained from meteorological stations located in or around sample sites from the China Meteorological Administration.

Data analysis: The number of plant species of each species in each plot was counted to calculate (i) the species richness (S) and (ii) the Simpson's diversity (D) index:

$$D = 1 - \sum P_i^2$$

where P_i is the ratio of number of species i to total number of plants at each quadrat and S is the number of species at each quadrat.

Rain use efficiency (RUE) based on above ground dry matter of each sampling plots was calculated by:

$$RUE = DM / MAP$$

where DM is above ground dry matter and MAP is mean annual precipitation of each site.

Finally, linear regression analysis was conducted to identify the relationship between above ground dry matter with species richness, diversity index and mean annual precipitation among the three site types. All statistical analyses were performed by using software package of SPSS 16.0 (SPSS Inc., Chicago, and IL., USA).

RESULTS

Above ground dry matter and above ground dry matter ratio of C3 and C4 plant: Across 20 sites within the study area, the largest mean above ground dry matter was found in

sites dominated by C4 plants (143.48±23.25) and the lowest in C3 and C4 mixed sites (123.08±3.06 g m⁻²). The ratio of above ground dry matter of C3 and C4 plants was found highest in the sites dominated by C3 plants (4.31±0.57), and the lowest was in sites dominated by C4 plants (0.59 ± 0.10, Table 1).

Species richness and Simpson's diversity index: The highest mean species richness index was found in C3 and C4 mixed sites (13.58±0.07) and the lowest was found also in sites dominated by C4 plants (12.73±0.29). The highest mean diversity index was found in sites dominated by C4 plants (0.61±0.02) and the lowest was found in C3 and C4 mixed sites (0.54±0.01, Table 2).

Precipitation and Rain use efficiency: The highest annual precipitation was found in C3 and C4 mixed sites (401.19±49.23) and the lowest was found also in sites dominated by C4 plants (282.72±20.40). But the highest rain use efficiency was found in sites dominated by C4 plants (0.50±0.05) and the lowest was found in also C3 and C4 mixed sites (0.35±0.01).

Relationships between productivity with diversity and mean annual precipitation: There was a significant positive linear relationship between above ground dry matter and species richness index in sites dominated by C3 plants ($ADM = 9.41 * (S) + 15.11$, $R^2 = 0.193$, $P < 0.05$; Fig. 2a) and C3 and C4 mixed sites ($ADM = 16.58 * (S) - 99.35$, $R^2 = 0.27$, $P < 0.05$; Fig. 2b) but there was no significant relationship for sites dominated by C4 plants (Fig. 1c). Similarly there was significant positive relationship between above ground dry matter with Simpson's diversity index in sites dominated by C3 plants ($DM = 194.1 * (D) + 25.19$, $R^2 = 0.217$, $P < 0.05$;

Table 2. Species richness and Simpson's diversity index in grassland of Inner Mongolia

Name of sites	Species richness			
	2007	2008	2012	Mean
Sites dominated by C3 plants	13.26 ±1.93	12.40 ±0.58	12.88 ±0.48	12.85 ±0.87
C3 and C4 mixed site	13.07 ±0.38	13.66 ±0.39	14.02 ±0.62	13.58 ±0.07
Sites dominated by C4 plants	12.25 ±0.85	12.16 ±0.46	13.79 ±0.25	12.73 ±0.29
Simpson's dominance index				
Sites dominated by C3 plants	0.61 ±0.01	0.59 ±0.01	-	0.60 ±0.01
C3 and C4 mixed site	0.56 ±0.03	0.51 ±0.03	-	0.54 ±0.01
Sites dominated by C4 plants	0.66 ±0.02	0.55 ±0.04	-	0.61 ±0.02

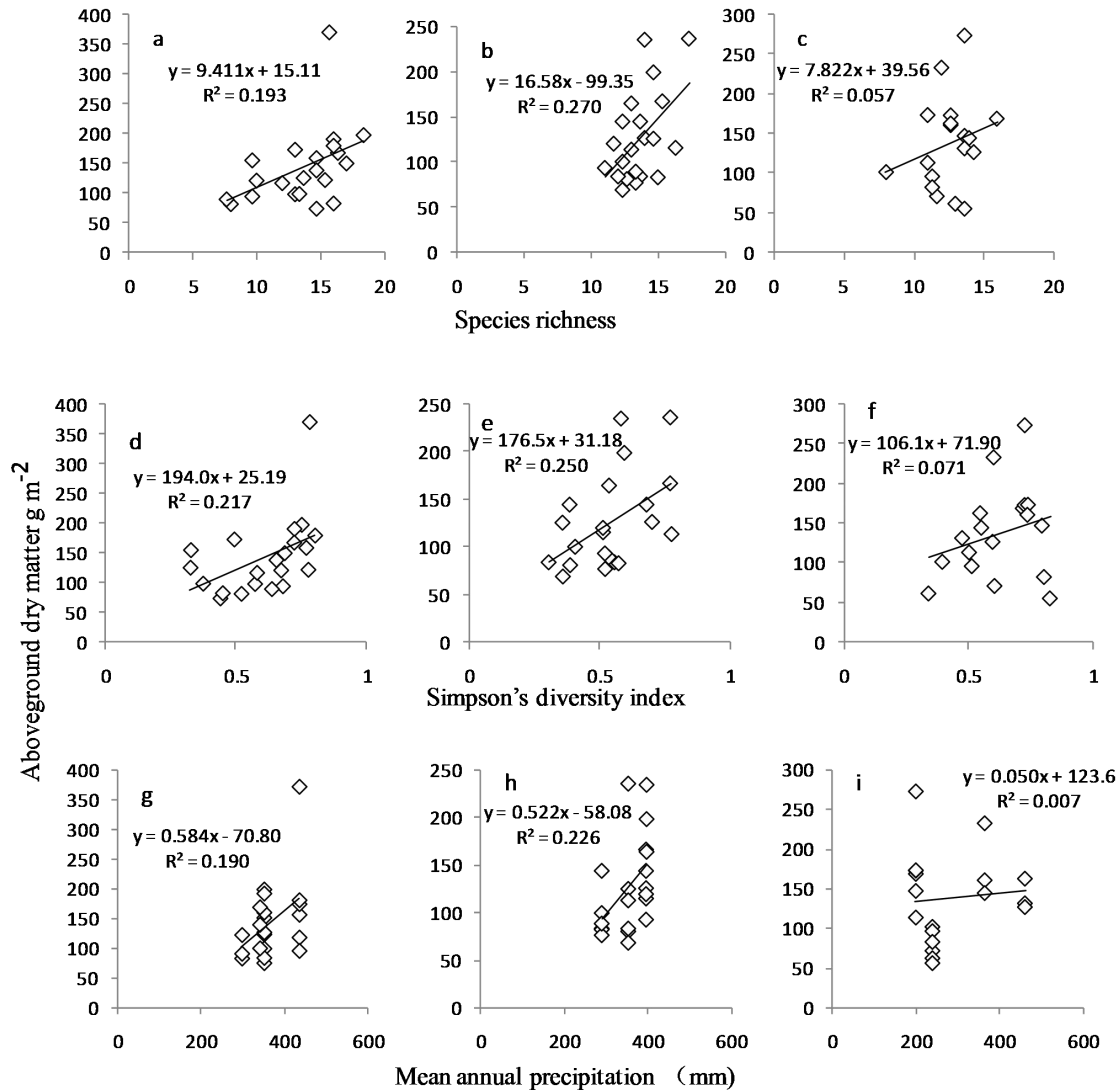


Figure 2. Relationship of above ground dry matter (g m^{-2}) with (a) species richness in sites dominated by C3 plants; (b) species richness in C3 and C4 mixed sites; (c) species richness in sites dominated by C4 plants; (d) Simpson's diversity index in sites dominated by C3 plants; (e) Simpson's diversity index in C3 and C4 mixed sites; (f) Simpson's diversity index in sites dominated by C4 plants; (g) mean annual precipitation in sites dominated by C3 plants; (h) mean annual precipitation in C3 and C4 mixed sites; (i) mean annual precipitation in sites dominated by C4 plants.

Fig. 2d) and in C3 and C4 mixed sites ($\text{DM} = 194.1 * (\text{D}) + 25.19$, $R^2=0.21$, $P<0.05$; Fig. 2e). However there was no significant relationship for sites dominated by C4 plants (Fig. 1f). Likewise there was significant positive relationship between above ground dry matter with mean annual precipitation in sites dominated by C3 plants ($\text{DM} = 0.58 * (\text{MAP}) - 70.80$, $R^2=0.190$, $P < 0.05$; Fig. 2g), C3 and C4 mixed sites ($\text{DM} = 0.52 * (\text{MAP}) - 58.08$, $R^2=0.266$, $P<0.05$; Fig. 2h). But there was no significant relationship for sites dominated by C4 plants (Fig.2i).

DISCUSSION

Species richness and biodiversity enhanced above ground productivity, although productivity differed with different environmental conditions and plant physiology. In our study we found that above ground dry matter is higher in sites dominated by C4 plants. This is because C4 grasses are often characterized by high maximum rates of photosynthesis, photosaturation at high light intensities, and high temperature optima for photosynthesis and growth (Barens,

1982). In sites dominated by C3 plants and C3 and C4 mixed sites, there was significant positive linear relationship between above ground dry matter and both the species richness index and Simpson's diversity index. In support of these positive relationships, there are some theoretical hypotheses such as the multivariate productivity–diversity hypothesis, which states that although species richness and biomass are both influenced by the level of resource supply, species richness is one of the determinants of productivity (Gross and Cardinale, 2007; Cardinale *et al.*, 2009). Our finding is not consistent with a significant positive relationship between plant diversity and productivity in all three site types (sites dominated by C3 plants, C3 and C4 mixed sites and sites dominated by C4 plants) in Inner Mongolia. We found that there was no significant productivity–diversity relationship in sites dominated by C4 plants. In support of our results, Dengler and Nelson (1999) explained that with a given resource supply and level of species richness, C4 plants would have a greater possibility of maximizing growth where as in sites dominated by C3 plants and C3 and C4 mixed sites, due to lower photosynthetic rate, more species may be needed to fully utilize a given resource supply and realize maximum yield (Gough *et al.*, 1994). As a result, a positive effect of species richness on productivity should be more evident in sites dominated by C3 plants and C3 and C4 mixed sites. Lambers *et al.* (2004) found that over yielding species (nitrogen competitors - C4 grasses - or nitrogen fixers) were not most productive in monoculture, and this did not result in a positive diversity–productivity relationship.

According to the predictions and observations of previous studies, plant growth strategies were mainly regulated by precipitation in the arid and semi-arid grassland of northern China because water availability is the dominant limiting factor for primary productivity in this region (Liu *et al.*, 2012). In our study we found significant positive linear relationships between above ground biomass within both sites dominated by C3 plants and C3 and C4 mixed sites. In addition, the differences in climatic conditions among different grassland ecosystems may affect the relationship between grass above ground dry matter and species richness (Ellis and Swift, 1988; Guo and Berry, 1998; Loreau *et al.*, 2001; Hooper *et al.*, 2005). According to present study, there was no significant relationship between mean annual precipitations and above ground dry matter in sites dominated by C4 plants (Fig. 1i). Mean annual precipitation was lowest in sites dominated by C4 plants compared to those sites dominated by C3 plants and C3 and C4 mixed sites (Table 3). However, above ground biomass was higher in C4 plants and this is because rain use efficiency was higher in sites dominated by C4 plants compared to C3 and C4 mixed sites (Table 3).

This study showed that C4 plant does not follow the general trend of increase in annual precipitation cause to increase

productivity which affects the positive relationship between above ground dry matter and species richness and diversity. This interpretation supports our hypothesis that the relationship between plant dry matter and diversity is dependent on plant functional type i.e. C3 or C4 plants.

Table 3. Differences between site type in mean annual precipitation and rain use efficiency (RUE, $\text{gm}^{-2} \text{mm}^{-1}$) based on above-ground dry matter in, 2007, 2008 and 2012.

Name of sites	Mean annual precipitation (mm)	RUE _{ADM} ($\text{g m}^{-2} \text{mm}^{-1}$)
Sites dominated by C3 plants	365.13±27.24	0.43±0.01
C3 and C4 mixed sites	401.19±49.23	0.35±0.01
Sites dominated by C4 plants	282.72±20.40	0.50±0.05
Mean	349.68±32.29	0.42±0.03

Conclusion: Our study concluded that the sites with C3 plants dominance and C3 and C4 mixed sites have positive productivity and diversity relationship following the general trend of increase in precipitation increases productivity. Although the sites dominated by C4 plants have higher productivity and higher rain use efficiency, it does not support the significant positive relationship between productivity and diversity.

Acknowledgments: The authors wish to thank Professor Paul A. Racey of University of Aberdeen for his useful comments on the manuscript. Research was funded by National Basic Research Program of China '973' (2012CB956204) and National Nature Science Fund (NSFC) Project (41271053, 41475104, 41075084).

REFERENCES

- Aarssen, L.W. 1989. Competitive ability and species coexistence: a plant's-eye-view. *Oikos*. 56:386-401.
- Aguiar, M.R., W.K. Lauenroth and D.P. Peters. 2001. Intensity of intra- and interspecific competition in coexisting short grass species. *J. Ecol.* 89:40-47.
- Bai, Y., J. Wu, Q. Pan, J. Huang, Q. Wang, F. Li, A. Buyantuyev and X. Han. 2007. Positive linear relationship between productivity and diversity: evidence from the Eurasian Steppe. *J. Appl. Ecol.* 44:1023-1034.
- Bai, Y., J. Wu, Q. Xing, Q. Pan, J. Huang, D. Yang and X. Han. 2008. Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. *Ecology* 89:2140-2153.
- Barnes, P.W., L.L. Tieszen and D.J. Ode. 1982. Distribution, production, and diversity of C3-and C4-dominated communities in a mixed prairie. *Can. J. Bot.* 61:741-751.
- Barnes, P.W. and A.T. Harrison. 1982. Species distribution

- and community organization in a Nebraska sand hills mixed prairie as influenced by plant/soil-water relationships. *Oecologia* 52:192-201.
- Cardinale, B.J., D.M. Bennett, C.E. Nelson and K. Gross. 2009. Does productivity drive diversity or vice versa? A test of the multivariate productivity-diversity hypothesis in streams. *Ecology* 90:1227-1241.
- Cheng, Y., T. Tsendeekhuu, N. Naran TUYA and T. Nakamura. 2008. Phytosociological study of steppe vegetation in Mongolia. *Grassland Sci.* 54:107-116.
- Dan, S., H. Li, L. Ping and X. De. 2013. Effects of climate change on vegetation in desert Steppe Inner Mongolia. *Nat. Resour. J.* 4:319-322.
- Dengler, N.G. and T. Nelson. 1999. Leaf structure and development in C4 plants. *Plant Biol.* 94:133-172.
- Doliner, L.H. and P.A. Jolliffe. 1979. Ecological evidence concerning the adaptive significance of the C4 dicarboxylic acid pathway of photosynthesis. *Oecologia* 38:23-34.
- Ellis, J.E. and D.M. Swift. 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. *J. Range Manage.* 41:450-459.
- Ehleringer, J.R. 1978. Implications of quantum yield differences to the distributions of C3 and C4 grasses. *Oecologia* 31:255-267.
- Fan, J., H. Zhong, W. Harris, G. Yu, S. Wang, Z. Hu and Y. Yue. 2008. Carbon storage in the grasslands of China based on field measurements of above- and below-ground biomass. *Climatic Change* 86:375-396.
- Gough, L., J.B. Grace and K.L. Taylor. 1994. The relationship between species richness and community biomass: the importance of environmental variables. *Oikos* 70:271-279.
- Guo, Q. and W.L. Berry. 1998. Species richness and biomass: dissection of the hump-shaped relationships. *Ecology* 79:2555-2559.
- Grace, J.B. and H. Jutila. 1999. The relationship between species density and community biomass in grazed and ungrazed coastal meadows. *Oikos* 85:398-408.
- Gross, K. and B.J. Cardinale. 2007. Does species richness drive community production or vice versa? Reconciling historical and contemporary paradigms in competitive communities. *The Am. Nat.* 170:207-220.
- Hastings, A., J.E. Byers, J.A. Crooks, K. Cuddington, C.G. Jones, J.G. Lambrinos, T.S. Talley and W.G. Wilson. 2007. Ecosystem engineering in space and time. *Ecol. Lett.* 10:153-164.
- Hooper, D.U., F.S. Chapin III, J.J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J.H. Lawton, D.M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A.J. Symstad, J. Vandermeer and D.A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monograph* 75:3-35.
- Huxman, T.E., M.D. Smith, P.A. Fay, A.K. Knapp, M.R. Shaw, M.E. Loik, S.D. Smith, D.T. Tissue, J.C. Zak, J.F. Weltzin, W.T. Pockman, O.E. Sala, B.M. Haddad, J. Harte, G.W. Koch, S. Schwinning, E.E. Small and D.G. Williams. 2004. Convergence across biomes to a common rain-use efficiency. *Nature* 429:651-654.
- Jing, Z., J. Cheng and A. Chen. 2013. Assessment of vegetative ecological characteristics and the succession process during three decades of grazing exclusion in a continental steppe grassland. *Ecol. Eng.* 57:162-169.
- Lambers, J.H., R. Harpole, W.S. Tilman, D.J. Knops and P.B. Reich. 2004. Mechanisms responsible for the positive diversity-productivity relationship in Minnesota grasslands. *Ecol. Lett.* 7:661-668.
- Le Houerou, H.N. 1984. Rain use efficiency: a unifying concept in arid-land ecology. *J. Arid. Environ.* 7:213-247.
- Liu, Y., Q. Pan, S. Zheng, Y. Bai and X. Han. 2012. Intra-seasonal precipitation amount and pattern differentially affect primary production of two dominant species of Inner Mongolia grassland. *Acta Oecol.* 44:2-10.
- Loreau, M. and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72-76.
- Ma, W., Y. Yang, J. He, H. Zeng and J. Fang. 2008. Above- and belowground biomass in relation to environmental factors in temperate grasslands, Inner Mongolia. *Science in China Series C: Life Sciences* 51:263-270.
- Ni, J., G.H. Wang, Y.F. Bai and X.Z. Li. 2007. Scale-dependent relationships between plant diversity and above-ground biomass in temperate grasslands, south-eastern Mongolia. *J. Arid Environ.* 68:132-142.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Ann. Rev. Ecol. Syst.* 4:25-51.
- O'Connor, T.G., L.M. Haines and H.A. Snyman. 2001. Influence of precipitation and species composition on phytomass of a semi arid African grassland. *J. Ecol.* 89:850-860.
- Oesterheld, M., J. Loreti, M. Semmartin and O.E. Sala. 2001. Inter-annual variation in primary production of a semi-arid grassland related to previous-year production. *J. Veg. Sci.* 12:137-142.
- Snyman, H.A. 2004. Soil seed bank evaluation and seedling establishment along a degradation gradient in a semi-arid rangeland. *Afr. J. Range. For. Sci.* 21:37-47.
- Still, C.J., J.A. Berry, G.J. Collatz and R.S. DeFries. 2003. Global distribution of C3 and C4 vegetation: carbon cycle implications. *Global Biogeochemical Cycles* 17:6-1.
- Xia, L. 1995. Modeling the response of vegetation in North-East China transect to global change. *J. Biogeog.* 22:515-522.
- Zhang, J.T. and Y. Dong. 2010. Factors affecting species diversity of plant communities and the restoration process in the loess area of China. *Ecol. Eng.* 36:345-350.