



Comparison of drought tolerances in a root water uptake model for two co-occurring grass species in Mongolia

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Abstract: Drought stress due to sparse rainfall is one of the main factors determining plant species composition in semi-arid ecosystems. The tolerance of two dominant perennial grasses of northeastern Asia, *Leymus chinensis* and *Stipa krylovii*, to continuously changing drought stress was compared. Their responses to the stress were evaluated in terms of the parameter values in Feddes model. The results indicated that transpiration in *S. krylovii* began to decrease at a higher matric potential (-10^2 cm) than in *L. chinensis*. *L. chinensis* has higher performance in transpiration rate at a higher matric potential. In contrast, it seemed that greater tolerance of *L. chinensis* for drought stress is inconsistent at lower matric potentials (-10^4 cm). Thus, the tolerance for drought stress was ambiguous but depended on the degree of stress. Furthermore, *S. krylovii* maintained a low transpiration rate under a lower matric potential, implying that this species is well-adapted to drought stress because it can continue transpiration, even under severe drought stress conditions. Notably, the estimated values for root water uptake according to Feddes revealed strategic responses in both plants for survival in semi-arid regions.

Key Words : *Stipa krylovii*; *Leymus chinensis*, root water uptake, drought stress, Feddes model

1. Introduction

Drought stress is a critical inhibitor of plant growth in semi-arid ecosystems and results from sparse and irregular rainfall. As typical semi-arid grassland, Hustai National Park in Mongolia is characterized by sparse and irregular rainfall. *Leymus chinensis* and *Stipa krylovii* are the

dominant perennial grasses in this area (Yuan et al., 2005; van Staaldunin and Anten, 2005). *L. chinensis* predominates in habitats with relatively abundant water (Chen et al., 2005). *S. krylovii* is a more abundant and important species in drier areas (Chen et al., 2005) such as the typical moderately grazed grasslands in Mongolia (van Staaldunin and Anten, 2005; Hoshino et al., 2009). With overgrazing, *S. krylovii* tends to be replaced by *L. chinensis* (Hilbig, 1995; Hoshino et al., 2009; van Staaldunin et al., 2007). Therefore, previous studies have suggested that these plants may be useful key indicators of grazing intensity; however, there is insufficient quantitative knowledge of their stress-response characteristics. Some studies have indicated that the two species have distinct differences in morphology, compensatory growth, and tolerance to drought stress (van Staaldunin and Anten, 2005; Shinoda et al., 2010), but little is known about their differences in real-time responses to drought stress and how these differences contribute to the distribution of the species.

Evaluation of the tolerances of these key plants to drought stress should help elucidate and predict the dynamics of species composition and net primary production in response to climate change and human activity in semi-arid ecosystems. Previous evaluations of drought stress on plants have been based on the assessment of dry matter production and dry matter content in various tissues at different inputs, such as under continuous wet or dry conditions (Wang, 2004; Chen et al., 2005; van Staaldunin and Anten, 2005; Yuan et al., 2005). Without understanding how a plant dynamically responds to stresses, predicting hydrological processes, vegetation growth, and shifts in such ecosystems is difficult. Macroscopic root water uptake (RWU) models, such as Feddes model (Feddes et al., 1978), deal with the nonuniform distribution of the matric potential by discretizing the soil and root profiles. Therefore, reliable evaluation of stress tolerance should be possible if such a model is used. Feddes model, which is based on stress-response functions and the active root distribution, is widely employed in user-friendly hydraulic sim-

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ulation models of soil-plant-atmosphere systems, such as HYDRUS (Šimůnek et al., 2006) and SWAP (van Dam et al., 1997). Notably, the plant-specific parameter values in Feddes model can be universal indices of the tolerance of plants to stress because they are assumed to be independent of the experimental conditions.

The objective of this study is to compare the tolerances of *S. krylovii* and *L. chinensis* to sequential changes in drought stress. Because net primary production is strongly related to transpiration and the prediction of transpiration rates under drought conditions is hydrologically important, the transpiration rate was the focus of the evaluation of tolerance to drought stress in this study.

2. Theory

In Feddes model, the rate of water uptake, S (day^{-1}) as a function of depth z (cm), which is a sink term in the continuity equation, is obtained by multiplying the RWU reduction coefficient α by the potential water uptake rate S_p (day^{-1}) (Feddes and Raats, 2004; Feddes et al., 1978):

$$S(z) = \alpha S_p(z) \quad (1)$$

To express the reduction in the water uptake rate in response to drought stress, the following equation was employed:

$$\alpha = \frac{1}{1 + \left(\frac{h}{h_{50}}\right)^p} \quad (2)$$

where h is the matric potential, and h_{50} and p are fitting parameters (van Genuchten, 1987). Note that h_{50} is the matric potential when the water uptake is 50 % of its potential rate; these parameters, therefore, represent simple indices of the stress tolerance of the plants. The potential water uptake (S_p) rate is proportional to both the normalized root density and root activity β (cm^{-1}) and the potential transpiration rate T_p (cm day^{-1}):

$$S_p(z) = \beta(z) T_p \quad (3)$$

The normalized root density β is defined as the density of active roots as a function of depth z that is normalized such that integrating over the root zone yields unity:

$$\beta(z) = \frac{\rho_r(z)}{\int \rho_r(z) dz} \quad (4)$$

where ρ_r is the density of the active roots, often represented by the root length density (cm^{-2}). Because the transpiration rate T_{cal} is the integral of S over the root zone, T_{cal} is calculated as follows:

$$T_{\text{cal}} = \frac{T_p}{\int \rho_r(z) dz} \int \alpha \rho_r(z) dz \quad (5)$$

In this study, numerical integration was performed with the Riemann sums at a spatial increment of 0.5 cm.

This model does not consider compensated water uptake, which describes the compensation for root water uptake reduction in dry layers by enhanced uptake in wet layers. However, since the magnitude of the compensated water uptake was assumed to be not so significant in our previous studies, we assume the simple root water uptake model is accurate enough if appropriate parameter values are used (Fujimaki et al., 2008; Fujimaki and Kikuchi, 2010; Yanagawa and Fujimaki, 2013).

3. Materials and methods

3.1 Experimental plants

Tillers of five *S. krylovii* and five *L. chinensis* plants were taken from Mongolia (lat. $47^\circ 46' 48''$ N, long. $105^\circ 54' 56''$ E, mean elevation 1378 m a.s.l.), where the climate is semi-arid and continental (mean annual temperature $+1^\circ\text{C}$) with a short growing season in summer (from June to August), during which time more than half of the precipitation is recorded (mean annual precipitation 232 mm, CV 31 %). These climatic data were obtained from the Hustai National Park climatic station for the years 1999–2005.

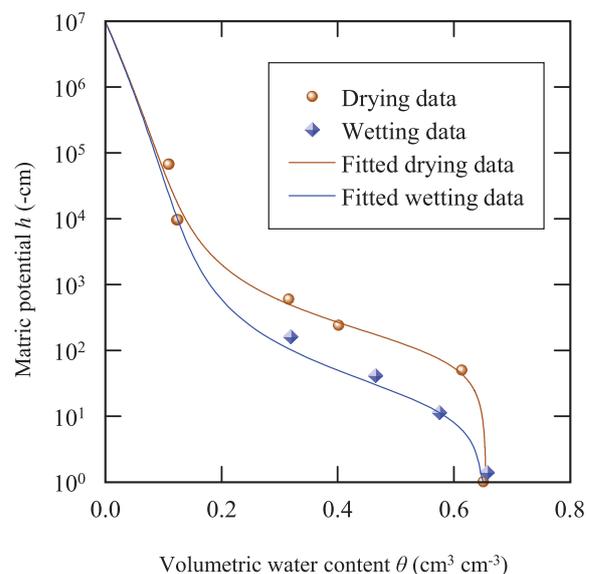


Fig. 1 Drying and wetting soil water retention curves for Kanto loam.

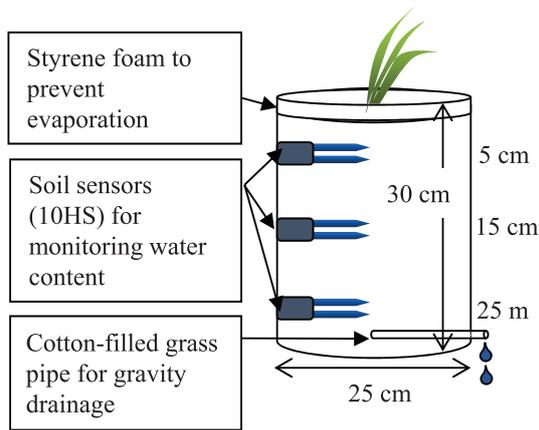


Fig. 2 Schematic of the experimental setup.



Fig. 3 Photos of *Stipa krylovii* (left) and *Leymus chinensis* (right).

Table 1 Experimental treatment and type of sensor for each column.

Plant	<i>Stipa krylovii</i>					<i>Leymus chinensis</i>				
	Column	S1	S2	S3	SR1	SR2	L1	L2	LR1	LR2
Treatment	Drought stress			No stress		Drought stress		No stress		
Sensor	Soil moisture and temperature			No sensors		Soil moisture and temperature		No sensors		

3.2 Experimental setup

The experiment was conducted in a greenhouse located in the Biotron Laboratory at the University of Tokyo. The internal temperature was maintained at approximately 25 °C during the day (06:00–18:00) and 20 °C at night (18:00–06:00), and the average humidity was 59 %. The day length was set at 15 h (05:00–20:00) by supplementing natural light with mercury-vapor lamps.

Ten columns (25 cm i.d. and 30 cm high) were placed in the greenhouse. Table 1 shows the experimental treatment and type of sensor for each column. Air-dried Kanto loam (sand 50 %, silt 44 %) was packed into the columns to a bulk density of 0.82 g cm⁻³. The water-retention curve for the Kanto loam obtained using the evaporation method for the drying curve and the hanging water method for the wetting curve, which was used to estimate the matric potential from the soil moisture content, is shown in Fig. 1. To minimize nonuniformity during packing, the mass of every 5 cm of packed soil was measured before the next soil increment was added. The soil surface was covered with white 1 cm-thick styrene foam to prevent evaporation, thus allowing only transpiration (Fig. 2). Cotton-filled glass pipes (1 cm o.d. and 15 cm long) were placed at the bottom of each column to allow gravity drainage through a hole in side of

the column at the bottom (Fig. 2).

To monitor the hourly volumetric water content, θ , and temperature in the soil, three dielectric moisture probes (10HS, Decagon Devices, Inc. Pullman, WA) were inserted horizontally into three columns for each species: S1, S2, and S3 for *S. krylovii* and L1 and L2, for *L. chinensis* (Table 1, Fig. 3). Insertion was performed such that the centers of the rods (there were three rods for each sensor) were located at depths of 5, 15, and 25 cm, respectively (Fig. 2). In addition, each type of moisture probe was calibrated at three points: the water content of the soil was measured for the air-dried soil, the saturated soil, and the soil at the end of the experiment.

Four reference columns, two (SR1 and SR2) for *S. krylovii* and two (LR1 and LR2) for *L. chinensis*, were used to measure the potential transpiration under continued irrigation with tap water for growth and 2000-fold diluted liquid fertilizer (N-P-K = 6-10-5, Hyponex Japan, Osaka, Japan) but were not equipped with soil moisture and EC probes. The water containing the liquid fertilizer was added to the reference columns using a sprinkling can within a few minutes, but without causing ponding, in order to replace the amount of water, that was taken up during the previous day (determined based on the decrease in weight).

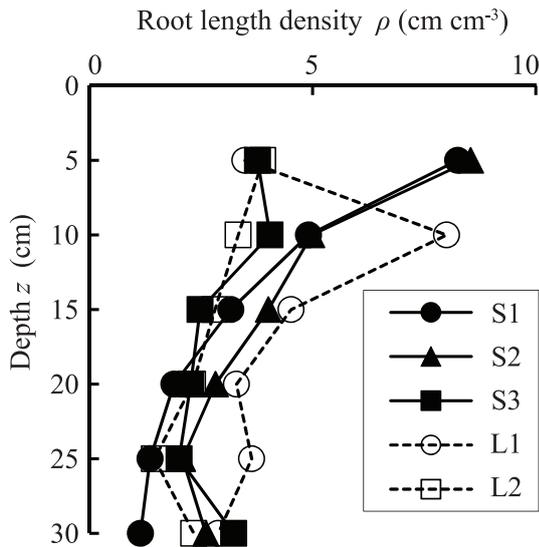


Fig. 4 Profiles of root length density at the end of experiment.

3.3 Experimental scheme

The method presented by Yanagawa and Fujimaki (2013) was followed. Although the drought stress period was the end of December, the experiment finished at the end of March. Consequently, it was possible that the root density at the end of the experiment was different from that of the drought stress period. Since the end of drought stress period is almost half of the whole experimental period, the data for the drought stress period was also inversely analyzed assuming half of the root depth at the end of the experiment while keeping the shape of the root density at the end of the experiment.

The daily transpiration rate was measured by manually weighing each column every night at 8 p.m. The potential transpiration was calculated by multiplying the mean value of the potential transpiration rate for the reference columns (SR1, SR2, LR1, and LR2) by correction factors for the individual differences in growth. Because T_p inevitably differs from plant to plant due to nonuniformity in micrometeorological conditions and genetic differences, a growth correction factor, η , was introduced for each plant:

$$\eta = \frac{1}{m-n+1} \sum_{i=n}^m \left(\frac{T_i}{T_{ri}} \right) \quad (6)$$

where T_{ri} is the average transpiration for the two reference columns, and m and n are the final and first day of analysis period, respectively. Thus, the value for η is the average value for the ratio of the transpiration on the i th day, T_i ,

to T_{ri} during the non-stress period ($m-n+1$). During the stress period, T_p was estimated by multiplying η by T_{ri} , assuming that the growth correction factor is invariant over the stress period.

One *S. krylovii* or *L. chinensis* tiller was transplanted into each column on October 7, 2008. The stress period was initiated after healthy plants were grown using irrigation with tap water ($EC < 0.01 \text{ dS m}^{-1}$) and 2000-fold diluted liquid fertilizer (1 dS m^{-1}). Because there were cotton-filled glass pipes for gravity drainage at the bottoms of the columns, the lack of oxygen supply should have been minimized. The water supply was completely stopped in order to initiate the drought stress period. The drought stress period was terminated when the relative transpiration (i.e., the actual transpiration rate divided by the potential transpiration rate) dropped to less than 75 %.

At the end of the experiment, soil samples were taken from each 5 cm layer. The roots were cut at the boundaries of each of the 5 cm layers using a pair of scissors and a sharp knife. The roots were then separated from the soil by sieving the air-dried soil samples through a 0.8 mm screen. The segments of the roots were scanned at 600 dpi to obtain digital images, and the total length of the root segments in each layer was automatically calculated using the SimpleDigitizer program (www.alrc.tottori-u.ac.jp/fujimaki/download/SimpleDigitizer) using the intersection method (Newman, 1966). The total root length density distribution for each column was then plotted (Fig. 4).

Consequently, the normalized root density, daily potential transpiration rate, and actual daily transpiration rate as well as hourly soil moisture and hourly matrix potential values calculated based on the soil moisture content of the Kanto loam (Fig. 1) were used to calculate the parameter values for the RWU reduction coefficient for each column. The program PERF, which is available at <http://www.alrc.tottori-u.ac.jp/fujimaki/download/windows.html>, was used to estimate the parameter values in the stress response function based on the Levenberg-Marquardt maximum neighborhood method (Marquardt, 1963) to minimize the sum of the root mean square error (RMSE) between the measured and calculated daily transpiration.

Table 2 Optimized parameter values and observed and calculated total amount of transpiration.

Column	<i>Stipa krylovii</i>						<i>Leymus chinensis</i>							
	S1		S2		S3		Average		L1		L2		Average	
Root Depth	Full	Half	Full	Half	Full	Half	Full	Half	Full	Half	Full	Half	Full	Half
h_{50}	-2021	-2389	-1580	-1561	-1424	-1410	-1675	-1787	-1200	-1337	-765	-683	-983	-1010
p	1.36	1.49	1.89	1.98	1.43	1.43	1.56	1.63	4.18	3.28	3.90	3.78	4.04	3.53
RMSE	0.07	0.08	0.09	0.08	0.05	0.04			0.13	0.12	0.10	0.13		
Period	12/4 -/27		12/4 -/26		12/4 -/25				12/4 -/23		12/4 -/24			
Total transpiration														
Observed	17.48		21.94		13.39		17.60		39.74		22.85		31.30	
Calculated	17.04	17.01	21.67	21.75	12.96	13.39	17.22	17.38	38.92	38.76	20.97	21.70	29.95	30.23

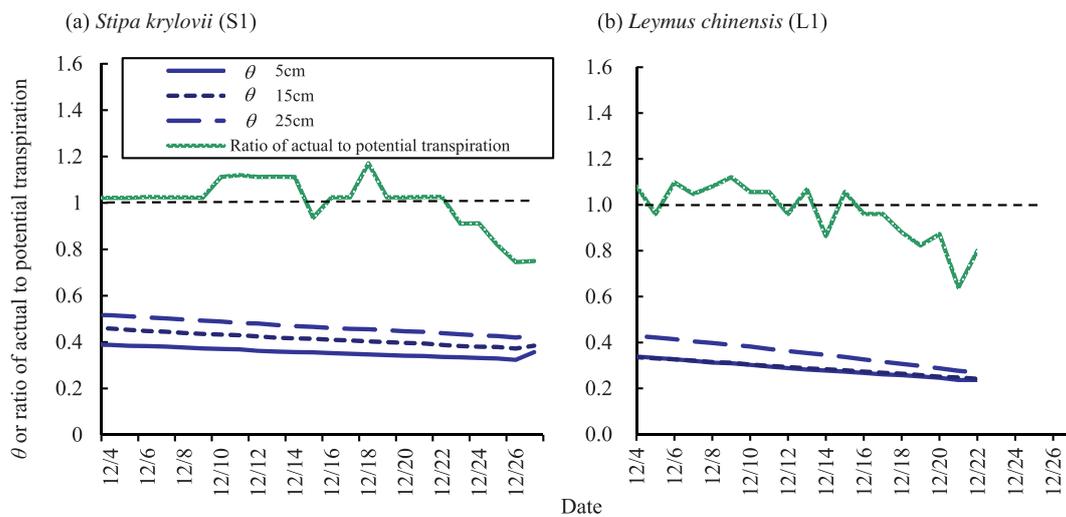


Fig. 5 Time series of volumetric water content (VWC) and ratio of actual to potential transpiration: (a) *Stipa krylovii* (S1) and (b) *Leymus chinensis* (L1).

4. Results

The time series for the volumetric water content and ratio of the actual to potential transpiration are shown in Fig. 5. The ratio of actual to potential transpiration started to decrease less than unity clearly when volumetric water content at the depth of 15 cm became less than 0.4. Table 2 lists the optimized parameter values and measured and calculated transpiration results for *S. krylovii* and *L. chinensis* after being subjected to drought stress assuming full and half root depths (Full and Half in Table 2) based on the root distribution at the end of the experiment (Fig. 4). The parameter values for drought stress and the total calculated transpiration results did not vary so much during the growing period regardless of the root depth. Therefore, the parameter values for drought stress (h_{50} , p) were con-

sidered to be reliable. The total transpiration for *L.chiensis* was higher than that of *S. krylovii* during the analysis period (Table 2).

Fig. 6 compares the measured and calculated ratios of the actual to potential daily transpiration for full and half root depths. The actual and potential transpiration were daily measured according to the weight of the column under stress and no-stress (reference) conditions, respectively. The calculated transpiration ratios were derived according to Eq. (5) based on the optimum sets of parameter values for h_{50} and p (Table 2). Large discrepancies between the measured and calculated values occurred when the potential transpiration was either very low or high. Except for such data, however, most of the calculated values were similar to the corresponding experimental results.

Since the parameter values for drought stress did not vary so much even if using the half root depth, the RWU

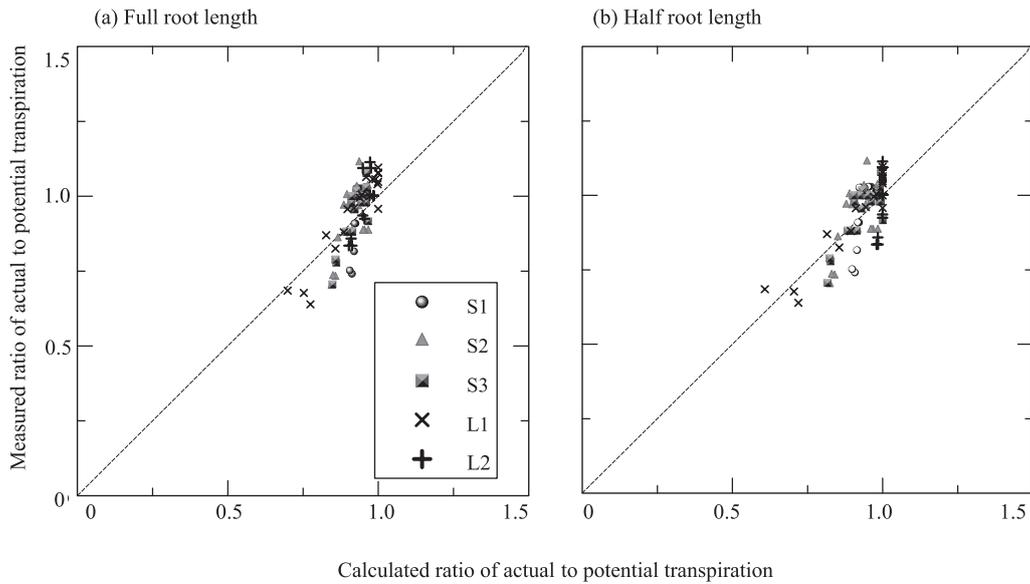


Fig. 6 Comparison of measured and calculated ratios of actual to potential daily transpiration: (a) full root length and (b) half root length.

reduction coefficient α according to equation 2 using obtained parameter values are shown only for the full root length condition in Fig. 7. Bold lines show the matric potential range of experiment. Each two or three columns were a set of replicates. As can be observed in this figure, the tolerance for drought stress varied with the degree of drought stress with the both condition of full and half root length. In addition, it was found that transpiration for *S. krylovii* began to decrease earlier than for *L. chinensis* under drying process.

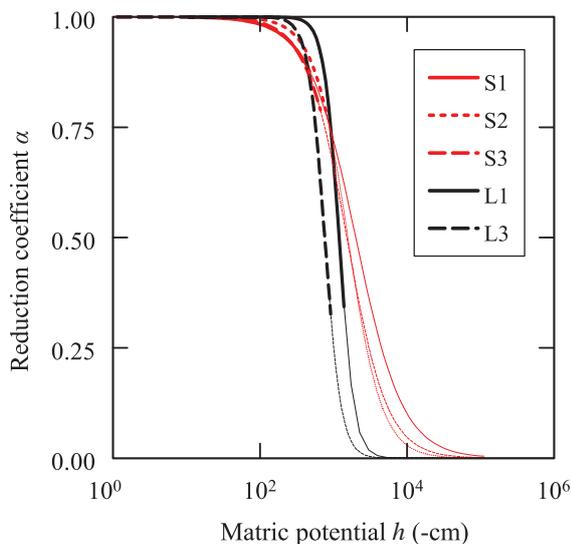


Fig. 7 Drought stress response functions for *Leymus chinensis* (L1 and L2) and *Stipa krylovii* (S1, S2, and S3).

The values for p were substantially greater for *L. chinensis* than *S. krylovii* (Table 2). The difference in the p values represents the difference in the sharpness of the reduction in the RWU beyond the threshold value for the two species. A low p value indicates a low sensitivity of the RWU to drought stress. In addition, the transpiration rate for *S. krylovii* decreased more gradually than that of *L. chinensis* (Fig. 7).

5. Discussion

Although the tolerance to drought stress of *S. krylovii* and *L. chinensis* has been reported (e.g., *S. krylovii* is considered more drought tolerant than *L. chinensis*; Chen et al., 2005), the results of the present study indicated that transpiration for *S. krylovii* began to decrease at a higher matric potential (-10^2 cm) than for *L. chinensis*. If the present results fully supported those of previous studies (Chen et al., 2005; van Staalduinen and Anten, 2005), then the S-shaped curve for drought stress in *S. krylovii* would have always appeared to the right of the curve for *L. chinensis*. However, the results of the present study indicate that the relationship between the drought stress responses of the two species changes with the degree of drought stress. A previous study implied a higher sensitivity of *L. chinensis* to drought stress (Wang, 2004). This sensitivity would correspond to the higher value of

p in *L. chinensis*. Unfortunately, the response at approximately -10^4 cm could not be observed directly, and thus remains to be investigated (bold lines in Fig. 7 show the matric potential range in the experiment). However, it can be concluded that because transpiration was greater for *L. chinensis*, *S. krylovii* is more suited to surviving drought conditions from the viewpoint of saving soil water. It means *S. krylovii* has a competitive advantage under continuously water limited condition such as in grassland. Since *L. chinensis* can use water more quickly, it seems that *L. chinensis* has a competitive advantage in plant communities with low density such as degraded bare grassland or river bank.

In addition, the results of the present study suggest that evaluation of stress responses using the parameters for Feddes model may provide more detail than previous studies when investigating continuous changes in the matric stress conditions for these two main species in Mongolia. Although the stress tolerances of these species were only qualitatively evaluated under continuous wet or dry conditions so far (Wang, 2004; Chen et al., 2005; van Staalduinen and Anten, 2005; Yuan et al., 2005), it is clear from the results that *L. chinensis* has a higher tolerance than *S. krylovii* only for drought stress conditions near -10^2 cm. Thus, obtaining the stress response functions of the dominant species allows us to predict plant growth and populations under various soil and climate conditions. The present study also demonstrates how soil physics can be applied to plant ecology.

6. Conclusion

We compared the tolerances of *S. krylovii* and *L. chinensis* to sequential changes in drought stress using a root water uptake model, Feddes model. Notably, transpiration in *S. krylovii* decreased at a higher matric potential (-10^2 cm) than in *L. chinensis*. In addition, transpiration in *S. krylovii* was less than that in *L. chinensis* during the analysis period. Thus, *S. krylovii* appears to be more adapted and thus may be more likely to survive drought conditions than *L. chinensis*.

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要 旨

乾燥ストレスは、半乾燥地域の植物生態系において重要な要素である。北東アジア地域の主要な草本である *Leymus chinensis* と *Stipa krylovii* について、乾燥条件を連続的に変化させ、乾燥耐性を調べた。ストレス応答パラメーターの推定には Feddes の吸水モデルを用いた。乾燥ストレスが低いときは、*L. chinensis* の耐乾性が高く、*S. krylovii* は乾燥ストレスが高いときにより高い耐性を示した。*S. krylovii* は、高い乾燥条件下でも蒸散速度を維持できるため、乾燥に適応した種であると考えられた。吸水モデルに基づくパラメーター推定によって、半乾燥地域において生き延びるための戦略的応答を評価することができた。

キーワード : *Stipa krylovii*, *Leymus chinensis*, 根による吸水, 乾燥ストレス, Feddes の吸水モデル