

Seasonal Dynamics in Resource Partitioning to Growth and Storage in Response to Drought in a Perennial Rhizomatous Grass, *Leymus chinensis*

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Abstract A natural grassland in northeastern China dominated by *Leymus chinensis* (Trin.) was subject to drought treatments to determine the seasonal dynamics in resource partitioning to shoot and storage organs in response to drought. The growing season was divided into six stages according to the phenology of *L. chinensis*. Plant samples of *L. chinensis* were collected at each stage to determine biomass, gross calorific value, relative water content, and key mineral contents of plant parts, including rhizomes, roots, leaves, and stems. Resource partitioning to shoot and storage organs as measured by biomass, gross calorific value, and N, K⁺, and Na⁺ contents varied significantly among phenologic stages. Drought treatment (natural precipitation, 50–60 % of field capacity) significantly reduced biomass, gross calorific value, relative water content of shoot, and N and K⁺ contents in both shoot and storage organs, but it enhanced rhizome : shoot ratio and Na⁺ content. A negative correlation in biomass, gross calorific value, and K⁺ and Na⁺ contents between shoot and storage organs was found throughout the growing season, which may have been accentuated by drought when soil moisture was limited. Our results indicate that resource partitioning to storage plays an important role in regulating plant growth of *L. chinensis*, especially under drought conditions.

Keywords Resource partitioning · Growth · Storage · Biomass · Gross calorific value · N · K⁺ · Na⁺ · Drought · Perennial rhizomatous grass · *Leymus chinensis*

Introduction

Research on plant responses to drought is becoming increasingly important as most climate change scenarios suggest an increase in aridity in many areas of the world (Chaves and others 2003; O'Connor and others 2001; Petit and others 1999; Shah and Paulsen 2003). On a global scale, the increase in drought (soil and atmospheric water deficits) and coincident high temperature pose the most important environmental constraints to plant growth, reproduction, and survival by altering competitive relationships, regeneration, photosynthesis, and respiration (Aloni and others 2001; Evers and others 2003; Shaw and others 2000). With increasing water shortage in many regions, a better understanding of plant responses to drought is vital for improved management practices and for predicting the fate of natural vegetation under climate change (Chaves and others 2003).

Resource partitioning to storage is one of the important strategies that plants use to cope with drought by storing resources in relatively safe organs (for example, roots and stems) to enable regrowth later. This has been well documented in crops (Bruce and others 2002; Gebbing and Schnyder 1999), grass forage (Wang 2005), and some legumes (Chaves and others 2002; Creelman and others 1990). Adaptations that promote the growth of below-ground organs due to drought are widespread. However, most research related to plant storage has focused on the storage of biomass and energy under drought and nutrient limitations (Greco and Cavagnaro 2003; McConaughay

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and Coleman 1999), but has shed little light on the storage of key minerals, in particular, nitrogen (N), potassium (K), and sodium (Na), in native plant species. Although there have been extensive research efforts (Chaves and others 2003; Iwasa and Kubo 1997; Meijden and others 2000) to explore plant strategies under drought stress, the function of stored resources in regulating plant growth has received little attention.

Drought is a major environmental factor that affects resource partitioning in plants, because plant growth is determined by photosynthesis, allocation of fixed carbon and energy, mobility of storage for growth and reproduction (Harper and Ogden 1970; Mooney 1972), and by climatic variables (for example, water limitation, light, and temperature). Sack and Grubb (2002) demonstrated that reduced watering frequency decreased specific leaf area but increased dry mass allocation to roots of seedlings in several woody species. Moreover, altering the growth-storage relationship is associated with water uptake ability of the plant and the amount of storage under drought conditions, which is maximized by increasing investment to roots (Joslin and others 2000). Several models have been developed to predict the optimal resource allocation to storage and growth (Iwasa and Kubo 1997; Meijden and others 2000), although the seasonal dynamics in resource allocation of native perennial grasses (especially mature plants) under drought remains unclear.

Leymus chinensis (Trin.) Tzvel. [*Aneurolepidium chinense* (Trin.) Kitag.], a perennial rhizomatous C_3 grass, is widely distributed on the eastern Eurasian steppe, with the main locations in China being the Manchurian Plain and the eastern part of the Mongolian Plateau (Li 1978). This species grows to 40–60 cm in height and produces thick and long belowground rhizomes with many adventitious roots at each node. Thick rhizome systems enable this species to survive drought when soil moisture can be less than 6% in dry seasons. Unlike monocarpic species, *L. chinensis* is capable of producing young shoots by both seeds and tillers (Li 1978), but regeneration is low in the field. This species usually begins booting in late May and flowering in early June with seed ripening in mid-July. Geographic demography and genetic diversity analyses revealed that moisture is a critical factor for the growth and distribution of this species (Qian and others 2000; Wang and others 2003). However, the regulation of storage resources (for example, biomass, energy, water, and nutrients) in plant growth of a species under drought has not been studied in detail, and this information is essential for formulating generalizations regarding plant growth regulation. In this study, we hypothesized that there is a negative correlation between partitioning to shoot and storage organs of any resource and this relationship can be accentuated by drought when soil moisture is limited.

Materials and Methods

Study Sites

The experiment was conducted in a natural *L. chinensis* grassland located in Changling county, Jilin province, China. The study site, located at latitude 44°41' N and longitude 123°44' E, is in the flat, low-lying southern part of the Manchurian Plain at about 140 m above sea level. Most of the grassland has a saline meadow chenzem, with 3–6% organic matter in the surface soil (0–30 cm) (Wang and Ripely 1997). Average soil pH is about 8.5, rising as high as 10 in the spring. The study site has not been grazed, fertilized, or burned for at least 5 years prior to this study, but transient flooding occasionally occurs in mid-August.

The study site has a continental monsoon climate, with large seasonal temperature variations. The main characteristics of the climate include a dry and windy spring, warm and wet summer with frequent droughts, cool autumn with early frosts, and long and cold winter with little snow cover. Mean annual air temperature is 5°C, varying from -20°C in January to 25°C in July. Mean annual precipitation is about 420 mm, of which 70% falls between June and August. Soil moisture content is below 6% in the dry season (mid-May to mid-June). A more detailed description of the climate in this region can be found in Wang and Ripley (1997).

Experiment Design and Sampling

An area within the study site with uniform soil and even distribution of *L. chinensis* was selected. Four 5-m × 20-m sampling plots, about 20 m apart, were established within the area. Two watering regimes or drought treatments were established: two plots with natural precipitation (drought treatment, 50–60% of field capacity) and two plots receiving additional water (watered treatment) when soil moisture content was below 10% (Table 1). All plant species within the plots other than *L. chinensis* were removed by hand weekly to eliminate interspecific competition. Samplings were carried out in late May, early June, late June, mid-July, mid-August, and mid-September, corresponding to phenologic stages of *L. chinensis*: early vegetative growth (EV), flower (FL), milk (MK), dough (DG), fructescence (FR), and late vegetative growth (LV), respectively.

Biomass Measurement

Ten sampling points within each plot and each phenologic stage were selected and a plant-soil column of

Table 1 Seasonal Variations in Physical and Chemical Properties (0–30 cm) of Soil and Climatic Variables in *Leymus chinensis* Grasslands, Northeast China

| | Treatment | Phenologic stage | | | | | |
|--|-----------|------------------|-------|-------|-------|-------|-------|
| | | EV | FL | MK | DG | FR | LV |
| Precipitation/water (mm) | Drought | 14.3 | 27.9 | 23.4 | 134.6 | 138.5 | 43.1 |
| | Watered | 25.8 | 51.2 | 56.9 | 134.6 | 138.5 | 43.1 |
| Soil moisture (%) | Drought | 3. 2a | 4.9a | 5.6 | 15.2b | 12.7c | 10.9d |
| | Watered | 10.2d | 10.1d | 10.2d | 15.4b | 12.8c | 10.9d |
| Soil pH | Drought | 9.0a | 8.8a | 8.9a | 8.2b | 8.2b | 8.2b |
| | Watered | 8.8a | 8.6 | 8.2b | 8.2b | 8.2b | 8.2b |
| Soil N (%) | Drought | 0.15a | 0.16a | 0.16a | 0.19b | 0.18b | 0.16a |
| | Watered | 0.15a | 0.18b | 0.17 | 0.20 | 0.18b | 0.15a |
| Soil K ($\mu\text{mol g}^{-1} \text{DW} \times 10^3$) | Drought | 1.97a | 1.95a | 1.98a | 1.85b | 1.85b | 1.89b |
| | Watered | 1.97a | 1.98a | 1.99a | 1.87b | 1.85b | 1.88b |
| Soil Na ($\mu\text{mol g}^{-1} \text{DW} \times 10^3$) | Drought | 28.2a | 26.9a | 27.4a | 19.1c | 19.0c | 19.5c |
| | Watered | 22.4b | 21.1b | 21.2b | 18.8c | 18.8c | 19.3c |
| Annual precip (30 yr) (mm) | | 12.4 | 19.6 | 22.1 | 132.9 | 128.8 | 39.3 |
| Mean annual temp (30 yr) ($^{\circ}\text{C}$) | | 9.4 | 15.3 | 22.1 | 25.8 | 22.6 | 14.8 |

EV = early vegetative growth; FL = flower stage; MK = milk stage; DG = dough stage; FR = fructescence stage; LV = late vegetative growth
 Values for each soil property are means of 6 observations except for soil moisture content which has 20 observations. Values with the same lowercase letters indicate no significant differences between drought treatments within each soil property ($p > 0.05$)

0.5 × 0.5 × 0.5 m was collected at each sampling point. These columns were brought back to the laboratory and soil particles were washed off with tap water. Plant materials were separated into rhizomes, roots, leaves, and stems and washed again with running tap water followed by distilled water. They were placed in perforated paper bags, oven-dried at 80°C for 48 h, and then weighed to determine the component biomass of *L. chinensis*. For calorific value and mineral (N, K⁺, and Na⁺) analysis, dry samples of these components were ground using a Wiley mill to pass through a 100-mesh screen.

Relative Water Content

Ten mature plants of *L. chinensis* were randomly selected within each plot at each phenologic stage and leaves, stems, rhizomes, and roots (about 5 g fresh weight [FW]) were sampled between 9:00 and 10:00 a.m. They were weighed immediately after detachment to obtain fresh weight. Soil particles surrounding rhizomes and roots were removed carefully before weighing. These samples were then placed into beakers (100 ml) filled with distilled water and allowed to sit overnight. The turgid fresh weight (TW) was measured the next morning. All samples were placed in perforated paper bags, oven-dried at 80°C for 48 h, and then weighed to obtain dry weight (DW). The relative water content (RWC) for growth (leaves and stems) and

that for storage (rhizomes and roots) were calculated separately using the formula $\text{RWC} = [(\text{FW} - \text{DW}) / (\text{TW} - \text{DW})] \times 100\%$ (Barr and Weatherley 1962).

Gross Calorific Value and Key Mineral Contents

Gross calorific value of plant components was determined using a Thermal Analyst 2000 calorimeter (DuPont/TA Instruments, Inc). About 0.5–1.0 g of ground subsamples was used for the determination of total nitrogen content for each plant component using the Auto-Kjeldahl method (Kjektec System 1026 Distilling Unit, Sweden). The N content was expressed as N per unit dry mass (DW). The contents of K and Na ($\mu\text{mol g}^{-1} \text{DW}$) were determined using 0.02 g of ground subsamples and flame photometry (Flame Photometer 410, Corning Halstead, UK). Ten measurements were used as replications for calorific value and mineral contents.

Physical and Chemical Characteristics of Soil

Soil water content (SWC, 0–30 cm) was determined gravimetrically at each sampling date. Soil pH was measured using a Model HS-3C pH meter (Shanghai Rex Instruments Factory). Key mineral contents of soil (N, K⁺, and Na⁺) were determined as described above using six

random samples. Weather data of the study site were recorded using a Campbell Scientific CR10 data logger.

Statistical Analysis

We define storage as resources (biomass, energy, water, N, K^+ , and Na^+) in rhizomes and roots, and growth as resources in shoots (leaves and stems). For the conversion of biomass to total energy content (kJ/m^2) in each plant part, the gross calorific value (kJ/g) was multiplied by biomass. Total N, K, and Na in shoot and storage organs (g/m^2) were converted using similar methods. Rhizome : shoot ratio and root : shoot ratio were calculated for each resource. Pearson's correlation analysis was used to examine the relationships between shoot and storage organs based on the above parameters over the growing season. Analysis of variance (ANOVA) was used to analyze treatment effect (drought and watered) and time effect. All statistical analyses were performed using SPSS v10.0 for Windows (SPSS Inc., Chicago, IL, USA).

Results

Biomass and Total Energy

Biomass and total energy of shoots (leaves and stems) of *L. chinensis* followed similar patterns over the growing season by increasing from early vegetative growth and peaking at the dough stage (Figure 1a, c). The two drought treatments also exhibited similar patterns over time in shoot biomass and energy. Not surprisingly, the watering treatment had significantly greater growth than the drought treatment over the growing season ($p < 0.01$), resulting in 71% and 48% more biomass and energy, respectively ($p < 0.01$).

Seasonal dynamics of storage in terms of biomass and energy differed between roots and rhizomes (Figure 1b, d). Biomass and energy of roots increased gradually from early vegetative growth to the fructescence stage, with significantly greater biomass and energy in the watered treatment than in the drought treatment ($p < 0.01$), whereas those of rhizomes dropped gradually from the early vegetative growth to the dough stage, and then increased to late vegetative growth. The rate of decrease in rhizome biomass and energy was faster in the watered treatment than in the drought treatment. Within the drought treatment, storage in roots was positively correlated with growth over the growing season for both biomass and energy ($r^2 = 0.95$, $p < 0.01$ and $r^2 = 0.94$, $p < 0.01$, respectively). Within the watered treatment, the correlation was significant only for root biomass ($r^2 = 0.939$, $p < 0.01$) but not for energy. Storage in rhizomes was negatively correlated with growth

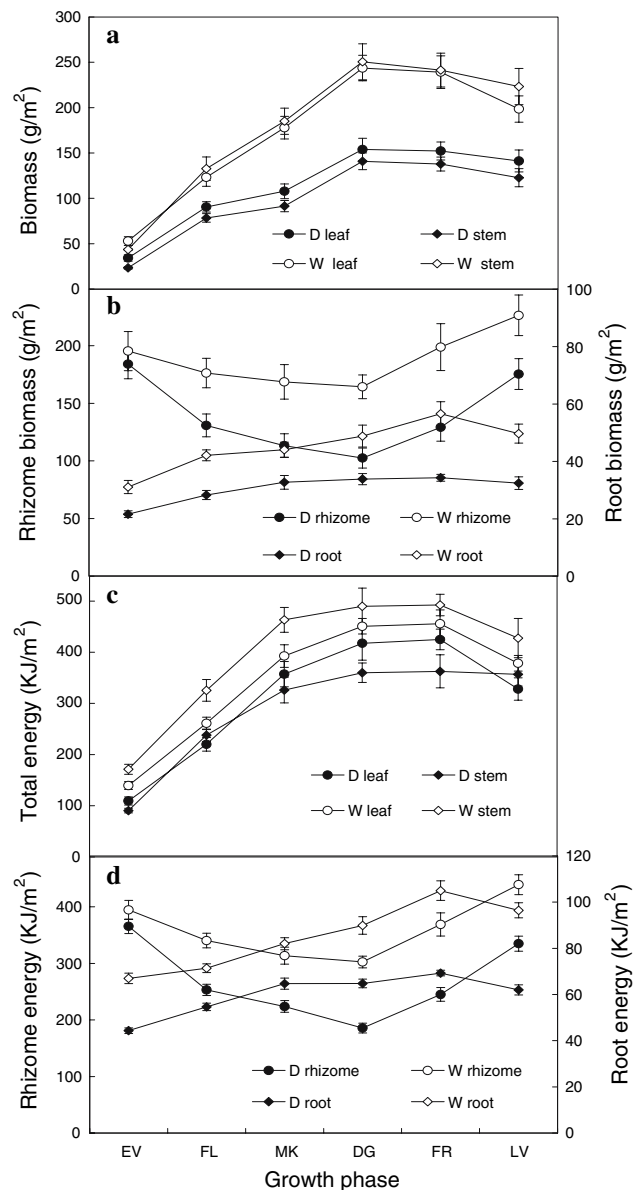


Fig. 1 Seasonal dynamics in biomass (a, b) and energy (c, d) allocation of *Leymus chinensis* under drought (D) and watered (W) treatments in northeast China. EV = early vegetative growth; FL = flower stage; MK = milk stage; DG = dough stage; FR = fructescence stage; and LV = late vegetative growth. Values are mean \pm SE of 20 observations for biomass and 10 observations for energy

within the drought treatment for biomass and energy ($r^2 = -0.84$, $p < 0.01$; $r^2 = -0.82$, $p < 0.01$), whereas the correlations were not significant within the watered treatment ($r^2 = -0.54$, $p > 0.05$; $r^2 = -0.37$, $p > 0.05$, respectively, for biomass and energy).

Rhizome : Shoot Ratio and Root : Shoot Ratio

From early vegetative growth to the milk stage, rhizome : shoot ratio and root : shoot ratio of *L. chinensis* in terms of

biomass and energy decreased significantly ($p < 0.01$) due to rapid increases in shoot biomass and energy, slower in increases in root biomass and energy, and decreases in rhizome biomass and energy (Table 2). A gradual increase in the rhizome : shoot ratio and root : shoot ratio from the milk stage to the late vegetative growth stage was found, which was likely caused by increasing biomass and energy allocation to storage in the later part of the growing season. The drought treatment resulted in a greater rhizome : shoot ratio and root : shoot ratio than that of watered treatment. The average rhizome : shoot ratio in the drought treatment was 59% greater ($p < 0.01$) than that in the watered treatment during the dry season (from early vegetative growth to milk stage), whereas that in rainy season (from DG to LV) was about 22% greater ($p < 0.05$) in terms of biomass and energy. There was no significant difference ($p > 0.05$) between treatments in root : shoot ratio in terms of biomass over the growing season, but the root : shoot ratio in terms of energy was 37% lower in drought than in watered treatment ($p < 0.01$).

Relative Water Content

Within the watered treatment, RWC of shoot and storage organs of *L. chinensis* did not change significantly ($p > 0.05$) over the growing season (Figure 2). Within the drought treatment, the difference in RWC between dry and rainy seasons was about 13% ($p < 0.05$) for growth and 5% ($p > 0.05$) for storage. During the dry season, growth in the drought treatment had 16% lower RWC ($p < 0.01$) than that in the watered treatment, although there was no

significant difference ($p > 0.05$) between treatments in the rainy season. Storage RWC did not differ significantly ($p > 0.05$) between treatments over the entire growing season.

Key Mineral Contents

Seasonal dynamics in the contents of the three major mineral elements followed different patterns (Figures 3, 4, 5). N content of both shoot and storage organs decreased over the growing season in both drought treatments; the reduction was over 60% (Figure 3a, b). Although stem N content decreased almost linearly with time, a rapid decrease between the early vegetative growth and flowering stages was observed in leaf N content. For root and rhizome N contents, two rapid drops were found between the early vegetative growth stage and the flowering stage, and between the dough and fructescence stages. The watered treatment resulted in 22% higher leaf N ($p < 0.01$) and 23% higher stem N ($p < 0.01$) than that of the drought treatment during the dry season, but there was no significant difference between the two treatments during the rainy season ($p > 0.05$). The content of N in storage was not significantly affected by drought treatments over the growing season ($p > 0.05$). The positive correlation in total N between shoot and storage organs was significant for plants in the watered treatment over the growing season ($r^2 = 0.76$, $p < 0.05$), although the correlation was not significant for plants in the the drought treatment ($r^2 = 0.41$, $p > 0.05$; Figure 3c).

Table 2 Dynamics in Rhizome : Shoot (RZ:SH) and Root : Shoot (RT:SH) Ratios in Terms of Biomass and Energy for *Leymus chinensis* as Affected by Drought Treatments over the Growing Season

| Stage | Biomass | | | | Energy | | | |
|-------|---------|---------|---------|---------|---------|---------|---------|---------|
| | RZ:SH | | RT:SH | | RZ:SH | | RT:SH | |
| | Drought | Watered | Drought | Watered | Drought | Watered | Drought | Watered |
| EV | 3.20 | 1.91 | 0.38 | 0.42 | 3.17 | 1.99 | 0.22 | 0.42 |
| FL | 0.77 | 0.51 | 0.17 | 0.14d | 0.73 | 0.43a | 0.12c | 0.13d |
| MK | 0.43a | 0.35 | 0.12c | 0.10c | 0.42a | 0.30 | 0.10c | 0.10c |
| DG | 0.27b | 0.28b | 0.11c | 0.09 | 0.25b | 0.27b | 0.07 | 0.12c |
| FR | 0.46a | 0.42a | 0.12c | 0.12c | 0.45a | 0.39a | 0.08 | 0.14d |
| LV | 0.88 | 0.62 | 0.16e | 0.14d | 0.91 | 0.65 | 0.09c | 0.17e |
| Mean | 1.00f | 0.68g | 0.17e | 0.17e | 0.99f | 0.67g | 0.11c | 0.19e |
| F | 1066.31 | 1012.39 | 1091.16 | 18.14 | 978.34 | 994.07 | 1034.78 | 29.32 |
| P | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |

EV = early vegetative growth; FL = flower stage; MK = milk stage; DG = dough stage; FR = fructescence stage; LV = late vegetative growth
 Values are mean of 20 observations for biomass and 10 observations for energy. Values with the same lowercase letters indicate no significant differences between drought treatments and between phenologic stages ($p > 0.05$)

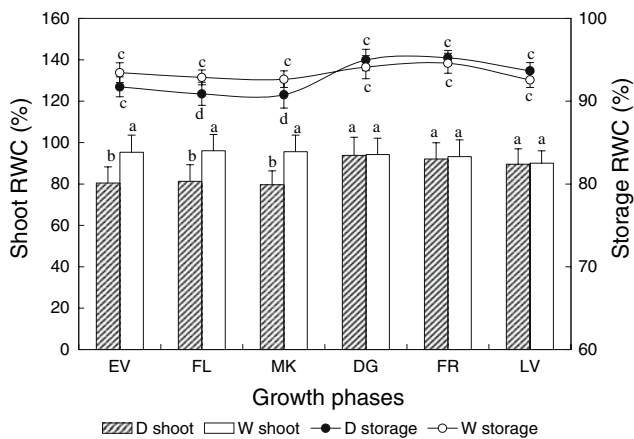


Fig. 2 Seasonal dynamics in relative water content (RWC) of *L. chinensis* under drought (D) and watered (W) treatments northeast China. EV = early vegetative growth; FL = flower stage; MK = milk stage; DG = dough stage; FR = fructescence stage; and LV = late vegetative growth. Values are mean \pm SE of 10 observations. Values with the same lowercase letters indicate no significant differences between treatments and phenological stag ($p > 0.05$)

The contents of K in growth decreased gradually over the growing season, but the reduction was greater in stems (70%) than in leaves (55%) (Figure 4a). Leaf and stem K contents were 14% higher for plants in the watered treatment than in the drought treatment during the dry season ($p < 0.05$), although they were not significantly affected by treatments during the rainy season ($p > 0.05$). Storage K contents were low compared to that of growth, but reductions were observed between the early vegetative growth and flower stages and between the dough and fructescence stages for rhizomes, whereas only between the early vegetative growth and flower stages for roots (Figure 4b). Rhizome K content in the watered treatment was 13% higher than that in drought during the dry season ($p < 0.05$), but the difference was not significant during the rainy season ($p > 0.05$). Root K content varied in a similar trend with that of rhizome over the whole growing season. There was a negative correlation in total K between shoot and storage organs over the growing season in both drought ($r^2 = -0.96$, $p < 0.01$) and watered ($r^2 = -0.91$, $p < 0.01$) treatments (Figure 4c). Total K averaged about 73% and 46% higher for shoot and storage organs, respectively, in the watered treatment than the drought treatment ($p < 0.01$).

The contents of Na had different patterns over the growing season between shoot and storage organs (Figure 5a, b). Leaf and stem Na decreased gradually until the dough stage (20–40%), and then increased 35–45% ($p < 0.01$). Rhizome Na did not decrease until the milk stage, whereas root Na increased gradually over the growing season. During the dry season, plants in the drought treatment had about 10% more growth Na

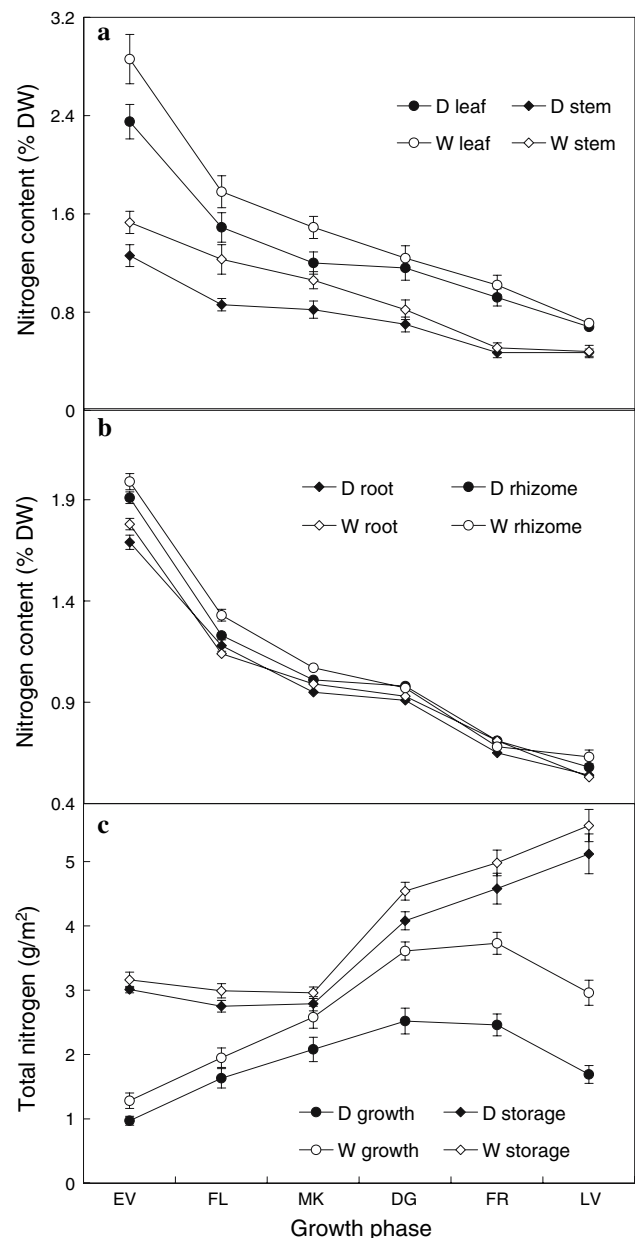


Fig. 3 Seasonal dynamics in N content (a, b) and total N in terms of shoot and storage organs (c) of *L. chinensis* under drought (D) and watered (W) treatments in northeast China. EV = early vegetative growth; FL = flower stage; MK = milk stage; DG = dough stage; FR = fructescence stage; and LV = late vegetative growth. Values are mean \pm SE of 10 observations

($p < 0.05$), 16% greater root Na ($p < 0.05$), and 26% greater rhizome Na ($p < 0.01$), respectively, compared to that in the watered treatment, but the treatment effects were not significant during the rainy season ($p > 0.05$). Total Na in growth increased over the growing season with more increase and greater amounts in the watered than in the drought treatment ($p < 0.01$, Figure 5c). Total Na in the watered treatment did not vary over the growing season ($p > 0.05$), but it decreased in the milk to dough stages in

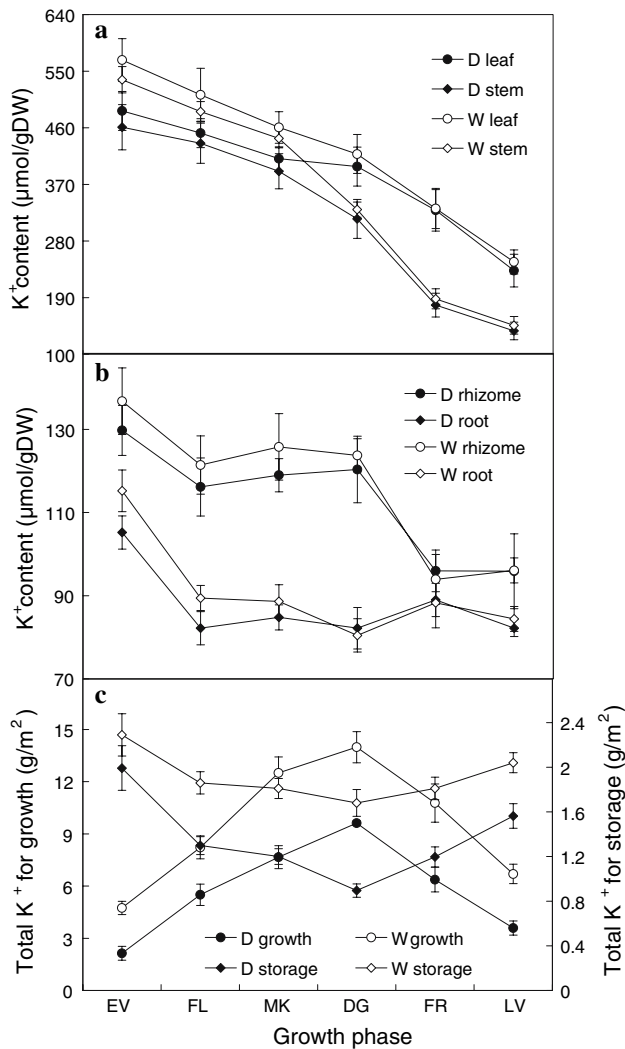


Fig. 4 Seasonal dynamics in K content (a, b) and total K in shoot and storage organs (c) of *L. chinensis* under drought (D) and watered (W) treatments in northeast China. EV = early vegetative growth; FL = flower stage; MK = milk stage; DG = dough stage; FR = fructescence stage; and LV = late vegetative growth. Values are mean ± SE of 10 observations

the drought treatment. There was a negative correlation between total Na in shoot and storage organs in the drought treatment over the growing season ($r^2 = -0.92, p < 0.01$), but not in the watered treatment ($r^2 = -0.53, p > 0.05$).

Discussion

Plant growth is determined by many factors, including net photosynthetic rate and allocation of fixed resources to growth, storage, and survival (Callaway and Delucia 1994; Harper and Ogden 1970). Differential resource allocation therefore has profound implications for plant growth, storage, and survival (Shipley and Meziane 2002; Wang

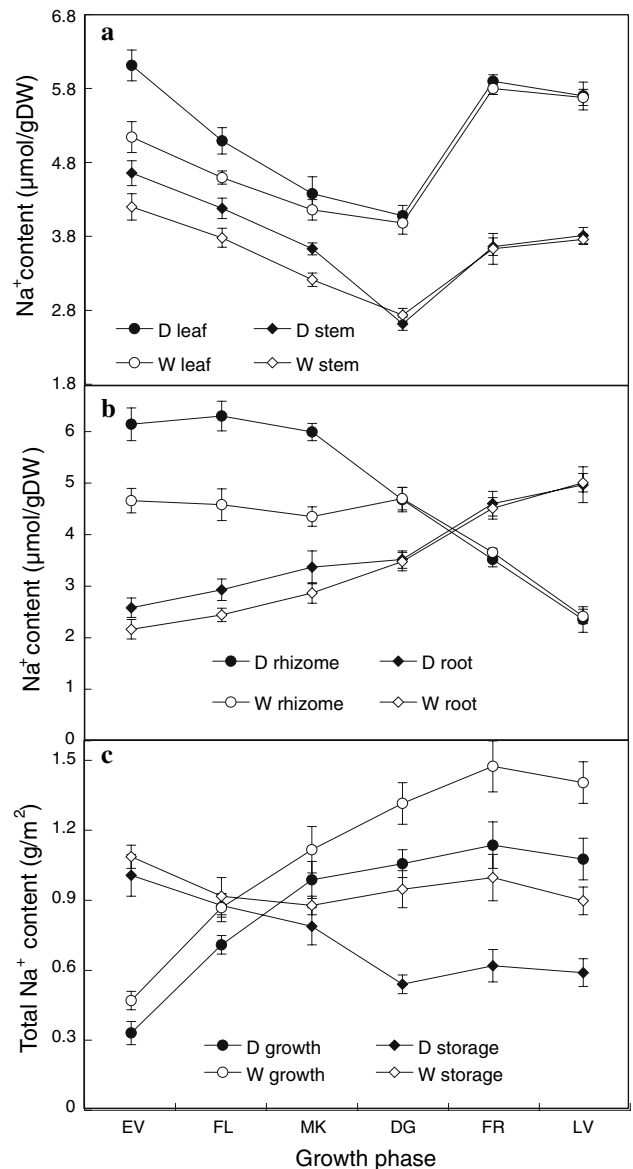


Fig. 5 Seasonal dynamics in Na content (a, b) and total Na in shoot and storage organs (c) of *L. chinensis* under drought (D) and watered (W) treatments in northeast China. EV = early vegetative growth; FL = flower stage; MK = milk stage; DG = dough stage; FR = fructescence stage; and LV = late vegetative growth. Values are mean ± SE of 10 observations

2005). Generally, plants adapted to low-stress and high-resource habitats preferentially utilize abundant resources for rapid growth and low-stress resistance. Conversely, plants adapted to resource-limited habitats or stressful environments develop mechanisms that allow them to balance storage and survival to grow more effectively (Davidson 1969; Garnier 1991; Grime 1977). In this study, the shoot and storage organ of *L. chinensis* in both biomass and energy were strongly affected by drought as expected. The positive correlations between root and plant growth in terms of biomass and energy are consistent with the

balanced-growth hypothesis (Davidson 1969; Garnier 1991), which states that plants preferentially allocate more resources to roots when water and nutrients become limited to growth. In *L. chinensis* grasslands, the adaptation to drought is reflected in the limited tradeoff between growth and root storage. By keeping a relatively stable balance between growth and root storage, the capacity of water and mineral uptake from soil when moisture is limited is maintained. This is supported by the small differences in the root : shoot ratios between the two drought treatments in the present study as well as by observations along large-scale transects (Wang and others 2003). In addition, the regulating role of roots in this species is not as critical as that of rhizomes because of the short root life span and relative small root biomass. Rhizome biomass was as high as four to five times the root biomass (Figure 1b). During the early growing season, both shoots and roots grew at the expense of stored reserves in the rhizomes (Wang 2001). However, most previous studies were based on short-term growth experiments (less than 4 months) or on species with relative simple life histories (Metcalf and others 2006), so they shed little light on perennial, mature plants with long-term growth and rhizome storage, and on storage regulation of plant growth in stressful environments.

The balanced-growth hypothesis is partly supported by the negative correlations between growth and rhizome storage in *L. chinensis* under drought conditions. The rhizome : shoot ratio in terms of biomass and energy was also relatively high for plants in the drought treatment (Table 1). The relatively high rhizome storage in biomass and energy can enhance the water and carbohydrate storage capacity under drought conditions, potentially improving recovery after droughts. However, the high biomass allocation to rhizomes may reduce primary production because of the increase in maintenance respiration of rhizomes (Wang and others 2003). This may explain why total biomass and energy of *L. chinensis* were significantly lower in the drought treatment. Previous studies on a large scale proved that biomass allocation of *L. chinensis* to rhizomes is negatively correlated with aridity (Wang and others 2003). These studies indicate that rhizome storage of this species plays an important role in regulating plant growth, such as carbohydrate, mineral elements, and water mobility when soil moisture becomes limited. Other studies have also demonstrated the importance of storage in crops (Bruce and others 2002; Gebbing and Schnyder 1999), grass forage (Wang 2005), and some legumes (Chaves and others 2002).

Relative water content (RWC) measures plant water status in terms of the physiologic consequences of cellular water deficit. Shoot RWC was more sensitive than that in storage in the drought treatment (Figure 2), mainly because of leaf transpiration (Wang and Gao 2001). This

explanation is confirmed by previous observations that leaf RWC decreased remarkably when plants were subject to drought (Wang and Gao 2001; Xu and Zhou 2006). Long-term drought, especially the reduction of leaf RWC, may affect net assimilation rate, stomatal conductance, and metabolic activity (Kaiser 1987; Wang and Gao 2001; Xu and Zhou 2006). This may explain why biomass and energy in growth were significantly lower under drought treatment than in the watered treatment. Relatively small variations in storage RWC of this species between drought and watered treatments over the growing season demonstrate that rhizomes have a high capacity for water storage under field conditions, which is important for regulating water supply, plant growth, and survival in rhizomatous grasses of arid regions.

Nitrogen, potassium, and sodium are the most important minerals for regulating the growth-storage relationship in *L. chinensis* in semiarid and saline grasslands of China. Nitrogen content is important because it is associated with the CO₂ assimilatory capacity of plants, and it is also an important determinant of forage nutritive value in grasslands (Sinclair and others 2000; Hu and Zhu 1987). Changes in plant K and Na contents are associated with salt tolerance, osmotic regulation, and enzyme activation in saline plants (Ge and Li 1992; Shi and Wang 2005). Nitrogen content in leaf, stem, root, and rhizome of *L. chinensis* in both drought and watered treatments decreased gradually over the growing season. The decline in leaf N is consistent with previous studies (Sinclair and others 2000; Xu and Zhou 2006), which results in low photosynthetic capacity of this species (Hu and Zhu 1987; Wang and Gao 2001). Reductions of N in stem, root, and rhizome were also observed in this study (Figure 3a, b). At the whole-plant level, the decline of N during the growing season suggests that there is a N-deficient stress in the grasslands, especially during the early growing season when soil moisture is limited. However, over the entire growing season, no significant correlation between shoot and storage organs in total N in the two drought treatments was found in this study, suggesting that N-deficient stress in grasslands may not be severe enough to inhibit plant growth of this species. The positive correlation between shoot and storage organs with respect to total N in the watered treatment over the growing season indicates ample soil water may enhance N utilization. Relatively higher total N in shoot and storage organs in the watered treatment rather than in the drought treatment may result in N-deficient stress because plants subject to ample soil water absorb more N from the soil relative to dry soil which results in limited soil N (Heckathorn and Delucia 1994).

Saline environments exert a major influence on plant growth by both reducing cell turgor and causing toxic salt accumulation in leaves (Garthwaite and others 2005;

Greenway and Munns 1980). The metabolism of K^+ and Na^+ is an important component for plants under salt stress (Cheeseman 1988; Shi and Wang 2005); for example, *Triticum aestivum* restricts Na^+ transport to leaf tissues and maintains high selectivity of K^+ over Na^+ (Corham and others 1997). The reduction in K and Na in leaves and stems of plants during the drought season is consistent with a previous study (Shi and Wang 2005) that suggested that leaf K and Na are diluted by rapid plant growth (Ge and Li 1992). However, the increase in leaf and stem Na during the late growing season was mainly due to Na uptake and accumulation in leaves and stems when plant growth was slow. The decline of rhizome K and Na contents during the late growing season was also due to the rapid increase in rhizome biomass (Figures 1b, 4b, 5b). The relatively higher Na content in plant parts in the drought treatment indicate that drought may enhance salt stress in grassland species. Drought together with high soil evaporation allows saline groundwater to rise, resulting in increased salinity of surface soils (Wang and Repily 1997). Negative correlations in total K and Na between shoot and storage organs of *L. chinensis* over the growing season suggest that these two minerals play important roles in regulating plant growth of this species, and these roles can be enhanced when soil moisture is limited. Saline stress (especially Na^+) inhibits plant growth of *L. chinensis* (Shi and Wang 2005; Wang and Ripley 1997), but this species is capable of excluding salts and the Na concentration is only 0.9% of that in the soil (Ge and Li 1992; Shi and Wang 2005).

There have been debates on resource allocation in plants, for example, whether there is a negative relationship between shoot and storage organs (Hilbert 1990; Iwasa and Kubo 1997; Wang 2005). Allocation of biomass, energy, K, and Na observed in this study supports our hypothesis that there is a negative relationship between shoot and storage organs over the growing season and this relationship may have been accentuated when soil moisture was limited. Correlations between shoot and storage organs in terms of relative water content and N do not support the hypothesis. Rhizome storage plays an important role in regulating plant growth of *L. chinensis*, especially under drought conditions.

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