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Original article

Relationships between tree increment, climate and above-ground biomass of grass: a case study in the typical steppe, north China

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Abstract

Meyer spruce (*Picea meyeri* Rehd. et Wils.) is a relict conifer, and Chinese leymus (*Leymus chinensis* [Trin.] Tzvel.) is a dominant grass in typical steppe of the Xilin River Basin, northern China. Herein, we evaluated the relationships between tree-ring width index of Meyer spruce, climate and above-ground biomass of Chinese leymus, and reconstructed above-ground biomass of Chinese leymus from 1955 to 1994 using tree rings. Both Meyer spruce and Chinese leymus exhibited significant positive ($P < 0.05$) growth response to May precipitation during the current growing season. In addition, the growth of Chinese leymus was significantly correlated ($P < 0.05$) with the sum of current July and August precipitation. Two predominant linear relationships between ring width and annual grass production were found, and each corresponding to different precipitation patterns in this region. With reference to seasonal precipitation patterns, the above-ground biomass of Chinese leymus from 1955 to 1994 was reconstructed using two models derived from tree-grass growth relationships. The comparison of climate-growth relationships between relict Meyer spruce and dominant Chinese leymus pointed to the different adaptation strategies of two ecosystem elements to the semi-arid steppe climates. The reconstruction of grass production could reduce the gap in our knowledge of the past dynamics of typical steppe, allowing verification of model estimates of natural climate fluctuations. This may be also an important step towards understanding the response of different ecosystem components to future climate change in the typical steppe, and delivering the baseline reference for a sound steppe management plan.

Keywords: Typical steppe; *Picea meyeri*; *Leymus chinensis*; Tree ring; Above-ground biomass; Seasonal precipitation pattern

1. Introduction

The threat of future increases in the atmospheric CO_2 concentration and associated climatic change has provided a strong impetus for the ecologists to model the plant responses to global environmental change (Steffen et al., 1992). As a sensitive region to climate change, semi-arid steppe may be among the first to show the effects of climate change, thereby playing an important role in mirroring the potential influence of global change (Houghton et al., 1996). The ability to predict probable influences of global change on ecosystem components requires detailed regional analyses of the responses of different vegetations to common climatic variables and how these responses are linked (Guyette and Rabeni, 1995). The Xilin River Basin in the eastern Inner Mongolian is one of the most representative and best-preserved typical steppe zone in China (Li et al., 1988), which received the even-increasing considerations for climatic change studies (Ye, 1992). However, a series of studies in this region have been hampered by the lack of adequate data of grass production (Ye, 1992). For example, Xiao et al. (1996) tried to assess the response of semi-arid steppe to the global warming using CENTURY model based on 8-year record of grass biomass. Due to a very limited dataset, it is not confident to infer a reliable conclusion. In order to comprehend the variation dynamics of steppe ecosystem in past several decades or over 100 years and provide an insight into the effect of future global change on semi-arid steppe, there remains an urgent need to develop new methods to reconstruct past grass production records based on a more reliable understanding of plant response to the environment.

To reconstruct the data not otherwise available, Kairiukstis et al. (1990) propose a model formulated on the basis of

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the correlation between two parallel biological processes that are under the effect of the same environmental factors. Such a model can overcome many difficulties in simulation modeling, and reduce the complexity in considering multiple factors that affect two growth processes. The studies have suggested that this approach can produce ideal results when the growth and development of the vegetation are strongly limited by environmental factors (Kairiukstis et al., 1990; Vaganov and Kachaev, 1992). Trees, unlike the grasses, can provide a consequent and documental growth process by producing annual rings, which serve as indicators of external environmental variations (Fritts, 1976; Hughes et al., 1982; Schweingruber, 1988; Cook and Kairiukstis, 1990; Wimmer and Vetter, 1999). With the advantage mentioned above, tree-ring time series offer a large potential to assess growth dynamics of other parallel growth processes. For example, tree-ring width series have been used in predicting crop yield (Yuan, 1989; Vaganov and Kachaev, 1992; Xia et al., 1994), investigating fish population dynamics (Vaganov et al., 1987; Guyette and Rabeni, 1995). To date, there have been few studies to compare the interannual growth variations between ligneous and herbaceous species, even though it could be fruitful for the different aspects of plant ecology.

The Xilin River Basin is dominated by the perennial grass, Chinese leymus (*Leymus chinensis* [Trin.] Tzvel., *Aneurolepidium chinense* [Trin.] Kitagawa.). Since the establishment of the Inner Mongolian Grassland Ecosystem Research Station of the Chinese Academyof Sciences in 1979, data on grass biomass has been collected which make the further investigations possible in the typical steppe. In sharp contrast to the typical steppe landscape, a small patch of forest containing about 100 individuals of Meyer spruce (*Picea meyeri* Rehd. et Wils.) is restricted to a shady slope of one sand dune. This patch of conifers is considered to be a remnant of a Meyer spruce forest (Cui et al., 1997; Feng et al., 1999; Liang et al., 2003). More recently, a 65-year standard tree-ring chronology of Meyer spruce has been developed in this forest stand (Liang, 2001; Liang et al., 2001b), which was characterized by a high sensitivity of radial growth to the precipitation in May of the current year and in August through October of the preceding year.

Trees and grasses possess characteristics that make them comparable objects of the study. In the Xilin River Basin, both Meyer spruce and Chinese leymus grow onlyduringthe warmer period. This creates annual growth increments (i.e. xylem rings in trees and annual above-ground increases in grasses), which allow the comparison between tree and grass interannual growth variations in the typical steppe. This is the basis for our decision to examine growth of both tree and grass in relation to their common growth-limiting factor (the precipitation).

Examining the covariance in growth of the two opposite extremes (relict conifer and dominant grass) coexisting in the typical steppe will aid in understanding the ecological processes that are sensitive to climate change, and bringing new insights into the adaptation strategies of two species to the semi-arid climates.

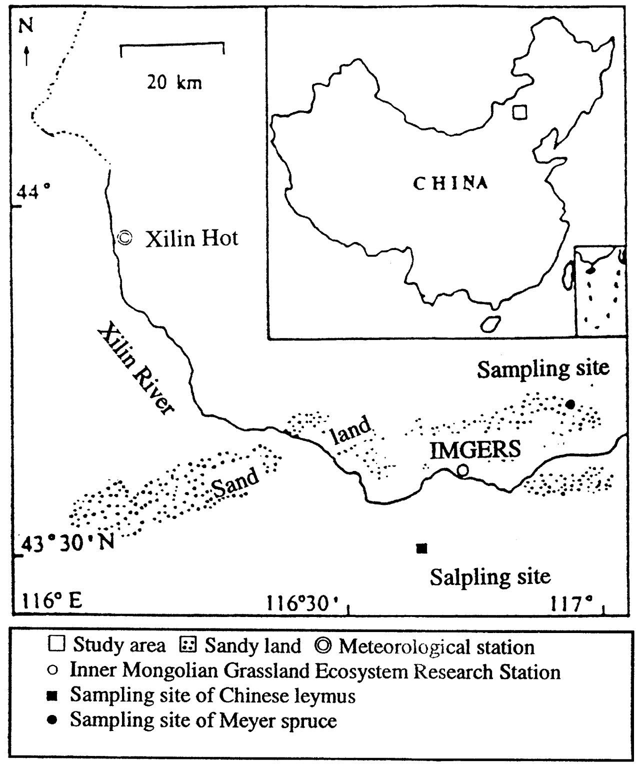

Fig. 1. Location map of meteorological station, sampling sites of Meyer spruce and Chinese leymus in typical steppe of the Xilin River Basin, east Inner Mongolia.

The purpose of this study is to compare the climate-growth relationships between Meyer spruce and Chinese leymus, and to detect the adaptation strategies of relict spruce and dominant grass to semi-arid steppe climate in the typical steppe. Furthermore, we examined the correlations among the variation in annual growth of two species, and then related the associations to climate variables. The attempt was also made to reconstruct the above-ground biomass of Chinese leymus using tree rings.

2. Materials and methods

2.1. Studied area and climate

The Xilin River Basin (Fig. 1) is located in the eastern Inner Mongolia (43°26'-44°20'N, 115°45'-117°15'E) with an area of 3900 km^2. The elevation varies from 900 m above sea level (asl) in the northwest lower reaches of Xilin River to 1400 m asl in the eastern hilly region (Chen, 1988). A sandy belt with a 10–15 km width is situated along the middle reaches of the Xilin River, while laval tableland characterizes the southern part of this region (Chen, 1988). Perennial and annual grasses are the dominant species and form the typical steppe landscape (Li et al., 1988).

Instrumental records of climatic data were obtained from the Xilin Hot Meteorological Station (43°57'N, 116°04'),

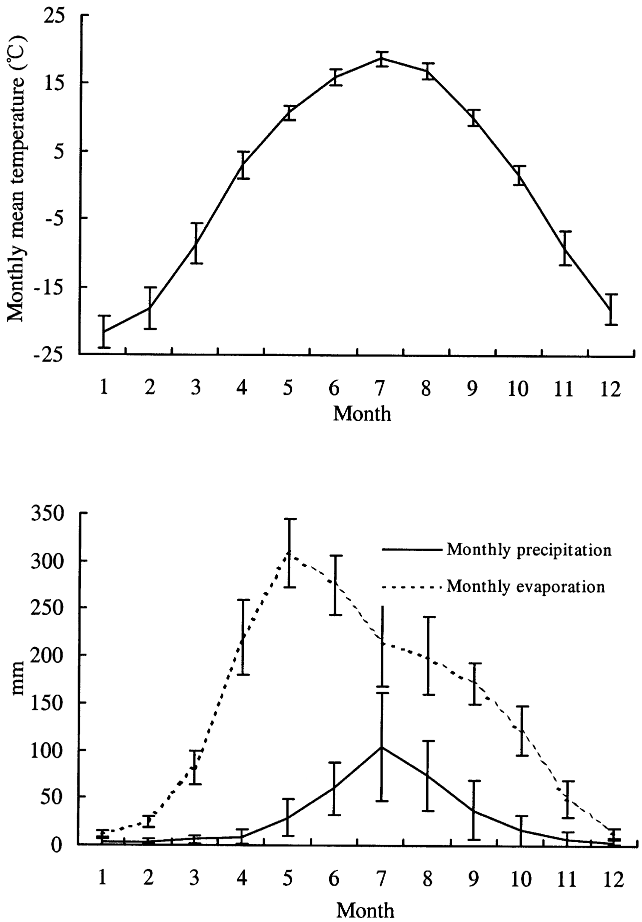

Fig. 2. Mean monthly temperature, precipitation and evaporation for the period 1954–1994 in the Xilin River Basin.

which has recorded continuous daily precipitation and temperature data since 1954. In the Xilin River Basin, a typical continental and semi-arid temperate steppe climate prevails, with cold, dry winters and warm, wet summers (Chen, 1988). The mean annual temperature is about –0.4 °C from 1954 to 1994 with a monthly minimum (January) and maximum (July) mean temperature of –21.6 and 18.8 °C, respectively Fig. 2). There are 5 months (May-September) with a mean temperature ≥5 °C in this region. The annual precipitation is about 350 mm with 60-80% falling between June and August (Fig. 2). This region also experiences wide fluctuations in annual rainfall, ranging from 180 to 500 mm. The annual potential evaporation is about 1700 mm, four to five times greater than annual precipitation (Fig. 2). Prevailing winds are from the north and northwest (Chen, 1988).

2.2. Sampling sites

A permanent experimental site (25 ha) for Chinese leymus (1265 m asl, 43°32’58’, 116°40’34’) was set up in 1979 at the Baiyin Xile livestock farm, about 60 km southeast of Xilin Hot (Fig. 1) (Jiang, 1988). Located far from water locations, this site is only slightly grazed by livestock and little affected by anthropogenic disturbance. To avoid livestock grazing, this site has been fenced for experimental data collection since 1980. The dark chestnut soil dominates this experimental site with plant litter on the soil surface, and the soil organic matter layer reaches 20-30 cm deep. Soil texture is 21% clay, 19% silt and 60% sand, on average (Wang and Cai, 1988; Xiao et al., 1996).

In the Chinese leymus site, there are 86 species of flowering plants, 11 of which are grass plants. The perennial xeric Gramineae Chinese leymus is the significantly dominant species (Li et al., 1988). Canopy cover ranges between 30 and 35%, and the height of the canopy varies from 30 to 40 cm. Chinese leymus is characterized by clonal growth with the perennial under-ground rhizoma (Li et al., 1988). It turns green at the end of April, and reaches peak above-ground biomass (PAB) in mid-August or early September. Thus, PAB represents the total maximum production of Chinese leymus within a year. Generally, the biomass of Chinese leymus begins to reduce in September and reaches senescence in early October (Li et al., 1988).

A patch (2 ha) of Meyer spruce is located on the shady slope of a sand dune (1315 m asl, 43°42’N, 116°54’E), in the eastern part of sandy belt (Fig. 1). This stand is characterized by the woodland sandy soil mainly composed of SiO_2 and silts (97.3%), and has low organic matter (less than 2.3%) (Wang and Cai, 1988). Compared to the chestnut soil, the sand soil has relatively low evaporation rates of soil moisture because of low capillary power in the usually dry upper sand profile (Wang and Cai, 1988).

Meyer spruce is an endemic conifer in mountainous regions of north-central China and is predominantly associated with cold and wet climates. Dry climates in the typical steppe are generally unfavorable for the natural growth and survival of most trees, and this patch of Meyer spruce forest was considered to be a remnant community of larger forest established during the forest optimum in the early Holocene (Cui et al., 1997; Feng et al., 1999; Liang et al., 2001a). Cambial activity of Meyer spruce begins in mid-April or early May, and the growth ceases in August coinciding with high temperature and strong evapotranspiration (Xu and Zou, 1998). The canopy coverage of Meyer spruce reaches 20–40% and its height ranges from 5 to 10 m.

2.3. Sampling techniques and data analysis

Data for above-ground biomass of Chinese leymus were collected in the beginning and middle of every month from May to September since 1980. Five 1 × 1 m quadrates were randomly chosen each time. All plants in the quadrates were cut at the ground surface and separated in terms of different species, and then oven dried at 60 °C to constant weight (Bai et al., 2000). Unlike tree-ring width series, 15-year grass production showed no age-related growth trend. In this study, the PAB of Chinese leymus from 1980 to 1994 was used.

A total of 42 cores from 21 dominant Meyer spruce trees were taken at breast height on 24 August 1994. Most cores ranged from 45 to 55 years. All cores were mounted, sanded, and visually cross-dated (Eckstein et al., 1984; Schweingruber et al., 1990). Ring width were measured to the nearest

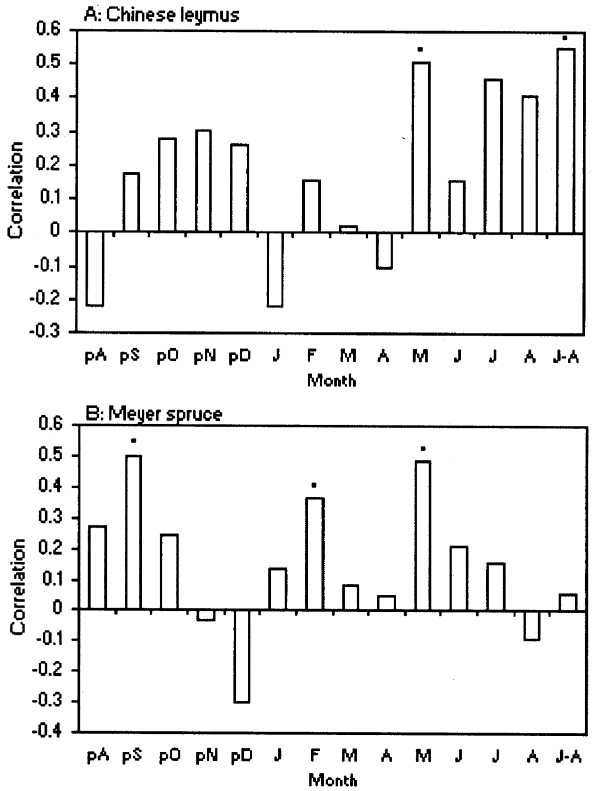

Fig. 3. Climate–growth relationships between PAB of Chinese leymus, tree-ring width indices and monthly precipitation from August of the previous year to August of the current year. The coefficients were calculated from a 15-year period (1980–1994) for Chinese leymus and a 40-year period (1955–1994) for Meyer spruce. Significant relationships between grass biomass and precipitation were found for May and for the sum of July and August of the growing season. Significance level at 95% level is indicated byone asterisk.

0.01 mm using University Model 4 system, with absolute dating verified statistically using the COFECHA program (Holmes, 1983; Grissino-Mayer, 1997). The measurement series were detrended using conventional standardization method (spline curves) that minimize non-climate variation in ring width due to age and stand dynamics and maximize high-frequency ring-width variance due to annual variations in climate (see Liang et al., 2001b for detail description on study sites, sampling, and processing of tree ring samples). At last, a 65-year standardized chronology was constructed, ranging from 1930 to 1994. But only the years from 1955 to 1994 were used, because the climatic data is not available during the period 1930-1955. Measured ring width is replaced by the ring width index (RWI) from this standardized chronology for all calculations.

Similar to the calculation of climate-growth relationships of Meyer spruce (Liang et al., 2001b), a Pearson correlation coefficient between PAB of Chinese leymus and corresponding monthly precipitation was calculated for the period 1980-1994 (Fig. 3). Fourteen monthly precipitation data from August of the previous year to August of the current year were used. All statistical procedures were evaluated at the 0.05 level of significance (*t*-test).

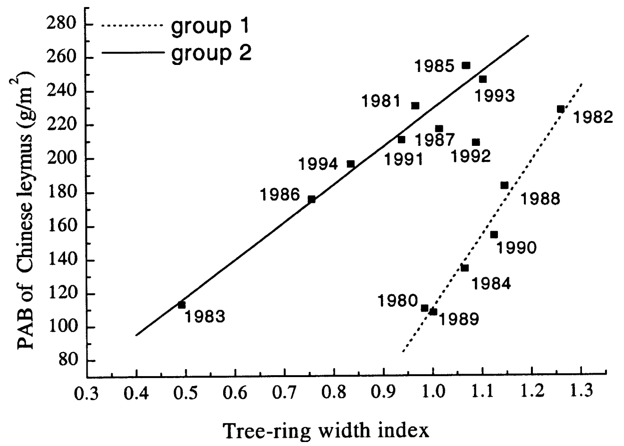

Fig. 4. Relationship between PAB of Chinese leymus and tree-ring width indices of Meyer spruce. Years from 1980 to 1994 can graphically be classified into two groups.

Due to the difference in many ecological aspects of the two species, the simple scatter plot was firstly used to reveal the tree-grass growth relationships (Fig. 4). This figure showed that two groups of years might exist. It was then necessary to try to explain the differences between these groups.

Correlation matrix PCA were performed including all years from 1955 to 1994 and using monthly rainfall and temperature data from August of the previous year to August of the current year. These analyses used successivelyall variables, rain variables only, temperature variables only, and a selection of the variables that appeared to be the most important to explain PAB and RWI variations and the separation of groups in Fig. 4.

Cluster analysis is a statistical method that can be used to assign cases into groups based on their properties in common (Everitt, 1993). In this study, a *K*-means cluster analysis (MacQueen, 1967) was performed to sort the years from 1954 to 1994 into homogeneous year-groups with respect to the three principal components of the PCA. Theses groups were displayed on PCA planes to confirm the two groups of Fig. 4 and to help interpret the differences between these groups. PAC and Cluster analyses were performed on ADE4 statistical software (Thioulouse et al., 1997).

3. Results

Fig. 4 showed that tree-grass growth relationship could be classified into two predominant groups with regard to their significant linear relationships. Synchronous growth patterns were found in the years 1980, 1982, 1984, 1988, 1989, 1990 (Group 1) and in the years 1981, 1983, 1985, 1986, 1987, 1991, 1993, 1994 (Group 2), while a intermediate situation was noticed in 1992. The correlation coefficient between the tree-ring chronology and PAB of Chinese leymus for all years was 0.14 (P = 0.40, n = 15): no significant correlation between the two growth processes could be noticed.

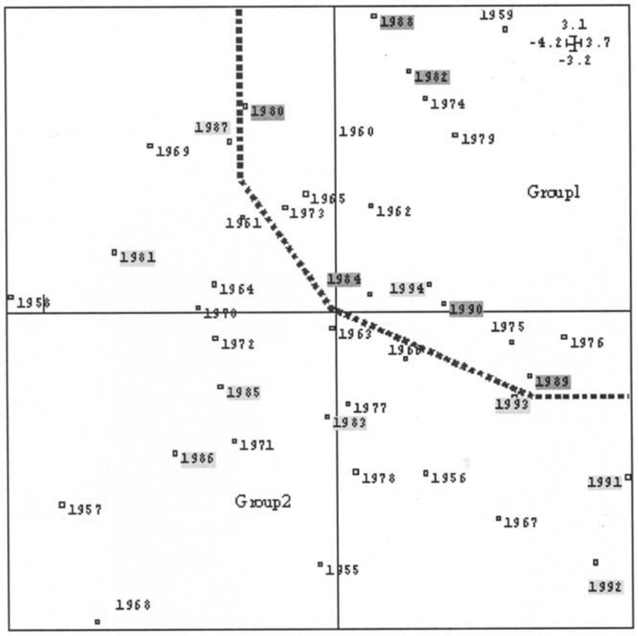

Fig. 5. A principal component analysis of the years (1955–1994) according to the monthly precipitation from August of the previous year to August of the current year. The years with similar precipitation pattern are classified into the same group and the years (1980–1994) in Group 1 and 2 were demarked by dark and gray color, respectively.

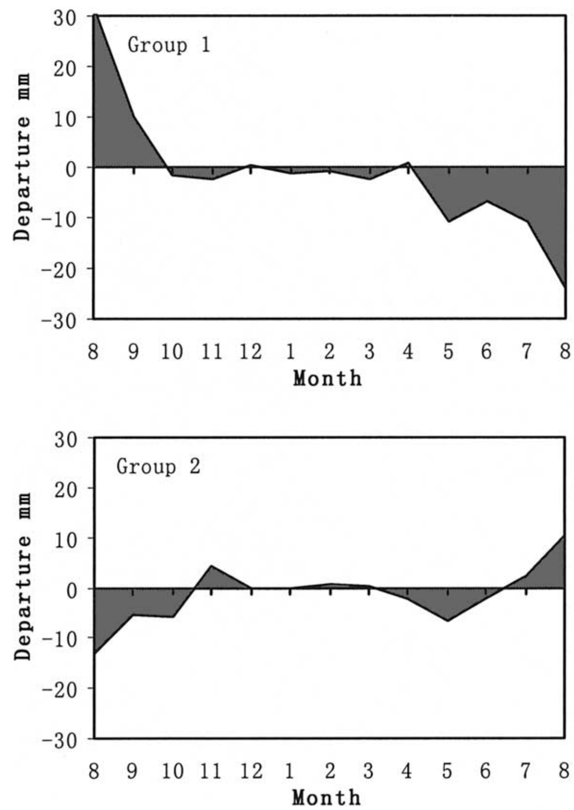

Fig. 6. The departure of monthly precipitation from the mean from the previous August to the current August. The year-group classification in this figure corresponds to Fig. 5. Group 1 was generally associated with high precipitation in the previous August through October and low precipitation in the current growing season; Group 2 corresponded to low-average precipitation in the previous fall and high precipitation in the current growing season. The precipitation in previous August-October is 147.3 mm (std 64.72 mm) and 82.15 mm (std 27.96 mm) in Group 1 and 2, and it is 173.82 mm (std 56.35 mm) and 229.21 mm (std 77.28 mm) in current May-August, respectively.

The two groups of years from Fig. 4 could be separated correctly by the PCA with all climatic variables. Displaying variables on this figure showed that summer rains and winter temperature seem to be important to understand the difference between the two groups. But other variables can participate to the separation of the groups, including winter rainfall. Some of these variables are probably redundant. Moreover, some monthly rainfall from autumn and part of winter, accounting for a few millimetres should not be significant. It was necessary to sort the variables that are really important for the growth of each species.

From Pearson correlation coefficients (Fig. 3), it appeared that the PAB of Chinese leymus was significantly correlated with May precipitation ($P < 0.05$) and the sum of July and August precipitation ($P < 0.05$). The re-analysis indicated that Meyer spruce also showed a significant positive response to the May precipitation during the current growing season, but showed no significant correlation with total precipitation in Julyand August ($P = 0.90$). Although the growth of Meyer spruce showed significant correlation with August-October precipitation in the previous year, Chinese leymus did not display such climate response.

The PCA on summer rains and winter temperature and the clustering analyses on the three principal components of this PCA confirmed the first analyses. The two groups of Fig. 4 appeared well separated in the first plane and in cluster groups (Fig. 5). The main variables that explained the separation of groups are previous year August and September rains (pP8, pP9), and winter temperature (pT12, T1, T2), and to a lesser extent current year summer rains (P7, P8) previous year August temperature (pT8) and current year temperature of March (T3).

In a last step, a simple ratio previous summer rains (pP8 + pP9) vs. mean winter temperature (pP12–P3) could completely differentiate the two predesigned groups. The ratio previous summer rains (pP8 + pP9) vs. current summer rains (P7 + P8) also separated the two groups of Fig. 4 except year 1990 which was misclassified, but did not fit as well with the years' groups from PCA and clustering: this last ratio seems to be implied in the differentiation of growth patterns but is not sufficient to explain all of it.

From all these analyses, it was possible to separate two groups of years in Fig. 4. The year 1992 that was in an intermediate position in Fig. 4 appeared in all analyses clearly linked with Group 2, even if it was sometimes close to the limit of the groups.

Based on the assumption that relationships between the grass production and the tree-ring width are stable over time, PAB of Chinese leymus was reconstructed from RWI of Meyer spruce for the period 1955–1994 (Fig. 6) using models from Fig. 4: Group 1: Y1 = 438.93X-327.81; R^2 = 0.92;

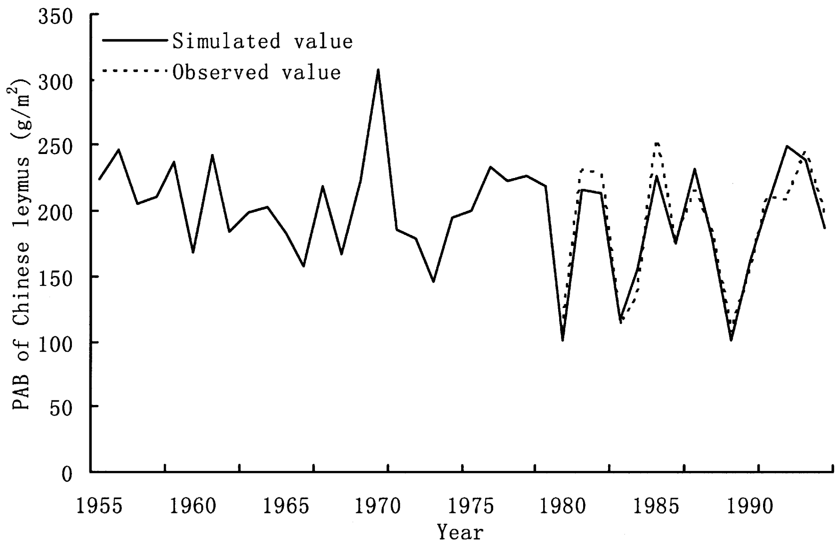

Fig. 7. The reconstruction of the PAB of Chinese leymus based on tree-ring width indices of Meyer spruce and the year-group classification in Fig. 5.

$P < 0.001$; Group 2: Y2 = 182.77X + 37.946; $R^2 = 0.79$, $P < 0.01$). The year 1992 was included in Y2 model. The correlation coefficient between reconstructed and observed PAB from 1980 to 1994 is 0.88 ($P < 0.01$) (Fig. 7).

4. Discussion

4.1. Comparison of the climatic response of Meyer spruce and Chinese leymus

May is the driest time within 1 year in the Xilin River Basin (Li et al., 1988), and water stress could be responsible for the synchronous positive correlation between May precipitation and the growth of the two species.

Different responses of Meyer spruce and Chinese leymus to the sum of July and August precipitation during the current growing season were probably associated with phenological characteristics of the two species. The climate in July and August was characterized by peak monsoon rains and high temperature within 1 year. As a dominant species in typical steppe, Chinese leymus can actively photosynthesize in response to optimal climates (Yang and Du, 1989), perhaps representing an evolutionary adaptation of this species to the semi-arid climates in the typical steppe. Chen and Wang (1985) observed that about 26 new above-ground tillers could be produced in an individual of Chinese leymus every day in Julyand August, and the above-ground biomass of Chinese leymus doubled from 25 July to 18 August in 1982. The non-significant correlation between radial growth and July-August precipitation implied that the rapid growth of Meyer spruce ceased in response to the high temperature in July and August, and only small part of latewood was formed during this period (Liang, 2001). As a climatically relict conifer species, Meyer spruce is clearly out-of-phase with the semi-arid steppe climates (Cui and Kong, 1992; Cui et al., 1997). The comparison of growth relationships between Meyer spruce and Chinese leymus also indicated the internal acclimatization of Meyer spruce to cold and wet climate rather than to semi-arid climates.

Meyer spruce and Chinese leymus respond to the precipitation in previous August through October in a different way, which may be attributed to the difference of the two species in physiological aspects and soil characteristics. The sandy substrate can effectively prevent soil moisture from evaporation. Thus, the rainfall in the previous August through October accounting for one-third of total annual precipitation was well stored in sandy soils and can be used by Meyer spruce in the following year (Liang et al., 2001b). As an evergreen conifer species, Meyer spruce might actively photosynthesize in previous August through September, which could allow most of the photosynthetic gain under the moist conditions to be stored, and has the strongest influence on current-year growth (Fritts, 1974; D'Arrigo and Jacoby, 1999; Rolland, 1993; Kozlowski and Pallardy, 1997; Oberhuber et al., 1998). In contrast, the precipitation during this period would be not utilized by Chinese leymus due to the strong soil water evaporation in chestnut soil.

4.2. Tree-grass growth relationships

Similar groups achieved with a simple scatter plot of the tree-grass relationship and principal component analysis of precipitation patterns from 1980 to 1994 indicated that tree increment and grass production were closely related to the seasonal precipitation patterns. Monthly precipitation patterns from 1980 to 1994 (Fig. 6) indicated that the tree-grass growth relationship of Group 1 was associated with high soil water availability in the previous August through October and low precipitation in the current growing season, which was favorable for the growth of Meyer spruce rather than that of Chinese leymus. Group 2 corresponded to low soil water in the previous fall and high precipitation in the current growing season. Most likely, the two different groups of tree-grass growth relationships (Fig. 3) are indicative of the difference in seasonal precipitation use of the two species. Thus, a similar seasonal precipitation pattern in different years resulted in a correspondent tree-grass growth relationship. Based on the physiological considerations of tree-grass growth relationships, tree-ring chronology of Meyer spruce with reference to seasonal precipitation patterns may bear a high potential to estimate Chinese leymus production in this region.

Former studies on reconstructing or predicting crop yield are based on one significant linear correlation between tree-ring width and crop yield (Yuan, 1989; Vaganov and Kachaev, 1992; Xia et al., 1994). In this study, two regression models derived from tree-grass relationships were used to reconstruct grass production from 1955 to 1994. Although the models were derived from 15-year investigation of spruce and grass growth variations, they were on the basis of strong biologically and physiologically reasonable links of the two growth processes, triggered by the common semi-arid climatic conditions. The reconstructed and observed grass production agreed fairly well from 1980 to 1994 and a low PAB in 1968 and 1973 also corresponded to lower precipitation in Julyand August, which further demonstrated the reliability of tree-ring width of Meyer spruce in reconstructing annual grass biomass.

Intraspecific and interspecific competition driven by seasonal precipitation variation may impose an important influence on above-ground biomass of Chinese leymus. The microclimatic difference may also affect the comparison of tree-grass growth relationships. Underground biomass of Chinese leymus was four times greater than the shoots in the Xilin River Basin (Li et al., 1988). The study of above-ground biomass alone could introduce a bias into assessment of the relationships between the above-ground biomass of Chinese leymus, climate and tree increment, which mayexplain why tree-grass growth relationship in the year 1994 cannot be accordingly revealed by the cluster analysis of monthly precipitation patterns. To gain a more comprehensive view of tree-grass growth relationships in this region, a forthcoming study will investigate daily and monthly growth dynamics of the two species.

5. Conclusion

Tree rings and annual grass biomass provide a rare forest-steppe association that can be used to assess the climatic response of diverse components of the ecosystem. The response of Meyer spruce and Chinese leymus to the precipitation in the current growing season and the previous fall reflect the physiological and phenological differences of the two species, and different adaptation strategies to the common semi-arid steppe climate. Two significant linear relationships were found, which were closely related to different seasonal precipitation patterns. This also confirmed that seasonal precipitation patterns in different years are strongly influential factors in the determination of tree and grass growth. The PAB of Chinese leymus was primarily reconstructed using two linear models based on tree-grass growth relationships. The reconstruction of grass production filled the gap of short-term record in annual grass above-ground biomass in recent decades, which will aid in understanding the past steppe dynamics, and allow to model the response of steppe ecosystem to climate change more realistically.

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