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Plant functional types and climate along a precipitation gradient in temperate grasslands, north-east China and south-east Mongolia

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Using data from three field surveys along a precipitation gradient of temperate grasslands in north-east China (the Northeast China Transect, NECT) and south-east Mongolia, the spatial distribution of six plant functional types (PFTs): C_3 species, C_4 species, grasses, shrubs, forbs and succulents and their relationships with climate were analysed. The spatial distribution of different PFTs varies in different regions and in different grassland types of the study area. The species richness in each PFT also has different relationships with climate (significantly or not). Generally, the number of C_3 species, C_4 species, grasses and forbs have positive relationships with precipitation and aridity. Shrubs have negative relationship with precipitation and aridity. Succulents were found to have no relationship with precipitation and aridity. Shrubs, grasses and forbs have stronger relationships with precipitation than C_3 and C_4 species. The relationships between C_3 species, forbs and aridity are more significant than with precipitation. On a regional basis, the combined effect of precipitation and temperature, the aridity, is more significantly correlated with the distribution of C_3 species and forbs, which are more dominant in the study area, than with C_4 species, grasses and succulents.

Keywords: aridity; climate change; land use; life-form (grass, forb and shrub); photosynthetic pathway (C_3 and C_4); plant functional types; precipitation gradient; steppe

Introduction

Temperate grasslands cover large continuous areas in Mid-Asia and are mainly controlled by the continental arid climate. They are sensitive to global climate change and have significant effects on the global carbon cycle (Sala *et al.*, 1996). The temperate steppes in northern China and southern Mongolia are the main

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components of Mid-Asian grasslands. They are major resources for local economic development, as well as natural regulators of local and regional environmental damages. However, large changes in climate and strong changes in land-use regimes have occurred and are expected to continue in the near future in this region. Steppes in north-eastern China and south-eastern Mongolia are strongly sensitive to environmental changes, such as climate change and natural (e.g. fire) and human disturbances (mostly changes in land-use regimes, e.g. over-grazing and the conversion of grassland into farmland). The response of the vegetation to future climate change is a major ecological question in this region. This question may be addressed through understanding the relationships between plant functional types (PFTs) and climate.

PFTs, groups of species that share traits (morphological and physiological attributes) play a similar role in an ecosystem, provide a logical link between physiological and life-history strategies at the plant level and process at the ecosystem level (Chapin, 1993; Paruelo & Lauenroth, 1996). PFTs are derived from traits based on species morphology, physiology and/or life history, and bioclimatic tolerance of species, depending on the aims and scales of the research (Prentice *et al.*, 1992; Smith *et al.*, 1993; Woodward & Cramer, 1996; Duckworth *et al.*, 2000). Studies on the relationships between PFTs and environments at local, regional and global scales, and along specific gradients such as climate, disturbance, and land use, have recently been emphasized (e.g. Aguiar *et al.*, 1996; Box, 1996; Woodward & Cramer, 1996; Díaz & Cabido, 1997; Smith *et al.*, 1997; McIntyre *et al.*, 1999; Pyankov *et al.*, 2000). The gradients in PFTs can help us to understand how plants will respond to environments and further global climate changes. This gradient approach has been expanded to the Terrestrial Transects (Steffen *et al.*, 1999) of the International Geosphere-Biosphere Program (IGBP). The Northeast China Transect (NECT), is one of the mid-latitude semi-arid IGBP Terrestrial Transects (Steffen *et al.*, 1999; Ni & Zhang, 2000), where the gradient is mainly controlled by precipitation. Grasslands occupy a large portion of this transect, from the middle to the west (Ni & Zhang, 2000). The general features of the transect have been described previously, including vegetation and climate variability (Ni & Zhang, 2000). The characteristics of photosynthesis of PFTs (Jiang *et al.*, 1999) and C_4 plant distribution related to environmental factors (Tang, 1999) were analysed. Some statistical and process-based modelling of vegetation and their responses to global change were also performed based on vegetation and/or PFTs (Li, 1995; Gao & Yu, 1998; Ni, 2000). Concerning the PFT research, Tang (1999) focused on the relationships between PFTs and climatic factors along the NECT. However, only the plants with C_4 photosynthetic pathway was taken into account in the field investigation (Tang, 1999). Other PFTs, such as shrubs and forbs, were poorly considered. Jiang *et al.* (1999) reported the response of photosynthesis of eight PFTs to environmental changes on the NECT, but there was lack of quantitative analyses of relationships between PFTs and climate.

The concept of PFTs can be applied at a range of spatial scales, from the plant community, through the ecosystem and landscape, to regional and global scales. The types of attributes that are important depend on the scale in question (Duckworth *et al.*, 2000). PFTs at the community to ecosystem levels have more classifications with greater details and more complex plant attributes for the linkage between ecosystem structure and function (Smith *et al.*, 1993; Aguiar *et al.*, 1996; Díaz & Cabido, 1997; Lauenroth *et al.*, 1997; Scholes *et al.*, 1997; Díaz *et al.*, 1998; Westoby, 1998; McIntyre *et al.*, 1999; Pillar, 1999; Walker *et al.*, 1999). PFTs at the landscape, regional, and global scales, however, have relatively coarse classifications to predict the broad distribution of vegetation and dynamics (Prentice *et al.*, 1992; Box, 1996; Paruelo & Lauenroth, 1996; Cramer, 1997; Leemans, 1997). In this study, the relatively coarse PFT classification will focus on the relatively broad distribution of grasslands along a precipitation gradient in temperate grasslands.

There are several questions to answer in this study. What is the spatial distribution of plant species in different functional types in grasslands of this region? What is the main climate factor that controls the distribution of PFTs? Are certain PFTs more sensitive to precipitation, temperature or both in a given longitudinal gradient? Along the grassland part of the NECT in north-eastern China and its westward expansion in south-eastern Mongolia, a precipitation gradient analysis of the geographical distribution of six PFTs: C_3 species, C_4 species, grasses, shrubs, forbs and succulents is performed using data from three field surveys. Then the relationships between PFTs and climatic variables (temperature, precipitation and aridity) are analysed. The tendency of species richness of PFTs in the face of continued changes in climate and land use is generally predicted.

Material and methods

Study area and field surveys

The NECT, located in mid-latitude temperate China, ranges from 42° to 46°N with a central line of 43·5°N in latitude and from 106° to 132°E in longitude (Ni & Zhang, 2000). In the middle and western parts of the transect, vegetation varies from agricultural fields and meadow steppes to typical steppes and desert steppes (Ni & Zhang, 2000), with annual mean precipitation ranging gradually from 400 to 600 mm in the middle to 100–200 mm in the west (Ni, 2000; Ni & Zhang, 2000).

The study was performed in the middle and western NECT and included its westward expansion to south-eastern Mongolia (Fig. 1). Three field surveys were conducted along the NECT in 1994 (the sampling number starting from 94-xx) and in 1997 (97 sxx), and in south-eastern Mongolia in 1998 (Mx). All field samples were

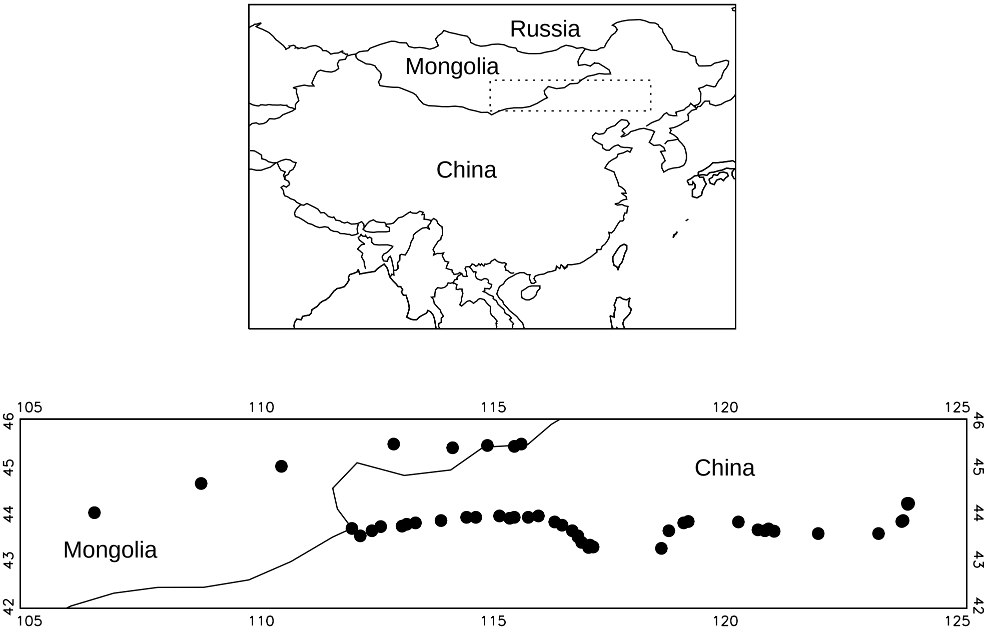

Figure 1. Locations of study area and sampling sites in temperate grasslands, north-east China (the middle and western parts of the Northeast China Transect, NECT) and south-east Mongolia.

collected between mid-July and early August when plants grew well and were expected to have the highest levels of production. Sites with the representative type of local vegetation and no or minimal human disturbances were chosen as plots. The distance between the adjacent sampling sites depended on the vegetation types, human disturbances and topography. The geographical position of each site was measured by the global positioning system (GPS). Vegetation was totally sampled at 49 sites (19 sites in 1994, 22 in 1997, and 8 in 1998) in the study area (Table 1). At each sampling site in the 1994 and 1997 surveys ten small plots, each within an area of $1 \times 1\,\mathrm{m}^2$, were made and formed a short transect ($1 \times 10\,\mathrm{m}^2$). In the 1998 survey three plots, each $1 \times 1\,\mathrm{m}^2$, were randomly selected at each sampling site ($60 \times 60\,\mathrm{m}^2$), with two plots in the opposite corners and one in the center. For the shrubs, the plot area was $10 \times 10\,\mathrm{m}^2$. The nest sampling method was used to justify the plot sizes. The grassland type was determined based on the dominant species in respect of structure in each site and information from the classification system of Chinese vegetation (Editorial Committee for Vegetation of China, 1980). The soil type was obtained from the field observation and based on the soil classification system in China (Xiong & Li, 1987). The number of species in each small plot was counted in the field and then summarized through all plots in a given sampling site. The species richness of each PFT at each site was recounted in the laboratory according to the assignment of plant species to PFTs.

PFTs

The plant species from all the samples in north-eastern China and south-eastern Mongolia were classified into six functional types, which were defined based on morphological, structural and functional attributes: C_3 species, C_4 species, grasses (graminoids), shrubs, forbs (non-graminoid herbs) and succulents (Paruelo & Lauenroth, 1996). All species were classified into C_3 and C_4 categories on the basis of the photosynthetic pathways from the previous identifications (Yin & Li, 1997; Yin & Wang, 1997; Jiang *et al.*, 1999; Tang, 1999). The PFTs of grass, shrub, and forb were classified according to the information from field investigation and herbarium. The succulent PFT includes the true succulents of the Crassulaceae and Chenopodiaceae families and a few succulent-like species of the Compositae (Asteraceae) and Tamaricaceae families.

Climate variables

The basic climate data used in this study area were constructed from records for 841 weather stations between 1951 and 1980 in China (Chinese Central Meteorological Agency, 1984) and many stations in surrounding countries (the CLIMATE database version 2·1, W. Cramer, Potsdam, pers. comm.). They were then interpolated into $10'$ latitude $\times 10'$ longitude grids by the smoothing spline method (Hutchinson & Bischof, 1983). The monthly mean temperatures and precipitation in each sampling site were obtained from the grid cell that covers the sampling site or from the nearest grid cell in the gridded climate data set.

Three climatic variables, mean annual temperature (MAT), mean annual precipitation (MAP) and an aridity index were used to analyse the relationship between PFTs and climate. Paruelo & Lauenroth (1996) have demonstrated that temperature and precipitation are important for certain species distribution, such as C_3 and C_4 species and shrubs. Along the longitudinal gradient in the study area, precipitation is the principal control on the interaction between vegetation and climate (Ni & Zhang, 2000), and therefore is the emphasis of this study. An aridity index (AI), the de Martonne aridity index (de Martonne, 1927) which is defined as

AI = MAP/(MAT+10), has been used worldwide in characterizing the arid climates and arid zones and recently in the study to relate C_4 species distribution to climate in Mongolia (Pyankov *et al.*, 2000). This aridity index was used in the present study.

The statistical method is the linear regression in both single variable and multivariable, using the SPSS 11.0 software package.

Along the longitudinal gradient from the NECT to south-eastern Mongolia, the MAT decreases from west to middle and then increases as longitude increases from middle to east. There is a region of low MAT (below zero) near 114°E to 117°E (Fig. 2(a)), resulting from the high elevation (1200–1400 m a.s.l.) in this region (Table 1). However MAP, the major driving factor on the gradient, is strongly correlated with longitude ($r^2 = 0{\cdot}86$). It increases sharply from *ca.* 100–500 mm from the western desert steppe via the middle typical steppe and meadow steppe to the eastern meadow (Fig. 2(b)). The AI also increases roughly from west to east, although not as clearly because there is a peak in the middle (Fig. 2(c)). AI is highest in the middle study area corresponding to the low MAT at the same longitudes (Fig. 2(a)).

Results and discussion

Grasslands at the 49 sites were classified into four types: meadow (six sites), meadow steppe (seven sites), typical steppe (22 sites) and desert steppe (14 sites). The meadow is mainly distributed in the easternmost part of the study area (123–125°E longitude), the meadow steppe in the middle east part (120–122°E), the typical steppe in the middle part (115°–120°E), and the desert steppe in the western part (<115°E). The structural dominant species change gradually from east to west: *Stipa grandis* P. Smirn., *Leymus chinense* (Trin.) Tzvel., *Chloris virgata* Swartz and *Filifolium sibiricum* (Linn.) Kitam. (meadow-to-meadow steppe), *Leymus chinense*, *Stipa grandis*, *Stipa krylovii* Roshev. and *Cleistogense squarrosa* (Trin.) Keng (typical steppe), *Stipa gobica* Roshev., *Stipa glareosa* P. Smirn., *Stipa klemenzii* Roshev., *Cleistogense songorica* (Roshev.) Ohwi, and species of *Caragana* Fabr. and *Artemisia* Linn. (desert steppe). In terms of the altitude, meadow and meadow steppe are mainly distributed in the lowland of North-east China Plain (160–443 m) and typical and desert steppes mainly in the Mongolian Plateau (626–1459 m).

Meadow had higher species richness of all PFTs in the natural range and lower species richness in the human disturbed areas. Meadow steppe had relatively low species richness. Typical steppe had relatively high species richness and the highest number of species occurred in this grassland. In contrast, desert steppe had very low species richness. The proportion of species richness in each PFT depended also on the grassland type (Fig. 3). Meadow was relatively rich in C_3 species, while meadow steppe was relatively poor in C_3 species. Typical steppe had high C_3 species richness, and the desert steppe's C_3 species richness was low along the gradient from east to west. The richness of C_4 species increased with longitude from west to east. Grasses had high species richness in the east and low numbers in the west. Forbs had the same spatial distribution as C_3 species. Shrubs, on the other hand, decreased from west to east. Desert steppe had high, typical steppe had medium and meadow steppe and meadow had low shrub species richness. A few succulent species occurred in the study area of the temperate grasslands. This functional type was found only at four typical steppe sites which are very close to the desert steppe. Generally, C_3 species and forbs had relatively high percentages in all grassland types, and therefore dominated grasslands in the study area. C_4 species occupied only a small proportion of grasslands (Fig. 3).

Despite the fact that only two plant attributes (life form and photosynthesis pathway) were taken into account in the PFT classification, these attributes and PFTs

Table 1. *Characteristics of 49 samples in temperate grasslands, north-east China and south-east Mongolia. Lon: longitude; Lat: latitude; Elev: elevation*

No.	Site name	Lon (d,m,s)	Lat (d,m,s)	Elev(m)	Vegetation	Dominant	Soil
94-04	Changling-Guangtai	123·55·28	44·12·34	242	Saline-alkali meadow	*Leymus chinense*	Dark meadow soil
94-05	Shuangliao-Yongjia	123·48·05	43·49·38	250	Lowland meadow	*Leymus chinense*	Dark meadow soil
94-06	Shuangliao-Xinglong	123·49·47	43·50·46	250	Lowland meadow	*Stipa grandis*	Dark meadow soil
94-07	Kailu-Liuheyong	121·02·55	43·36·38	230	Meadow steppe	*Leymus chinense*	Chernozem
94-08	Chifeng-Shaogen southeast	120·55·40	43·39·40	270	Meadow steppe	*Cleistogenes squarrosa*	Chernozem
94-09	Chifeng-Shaogen	120·41·47	43·38·48	265	Meadow steppe	*Leymus chinense*	Chernozem
94-10	Bairin Zuoqi	119·06·13	43·47·44	740	Typical steppe	*Stipa grandis*	Chestnut soil
94-11	Hexigten Qi-Wuzhou	117·08·47	43·16·32	1320	Typical steppe	*Agropyron cristatum* + *Artemisia*	Chestnut soil
94–13	Hexigten Qi-Baorihuzhao	117·02·57	43·16·29	1310	Typical steppe	*Stipa krylovii*	Chestnut soil
94-14	Hexigten Qi-Dali Nur	116·54·00	43·23·02	1280	Typical steppe	*Leymus chinense* + *Cleistogenes squarrosa*	Chestnut soil
94-15	Xilingol-Wulangou	116·28·41	43·44·40	1230	Typical steppe	*Stipa grandis* + *Leymus chinense*	Chestnut soil
94-16	Xilingol-Bayanhushuo	116·18·38	43·49·30	1150	Typical steppe	*Stipa grandis* + *Artemisia frigida*	Chestnut soil
94-17	Xilingol-Huermutaihua	115·44·54	43·54·58	1170	Typical steppe	*Stipa grandis* + *Stipa krylovii*	Chestnut soil
94-18	Abag Qi	115·08·28	43·57·08	1210	Typical steppe	*Artemisia frigida* + *Stipa grandis*	Chestnut soil
94-19	Abag Qi-West	114·36·48	43·55·17	1080	Desert steppe	*Stipa gobica*	Brown soil
94-20	Sonid Zuoqi-Bailayingaobao	113·52·24	43·50·36	1100	Desert steppe	*Artemisia frigida* + *Stipa gobica*	Brown soil
94-21	Xilingol-Daolungeyin	113·02·25	43·43·36	1020	Desert steppe	*Stipa gobica*	Brown soil

94-22	Erenhot-West	112·23·13	43·38·32	980	Desert steppe	*Allium polyrhizum* + *Stipa gobica*	Brown soil
94-23	Xilingol-Bulinhuduge	112·07·43	43·31·26	990	Desert steppe	*Stipa gobica*	Brown soil
97s09	Changling-Southeast	123·57·22	44·13·18	243	Saline-alkali meadow	*Chloris virgata* + *Leymus chinense*	Dark meadow soil
97s10	Changling	123·56·15	44·12·26	243	Farmland	*Leymus chinense*	Dark meadow soil
97s11	Shuangliao	123·18·24	43·33·58	160	Lowland meadow	*Serratula centauroides* + *Heteropappus altaicus*	Dark meadow soil
97s12	Tongliao	121·59·46	43·34·05	207	Meadow steppe	*Chloris virgata* + *Iris lactea* var. *chinensis*	Chernozem
97s13	Kailu	121·02·46	43·36·55	280	Meadow steppe	*Suaeda glauca*	Chernozem
97s14	Kailu-West	120·50·37	43·38·11	315	Meadow steppe	*Tribulus terrestris*	Chernozem
97s15	Ar Horqin Qi	120·16·40	43·48·37	443	Meadow steppe	*Enneapogon borealis*	Chernozem
97s16	Bairin Youqi	119·11·34	43·49·56	626	Typical steppe	*Lespedeza davurica*	Chestnut soil
97s17	Bairin Youqi-West	118·47·20	43·37·52	673	Typical steppe	*Arundinella hirta*	Chestnut soil
97s18	Ongniud Qi	118·36·48	43·14·43	664	Typical steppe	*Atraphaxis manshurica* + *Caragana microphylla*	Chestnut soil
97s19	Hexigten Qi-East	117·04·45	43·18·56	1300	Typical steppe	*Koeleria cristata* + *Artemisia frigida*	Chestnut soil
97s20	Hexigten Qi	116·49·30	43·30·20	1459	Typical steppe	*Filifolium sibiricum* + *Carex pediforimis*	Chestnut soil
97s21	Hexigten Qi-West	116·49·29	43·31·03	1448	Typical steppe	*Leymus chinense*	Chestnut soil
97s22	Hexigten Qi-North	116·42·03	43·38·32	1248	Typical steppe	*Cleistogenes squarrosa* + *Festuca dahurica*	Chestnut soil
97s23	Xilinhot	115·58·21	43·56·40	1060	Typical steppe	*Stipa grandis* + *Cleistogenes squarrosa*	Chestnut soil
97s24	Xilinhot-West	115·26·56	43·54·33	1182	Typical steppe	*Stipa krylovii* + *Cleistogenes squarrosa*	Chestnut soil
97s25	Erenhot-East	113·08·25	43·45·54	1065	Desert steppe	*Stipa klemenzii*	Brown soil
97s26	Erenhot	112·34·07	43·43·14	977	Desert steppe	*Stipa klemenzii*	Brown soil
97s27	Erenhot-West	111·57·26	43·40·48	993	Desert steppe	*Stipa gobica*	Brown soil
97s28	Sonid Zuoqi	113·19·02	43·47·35	1033	Desert steppe	*Stipa gobica* + *Artemisia xerophytica*	Brown soil

Table 1—*Continued.*

No.	Site name	Lon (d,m,s)	Lat (d,m,s)	Elev(m)	Vegetation	Dominant	Soil
97s29	Sonid Zuoqi-East	114·25·23	43·54·45	1012	Typical steppe	*Reaumuria soongorica* + *Salsola passerina*	Chestnut soil
97s30	Abag Qi	115·20·59	43·53·51	1199	Typical steppe	*Cleistogenes songorica* + *Stipa grandis*	Chestnut soil
M1	Bichigt	115·36·04	45·29·51	1234	Typical steppe	*Leymus chinense*	Chestnut soil
M2	Lkhachinvandad	115·27·12	45·27·16	1226	Typical steppe	*Stipa grandis*	Chestnut soil
M3	Shilinbogt Mt·	114·51·54	45·28·00	1350	Typical steppe	*Leymus chinense*	Chestnut soil
M4	Dariganga	114·07·25	45·25·25	1450	Desert steppe	*Stipa krylovii*	Brown soil
M5	Ongon	112·51·29	45·30·12	1131	Desert steppe	*Cleistogenes squarrosa* + *Carex duriuscula*	Brown soil
M6	Sainshand	110·26·08	45·01·07	960	Desert steppe	*Stipa glareosa*	Brown soil
M7	Saihandulaan	108·42·24	44·38·53	1168	Desert steppe	*Caragana pygmaea* + *Cleistogenes songorica*	Brown soil
M8	Manlai	106·24·15	44·01·20	1284	Desert steppe	*Stipa gobica*	Brown soil

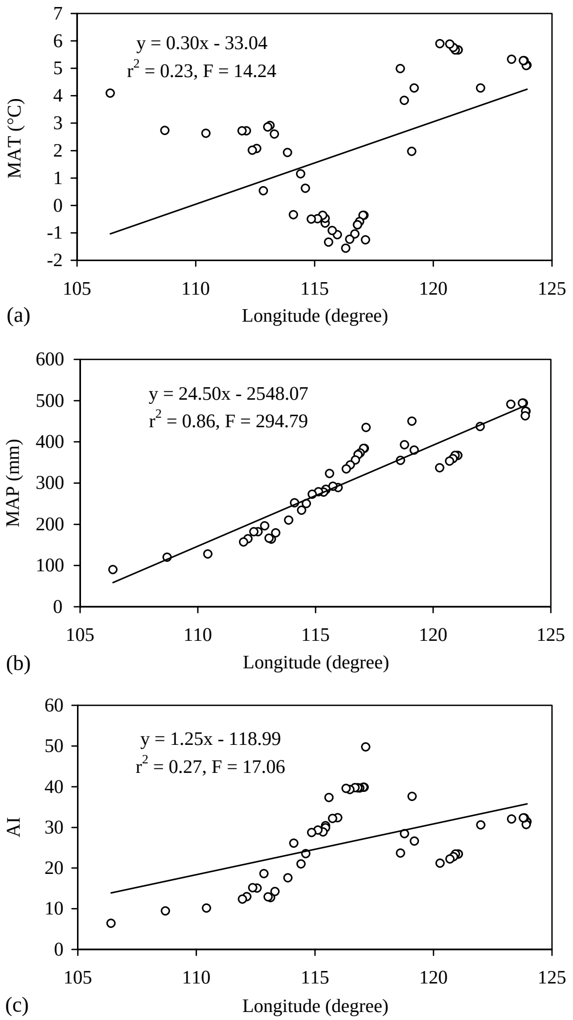

Figure 2. Spatial distribution of (a) annual mean temperature (MAT), (b) annual precipitation (MAP) and (c) aridity index (AI = MAP/(MAT+10)) along the longitudinal gradient in north-east China and south-east Mongolia.

characterized well the grassland ecosystems in the study area. The gradient distribution of PFT richness varied in different regions and in the different grassland types of the study area (Fig. 3). Many environmental factors, such as macroclimate, soil and topography as well as likely human disturbance and microclimate, may result in these differences. Although the study area was focused on a longitudinal gradient and the relationships between ecological parameters and longitude existed, the geographical coordinates (especially longitude) are spatial descriptors that do not have sufficient ecological meaning. However, the spatial gradients in vegetation and climate observed in the study area allowed the relationships between PFT distribution and climate to be clearly represented along the longitudinal gradient. In fact, the species richness in each PFT showed weak relationships with longitude, but instead it significantly responded to gradual changes of climate, especially MAP and AI (Figs 4 & 5). Climate data are more useful for mechanistically describing the spatial distribution of PFT richness than geographic coordinate of longitude, because more

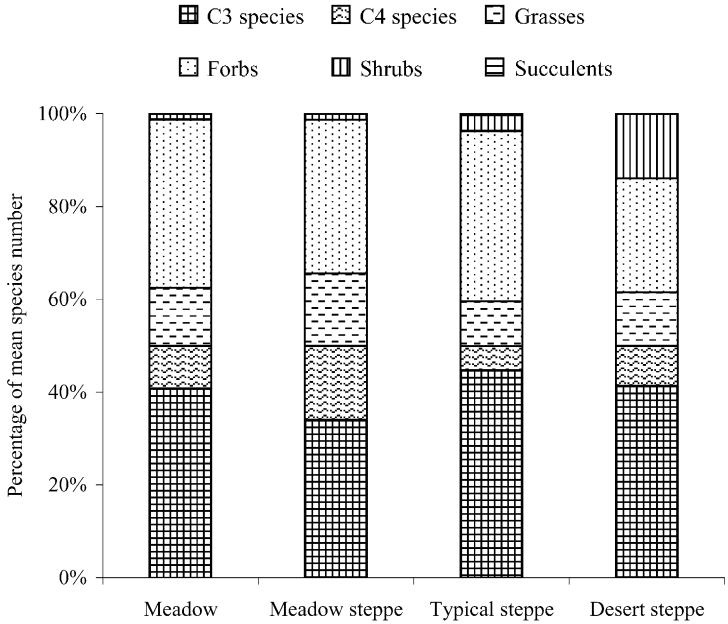

Figure 3. Proportion of mean species richness of six PFTs in each grassland type.

information such as the influence of jet streams, rain shadow effects, prevailing winds and pressure systems are inherent in climate data.

Species richness of all PFTs and species richness in each PFT excluding succulents had significant relationships with both MAP (Fig. 4) and AI (Fig. 5). Shrub richness had negative relationships with MAP and AI. Succulent richness had no relationship with MAP and AI. Species richness of other PFTs such as C_3 species, C_4 species, grasses and forbs had positive relationships with MAP and AI. However, the degree of correlation between different PFTs and climate varied (r^2 = 0·004–0·42 for MAP and r^2 = 0.0001–0·43 for AI). Shrubs, grasses and forbs had higher correlations with MAP than C_3, C_4 and all species (Fig. 4). Forbs, C_3 species and all species had higher correlations with AI than shrubs, grasses and C_4 species (Fig. 5). The relationships between all species, C_3 species, forbs and AI were more significant than those PFTs with MAP. The relationships between C_4 species, grasses, shrubs and AI, in contrast, were weaker than those PFTs with MAP (Figs 4 & 5).

The multivariable linear regression (Table 2) also showed that, species richness of C_3 species and forbs had higher relationships with MAT, MAP and elevation than all PFTs, C_4 species and grasses with median relationships. In contrast, species richness of shrubs and succulents had the lower relationships with MAT, MAP and elevation than other PFTs. The relationships between MAP and species richness of PFTs were higher than MAT and elevation, indicating that MAP is a control factor on the transect (Table 2).

It has been widely accepted that temperature is the principal control on the distribution of C_3 and C_4 species. Precipitation and its seasonal distribution are also important (Paruelo & Lauenroth, 1996; Tang, 1999). However, the limited south–north distribution range of the given longitudinal gradient in this study restricted examination of how C_3/C_4 species richness responds to MAT. In a large study area such as the whole of Mongolia, however, C_4 species would be more dependent on temperature (Pyankov *et al.*, 2000). C_3 and C_4 grasses increased with MAP in grasslands and shrublands of North America (Paruelo & Lauenroth, 1996). This

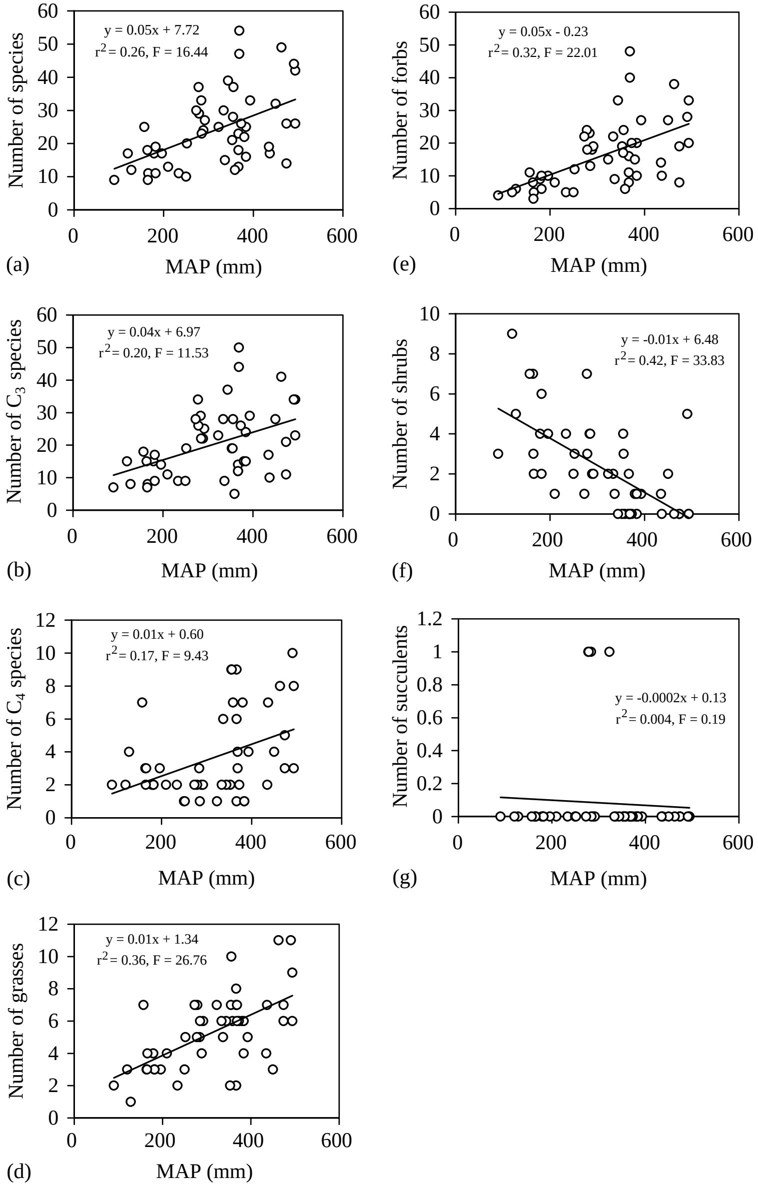

Figure 4. Relationships between species richness of (a) all PFTs, (b) C_3 species, (c) C_4 species, (d) grasses, (e) forbs, (f) shrubs, and (g) succulents and mean annual precipitation (MAP).

result was confirmed by the positive relationships between both C_3 and C_4 species richness with MAP in grasslands of north-eastern China and south-eastern Mongolia (Fig. 4(b, c). The same positive relationships were also consistent for grasses and forbs (Fig. 4(d, e)). Shrubs had a negative relationship with MAP both in North America (Paruelo & Lauenroth, 1996) and in north-eastern China and south-eastern Mongolia (Fig. 4(f)). Elevation is an important factor in controlling plant distribution. In this study however, the absolute elevation of the plateau is relatively high (above 1000 m),

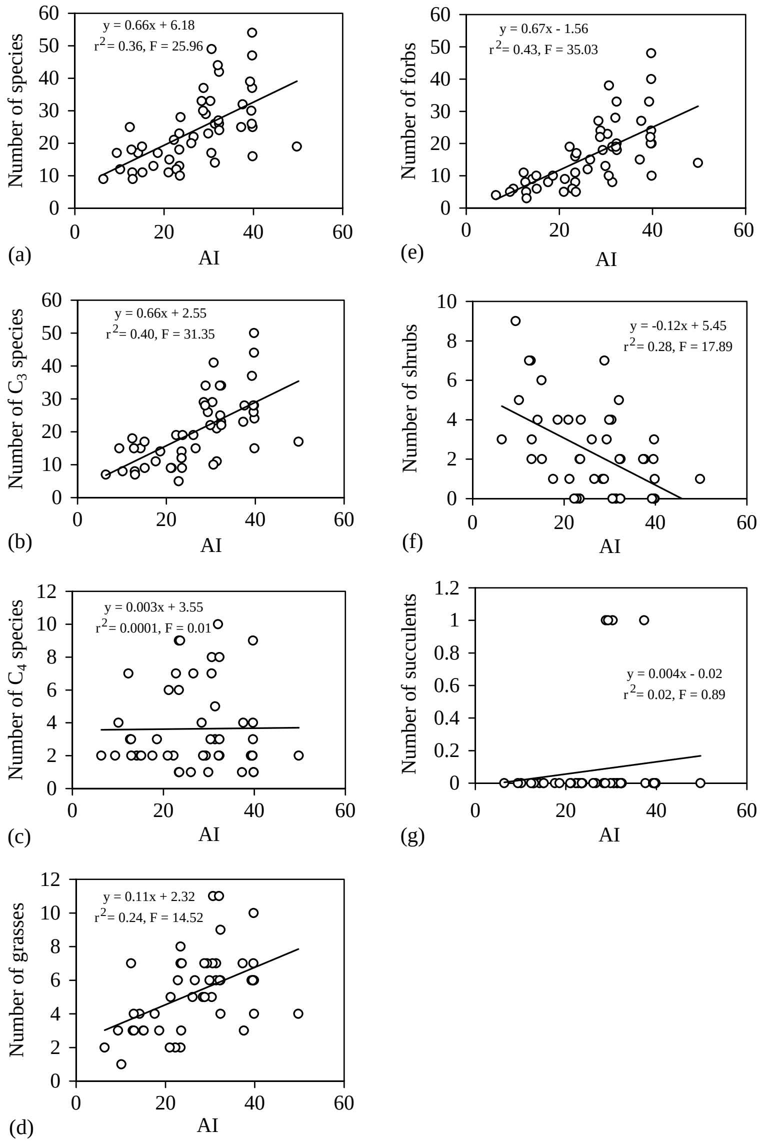

Figure 5. Relationships between species richness of (a) all PFTs, (b) C_3 species, (c) C_4 species, (d) grasses, (e) forbs, (f) shrubs, and (g) succulents and aridity index (AI = MAP/(MAT+10)).

but the relative elevation on the plateau is low. Therefore, the relative elevation does not significantly influence the distribution of plant species in the study area.

The C_3 species and forbs richness had higher proportion than other PFTs in all grassland types (Fig. 3). The proportion of C_3 species and forbs in species richness of all PFTs is highest at those longitudes (roughly typical steppe) where MAT is low and AI is high (Fig. 2). Furthermore, C_3 species and forbs had more significant relationships with AI (Fig. 5(b–e)) than MAP (Fig. 4(b-e)). Thus, as with all species, the C_3 species and forbs indicated that climatic control of PFT distribution in grasslands of north-eastern China and north-eastern Mongolia is not only precipitation but

Table 2. *Multivariable regression of species richness with mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm) and elevation (ELEV, m)*

Species richness	Regression	r^2	F	Significance			Sample number
				MAT	MAP	ELEV	
All PFTs	$Y = -10{\cdot}34 + 0{\cdot}009\mathrm{MAT} + 0{\cdot}08\mathrm{MAP} + 0{\cdot}01\mathrm{ELEV}$	0·40	9·98	0·064	0·000	0·381	49
C$_3$ species	$Y = -12{\cdot}39 - 0{\cdot}34\mathrm{MAT} + 0{\cdot}07\mathrm{MAP} + 0{\cdot}01\mathrm{ELEV}$	0·46	12·54	0·005	0·001	0·094	49
C$_4$ species	$Y = 0{\cdot}80 + 0{\cdot}45\mathrm{MAT} + 0{\cdot}007\mathrm{MAP} - 0{\cdot}0002\mathrm{ELEV}$	0·39	9·57	0·000	0·002	0·000	49
Grasses	$Y = 1{\cdot}52 - 0{\cdot}07\mathrm{MAT} + 0{\cdot}01\mathrm{MAP} - 0{\cdot}0001\mathrm{ELEV}$	0·37	8·71	0·305	0·000	0·030	49
Shrubs	$Y = 9{\cdot}23 - 0{\cdot}16\mathrm{MAT} - 0{\cdot}01\mathrm{MAP} - 0{\cdot}002\mathrm{ELEV}$	0·24	3·21	0·240	0·003	0·393	34
Forbs	$Y = -21{\cdot}55 + 0{\cdot}36\mathrm{MAT} + 0{\cdot}08\mathrm{MAP} + 0{\cdot}01\mathrm{ELEV}$	0·48	13·76	0·066	0·000	0·047	49
Succulents	$Y = 1{\cdot}73 - 0{\cdot}02\mathrm{MAT} - 0{\cdot}002\mathrm{MAP} - 0{\cdot}00003\mathrm{ELEV}$	0·16	1·46	0·373	0·023	0·152	27

also temperature. The combined effects of precipitation and temperature, i.e. the aridity, are, to some extent, most important to certain PFT spatial distribution.

The de Martonne index of aridity uses combinations of temperature and precipitation, in order to make some allowance for the increasing evaporation with higher temperatures. The absolute minimum values of this index indicate the maximum aridity of climate, considering the (MAT+10) is a proxy for potential evapo-transpiration. But, other climatic variables such as humidity also influence aridity. Factors such as seasonal timing of rainfall are also critical in determining aridity. However, this index has been widely used because it is simple and a true sliding scale without artificial break points. It is reasonable and acceptable in this study.

The continued climate change is expected to result in increases of temperature, precipitation and potential evapo-transpiration in this study area (Ni & Zhang, 2000). Under this condition, the number of C_3, C_4, grasses and forbs would be predicted to increase and shrubs to decrease in the study area, especially in the western dry part. In general, the grassland types will shift westward. If human land uses such as farming and grazing lead to grassland degradation and further desertification, the aridity would strongly increase. It is suggested that the number of shrubs would increase and other PFTs decrease. However, the land uses itself would reduce the richness of all species and PFTs.

Conclusions

Quantitative analyses of the relationships between PFTs and climatic variables provided insights into the gradient distribution of vegetation in north-eastern China and south-eastern Mongolia. Temperature has been recognized as an important control on the distribution of C_3 and C_4 species, but this point was not confirmed in this study due to limited latitudinal study area and therefore limited variability on the C_3/C_4 distribution. Precipitation was also an important control not only on C_3 and C_4 species but also on grasses, forbs and shrubs. On a regional basis, the combined effect of precipitation and temperature, the aridity, was more significantly correlated with the distribution of C_3 species and forbs, which are dominant in the study area, than with C_4 species, grasses and succulents. Four PFTs: C_3 species, C_4 species, grasses and forbs showed a positive relationship with precipitation and aridity while shrubs showed a negative relationship. Thus, the relative importance of those four PFTs decreased and that of shrubs increased in dry environments.

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