Variation of Water-Use Efficiency of Leymus chinensis and Cleistogenes squarrosa in Different Plant Communities in Xilin River Basin, Nei Mongol

CHEN Shi-Ping, BAI Yong-Fei, HAN Xing-Guo

(Laboratory of Quantitative Vegetation Ecology, Institute of Botany, The Chinese Academy of Sciences, Beijing 100093, China)

Abstract: Water is usually considered to be a key limiting factor for the growth and reproduction of steppe plants in the Xilin River Basin, Nei Mongol. Foliar δ13C values, an indicator of long-term intercellular carbon dioxide concentration and thus of water-use efficiency (WUE) in plants, were measured on Leymus chinensis (Trin.) Tzvel. and Cleistogenes squarrosa (Trin.) Keng. in six communities of different habitats in the Xilin River Basin. The foliar δ13C values of both species tended to increase with decreasing soil water content (SWC) and a significant negative correlation was found between foliar δ13C values and SWC in different soil layers, indicating that the two species could change WUE according to water availability. We also found relatively constant leaf water contents (LWC) of the two species in different habitats. Our results implied that the two steppe species might have adapted to different soil water regimes either through adjusting stomatal conductance to get a proper WUE, or through enhancing the osmosis-regulating ability to keep a relatively stable LWC. Our findings could partially explain why the two plant species have a wide distribution range and become dominant in the Xilin River Basin.

Key words: Xilin River Basin; Leymus chinensis; Cleistogenes squarrosa; water-use efficiency; δ13C value.

Water-use efficiency (WUE), i.e. the amount of carbon biomass produced per unit water transpired by the plant, is one such trait that can contribute to productivity when water resources are scarce (Wright et al., 1988). WUE is traditionally determined either as the ratio of photosynthesis (A) to transpiration (E) over short time or as the ratio of dry matter accumulation to water consumption over a longer time interval, for instance, a growing season. The former gives instantaneous estimates of WUE (A/E) and the latter gives a long-term WUE. The long-term method cannot be easily determined because it could need a tremendous amount of labor input in addition to practical difficulties involved in the simultaneous measurement of transpiration and root biomass in the field (Wright et al., 1988). The instantaneous method, although easily conducted, may not necessarily correlate with long-term plant performance (Martin and Thorstenson, 1998). Clearly, new, reliable methods for measuring WUE of plants need to be employed.

More recently, δ13C has been developed as a tool to measure WUE, because a strong positive correlation is found between δ13C and WUE (Farquhar et al., 1989). δ13C is partly determined by C/C0, the ratio of CO2 concentrations in the leaf intercellular spaces to that in the atmosphere (Farquhar et al., 1982, 1989; Farquhar and Richards, 1984). This ratio differs among plants because of the variation in stomatal opening (affecting the supply rate of CO2), and the variation in the chloroplast demand for CO2. So the carbon isotope ratio of plant tissue provides an integrated measurement of internal plant physiological and external environmental properties influencing photosynthetic gas exchange over the time when the carbon was fixed (Smedley et al., 1991).

The application of stable isotope technique to ecological studies was limited in China (Sun et al., 1993; Lin et al., 1994, 1995; Yan et al., 1998; Liang et al., 2000; Su et al., 2000; Qu et al., 2001). Most of the ecological research using stable isotopes in China was mainly found in geological field, and the limited literature so far reported in terrestrial ecosystems was focused on forest ecosystems, while studies on grassland ecosystems were rare.

Xilinogol grassland belongs to arid and semi-arid grassland zone. Water is the most important factor limiting ecosystem productivity. In general, it appears that species native to arid or semi-arid environments show no change or an increase in WUE with decreasing water supply (Toft et al., 1989). Cohen (1970) predicted that the water-use pattern should become more conservative during drought.

In this study, δ13C values of two common C3 and C4 grasses, i.e. Leymus chinensis and Cleistogenes squarrosa, were determined in six different communities in the Xilin River Basin. The main objectives of our research work are: 1) to study the variations of the water-use pattern in different habitats and to test Cohen’s hypothesis; 2) to find the strategies of two plant species to adapt to different habitats, especially different soil moisture regimes, through comparing the variations of their WUE in different communities.
1. Materials and Methods

1.1 Study site

XiLing River Basin (43°26' N - 44°29' N, 115°32' E - 117°12' E) is located in the typical steppe zone of Nei Mongol Plateau, close to the Da Hinggan Ling Mountains on the eastern edge. Topographically, this area, being about 10,000 km² in size, declines gradually from east to west, varying from 1,500 to 950 m in elevation. Chestnut and dark chestnut soils are the zonal soil types. The study area has semi-arid continental temperate steppe climate with dry spring and moist summer. Based on the records of 22 meteorological stations around the XiLing River Basin, the annual precipitation decreases gradually from 400 mm in the southeast to 250 mm in the northwest. Annual mean temperature increases from southeast to northwest, ranging from 0.5 to 2.1 °C.

1.2 Flots selection

Our study was conducted in the Nei Mongol Grassland Ecosystem Research Station (MGERS), the Chinese Academy of Sciences, which is located in the middle reaches of the XiLing River. Six plant communities were selected. They were dominated by Achnatherum splendens, Filolium sibiricum, Leymus chinensis, Stipa grandis, Caragana microphylla and Artemisia frigida, respectively. These six communities could represent a soil water gradient depending on relative elevation and soil types. They were salt meadow, meadow steppe, typical steppe and degraded typical steppe communities, respectively (Table 1).

1.3 Plant materials

Leymus chinensis, one of the most important species in Nei Mongol Steppe with wide ecological amplitude, is a perennial rhizome C3 grass and intermediate xerophytic steppe species. Cleistogenes squarrosa a perennial bunch C3 grass and typical xerophytic steppe species, is a dominant species in the lower layer of L. chinensis and Stipa spp. grassland communities.

1.4 Sampling and analyses

From 23 to 25 August 2001, a sampling transect was randomly positioned in each plant community and five spots in the line were selected for sampling. Distance between two spots was about 30 m. Fully expanded leaves from at least 10 individuals of each plant species were collected in every spot, dried at 70 °C, ground to 80 mesh and analyzed. The leaf water content was determined at the same time through weighing the fresh and oven-dried leaves. Since C. squarrosa was a rare species in the Filolium sibiricum community, plot 2 was excluded in its sampling. Soil water content of three layers (0 - 20 cm, 20 - 40 cm, 40 - 60 cm) was determined at every spot through weighing the wet and oven-dried soils.

Carbon isotope composition was measured by Finnegan MAT252 mass spectrometer in the Stable Isotope Laboratory, Institute of Geography and Geophysics, the Chinese Academy of Sciences.

\[ \Delta^{13}C_l (\text{‰}) = \frac{(13^C/12^C)_{\text{leaf}} - (13^C/12^C)_{\text{soil}}}{(13^C/12^C)_{\text{soil}}} \times 1000 \]

where \( \Delta^{13}C_l \) is leaf \( ^{13}C \) value, \( (13^C/12^C)_{\text{soil}} \) and \( (13^C/12^C)_{\text{leaf}} \) are the carbon abundance ratios of the leaf and the standard PDB, respectively.

1.5 Meteorological data

Meteorological data, including air temperature, precipitation and relative humidity, were collected from the Nei Mongol Grassland Ecosystem Research Station (Fig. 1).

1.6 Statistical analyses

Statistical analyses (variance and correlation) were conducted, and means were compared using the statistical procedures of the Microsoft Excel 2000 (ANOVA for significant mean differences in soil water content (SWC), leaf water content (LWC) and \( ^{13}C \) of two grasses among different communities and correlation analyses).

2 Results

2.1 Variation of SWC in different communities

The SWC gradually decreased from plot 1 to plot 6 (Fig. 2). As a whole, A. splendens and F. sibiricum communities had the highest SWC and the best soil water status; L. chinensis community took the second place; S. grandis, C. microphylla and A. frigida communities had the lowest SWC and were driest.

2.2 Variation of LWC of L. chinensis and C. squarrosa in different communities

As to LWC of L. chinensis, no significant difference was found between communities (Fig. 3). For C. squarrosa, LWC of plots 1 and 6 was significantly higher than that of plots 3, 4 and 5. These results indicated that both L. chinensis and C. squarrosa could postpone dehydration when soil moisture is depleted and keep a relatively stable water status in vivo under different SWC conditions.

Table 1 Characteristics of the study sites in XiLing River Basin, Nei Mongol

<table>
<thead>
<tr>
<th>Plot No.</th>
<th>Community type</th>
<th>Situation</th>
<th>Altitude (m)</th>
<th>Soil type</th>
<th>Land use type</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Achnatherum splendens</td>
<td>43°34'.925 N, 116°40.629' E</td>
<td>1 190</td>
<td>Meadow soil</td>
<td>Grazing pasture</td>
</tr>
<tr>
<td>2</td>
<td>Filolium sibiricum</td>
<td>43°32'.418 N, 116°49.643' E</td>
<td>1 380</td>
<td>Dark chestnut soil</td>
<td>Mowing field</td>
</tr>
<tr>
<td>3</td>
<td>Leymus chinensis</td>
<td>43°32'.895 N, 116°40.708' E</td>
<td>1 250</td>
<td>Dark chestnut soil</td>
<td>Fenced plot</td>
</tr>
<tr>
<td>4</td>
<td>Stipa grandis</td>
<td>43°32'.322 N, 116°33.117' E</td>
<td>1 180</td>
<td>Chestnut soil</td>
<td>Fenced plot</td>
</tr>
<tr>
<td>5</td>
<td>Caragana microphylla</td>
<td>43°35'.748 N, 116°44.419' E</td>
<td>1 210</td>
<td>Chestnut soil</td>
<td>Fenced plot</td>
</tr>
<tr>
<td>6</td>
<td>Artemisia frigida</td>
<td>43°37'.967 N, 116°39.397' E</td>
<td>1 180</td>
<td>Chestnut soil</td>
<td>Heavily grazed</td>
</tr>
</tbody>
</table>
Fig. 1. Weather conditions of Nei Mongol Grassland Ecosystem Research Station in 2001.

Fig. 2. Variation of soil water content (SWC) of three soil layers in six plots. Plot 1 to plot 6 represent Achnatherum splendens community, Filipendula ulmaria community, Leymus chinensis community, Stipa grandis community, Caragana microphylla community and Artemisia frigida community, respectively. The same letter denotes non-significant difference, while different letters denote a significant difference ($\alpha = 0.05$).

Fig. 3. Variation of leaf water content (LWC) of Leymus chinensis and Cleistogenes squarrosa in different plots. A. Leymus chinensis. B. Cleistogenes squarrosa (no plot 2).

2.3 Variation of $\delta^{13}C$ of L. chinensis and Cleistogenes squarrosa in different communities

The foliar $\delta^{13}C$ of L. chinensis was more negative than that of C. squarrosa, which was mainly caused by their different photosynthetic pathways. C$_3$ and C$_4$ plants have distinct isotopic composition because of the difference in their primary carboxylating enzyme (Rubisco...
and PEP carboxylase for C₃ and C₄ plants, respectively. C₃ plants have δ¹³C values of approximately -28‰ whereas C₄ plants are approximately -14‰ (O’Leary, 1988; Farquhar et al., 1989).

For L. chinensis, the δ¹³C value in plot 1 is most negative, plots 4, 5, 6 the most positive, and plots 2, 3 in the middle (Fig. 4). Similar trends were also found in the δ¹³C of C. squarro sa except in plot 5, which was more negative than that in plot 4 and plot 6. The more negative δ¹³C in plot 5 might be due to the relatively low intensity of irradiance. Although the SWC of plots 4, 5 and 6 is similar, the mean height of plants and biomass per unit area of plot 5 were much higher than those of plots 4 and 6 (the average height of plant in plots 5, 4 and 6 were 22.69, 16.28 and 8.97 cm; biomass were 240.22, 81.46 and 113.44 g/m², respectively). As a lower layer component of these plant communities, C. squarro sa in plot 5 was more shaded than in plots 4 and 6. Since the decrease of irradiance level will result in a decrease of δ¹³C value and the reduction of WUE, the δ¹³C of C. squarro sa of plot 5 should be relatively more negative than that of plots 4 and 6.

Fig. 4. Variation of δ¹³C value of Leymus chinensis and Cleistogenes squarro sa in different plots. A. Leymus chinensis. B. Cleistogenes squarro sa (no plot 2).

2.4 Relationship between SWC and δ¹³C

Significantly negative correlation was found between SWC and δ¹³C of L. chinensis and C. squarro sa (Fig. 5). For C. squarro sa, a more significantly negative correlation exists between SWC and δ¹³C excluding plot 5, because of the more negative δ¹³C in plot 5. Since δ¹³C is generally considered as an indicator of WUE of plants, the WUE of L. chinensis and C. squarro sa was also negatively correlated with soil water content (SWC), that is, the WUE increased with the decrease of SWC.

Fig. 5. Correlation between soil water content (SWC) and δ¹³C value of Leymus chinensis and Cleistogenes squarro sa. A. Leymus chinensis, B. Cleistogenes squarro sa. C. Cleistogenes squarro sa (excluding plot 5).

3 Discussion

δ¹³C value is a sensitive indicator of WUE in natural ecosystems (Toft et al., 1989). More negative foliar δ¹³C indicates higher C₃/C₄ ratios, resulting from either lower chlornoplast demand for CO₂ or greater stomatal conductance affecting the supply rate of CO₂ and transpiration, and hence plant water-use efficiency (Ehleringer and Cooper, 1988; Farquhar et al., 1989). Stable carbon isotope discrimination therefore provides a useful measure of integrated carbon/water balance in plants over longer periods, and is generally well correlated with plant water-use efficiency (Farquhar et al., 1988). Up to now, it is generally accepted that water-use efficiency is correlated with δ¹³C values in C₃ and C₄ plants (Peterson and Fry, 1987; Ehleringer and Cooper, 1988; Johnson et al., 1990; Madhavan et al., 1991; Henderson et al., 1992, 1998; Ehleringer, 1993; Ebdon et al., 1998; Arslan et al., 1999; Su et al., 2000). Stable carbon isotope fractionation δ¹³C in desert plants is partially determined by environmental conditions, such as water availability and vapor pressure deficit of air (VPD) (Farquhar et al.,
Ehleringer and Cooper (1988) found that along a soil moisture gradient from the relatively wetter wash to the relatively drier slope, leaf carbon isotope ratios increased in all species, indicating that water-use efficiency increased as soil water availability decreased. Stewart et al. (1995) observed an increase in δ¹³C with decreasing rainfall. Similar results were also documented (Comstock and Ehleringer, 1984, 1992; Sobrado and Turner, 1986). In a more recent research along grassland zone of the Northeast China Transect (NECT), Su et al. (2000) found that δ¹³C value and WUE of L. chinensis decreased with increasing annual average precipitation and air temperature. The results in this paper are consistent with the findings of the researchers above.

In this study, for L. chinensis and C. squarrosa, a strong negative correlation existed between δ¹³C value and SWC of three soil layers in six different habitats, that is, WUE of the two plant species increased with the decrease of soil water availability. As water was withheld, an increase in A/E, and concomitant decrease in Ci, was demonstrated in some plant species (Toft et al., 1989; Ehleringer, 1995; Lin et al., 1996). Since the increase in WUE was brought about by either a decrease in g (stomatal conductance) without a change in A, or by a greater relative decrease in g compared to A (Toft et al., 1989), the variation of WUE in our experiment might be caused by stomatal action. Decreasing water availability can result in the decrease of transpiration by increasing stomatal closure and hence enhancing water-use efficiency of plants.

Passioura (1982) hypothesized two contrasting strategies that plants may have evolved in arid and semiarid lands: conservative and prodigal, which represent plant populations with higher or lower WUE, respectively. Cohen (1970) proposed a model, which predicted that the water-use pattern should become more conservative during drought. Our data from community-wide study supported Cohen’s hypothesis. A more positive δ¹³C value indicates a more conservative water-use pattern. When water availability decreased, Leymus chinensis and Cleistogenes squarrosa employed more conservative water-use patterns. The two plant species in typical steppe and degraded typical steppe communities (plots 4, 5 and 6) have a conservative water-use strategy, especially in extended drought because it can regulate stomata in different water availability habitats; whereas the populations in salt meadow and meadow steppe communities (plots 1 and 2) have a prodigal water-use strategy which maintains higher stomatal conductance and thus probably enables higher yields. Other studies have also shown similar patterns of δ¹³C in response to drought (Ehleringer, 1993; Wand et al., 1999; Li, 2000). In the deserts of western North America, higher (less negative) δ¹³C values are typically found in species exposed to prolonged droughts in arid deserts (Ehleringer, 1993), or to long-lived species (Schuster et al., 1992), which run a higher risk of experiencing serious drought during their lifetime. Short-lived species and those occupying wetter microhabitats, such as washes, tend to have a lower (more negative) δ¹³C and lower water-use efficiency under conditions of high water availability. Their δ¹³C values therefore indicate a reasonable overall level of water-use efficiency and a survival strategy during water stress.

LWC of L. chinensis and C. squarrosa kept relatively constant in six different habitats, which suggested that these two plant species could keep a relatively stable water status in different SWC conditions. Osmotic adjustment is generally considered to be the main mechanism for turgor maintenance under water-deficient conditions, which enables plants to maintain metabolic activity, growth and productivity during drought. Studies on the physio-ecological mechanisms of four plant species under drought stress in Xilin River Basin showed that L. chinensis had strong ability to adjust osmosis and water retention, and C. squarrosa had high activity of protective enzyme system.

In conclusion, as two abundant plant species in the typical steppe communities of Xilin River Basin, both L. chinensis and C. squarrosa grow well under different soil water status. Two mechanisms might be employed by these two species: either through adjusting stomatic conductance to get a proper WUE or through enhancing osmosis-regulating ability to keep a relatively stable LWC. Water-use efficiency features may significantly influence the outcome of competitive interactions (Cohen, 1970), and may finally determine species composition in the community. From a physiological perspective, traits that influence water loss and the ability to compete for limited soil water should determine which plants will be able to colonize the given locations along these gradients (Schuster et al., 1992), which might partially explain why these two plant species had wide distribution range and became dominant in the Xilin River Basin.

As an indicator of WUE, δ¹³C of leaves provides useful information for studies on the strategies of grasses in response to different water regimes. Further research on other grasses in the six different communities is recommended to understand the water use strategies of other grasses as well as the entire communities.

References:


