

Seed production, mass, germinability, and subsequent seedling growth responses to parental warming environment in *Leymus chinensis*

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Abstract. Understanding how the seed yield and seed quality respond to global warming is crucial for understanding how new grassland establishment responds to global change. This study evaluated *Leymus chinensis*, a dominant perennial grass widely distributed in the eastern regions of the Eurasian grassland zone, as a model to investigate the effect of increasing ambient temperature on seed production, seed mass, germinability, and subsequent seedling growth. As the temperature rose, there were significant reductions in the number of flowering plants and in seed number per square metre but significant increase in the number of florets and the number of seeds per plant. Increasing temperature decreased the proportion of light weight seeds, increased the proportion of heavy weight seeds and led to a significant increase in the mean dry weight. Germination success, germination rate and the root : shoot ratio of light weight seeds were reduced, while heavy weight seed did not appear to be affected by elevated temperatures. Finally, germinating seeds per unit area was reduced by increased temperature. The reduction in the number of germinating seeds with increasing temperature implies that continued global warming will further constrain new grassland establishment of *L. chinensis* in the eastern regions of Eurasia.

Additional keywords: germination, global warming, seed production, seedling growth, temperate grassland.

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Introduction

New grassland establishment and degraded grassland renewal are highly dependent on seed production and seed quality (Grime and Campbell 1991; Hovenden *et al.* 2008). Seed production has been shown to be influenced by several seed yield components, such as the number of flowering plants, seed number per spike and thousand-seed weight. Seed quality is often correlated with seed weight and has a large influence on seed germination success (GS, seeds were considered to have germinated after radicle emergence) and subsequent growth because of ‘maternal effects’ (Howe and Richter 1982; Stanton 1984). A large, well developed seed stores more nutrients, which leads to an increased growth rate and an improvement in the ability of the seedling to survive competition in harsh environments (Howe and Richter 1982; Huxman *et al.* 1998; Steinger *et al.* 2000; Hovenden *et al.* 2008).

In the 21st century, climate change, mediated by greenhouse gas emissions is predicted to raise the mean global temperature by 1.8–4.0°C (IPCC 2007). Given the importance of temperature on plant life cycles, climate warming simulation experiments

can provide important information about the impact of temperature on aspects of the plant life cycle, such as phenology and seed production in different areas. Current estimates indicate that the first half of this century might result in an increase in average seed yield in high-latitude regions, whereas seed yield would decline in semi-arid and tropical regions (Tubiello *et al.* 2007). Compared with the substantial body of research on climate change effects in high-latitude or arctic regions (Klady *et al.* 2011), there has been little such research in temperate semi-arid areas. A few reports have suggested that increased temperature had no effect on seed number, but results for *Austrodthonia caespitosa*, a dominant grass in Australian temperate grassland reported a reduction in seed mass (Hovenden *et al.* 2008). The decrease in seed mass was attributable to an increase in the number of light seeds (Hovenden *et al.* 2008). This means that there is a decrease in stored nutrients within the seeds and a reduction in ‘maternal effects’, leading inevitably to reduced seed germinability and subsequent seedling growth. It is, therefore, necessary to study the effects of global warming on seed production and

seed quality so that the success of new grassland establishment and degraded grassland renewal in semi-arid regions, which is heavily dependent on seed viability, can be predicted.

In semi-arid and arid regions, primary constraints on plant growth and reproduction include low soil water content and high ambient temperature (Dermody *et al.* 2007). Undoubtedly, continued global warming will further increase air and soil temperatures and reduce soil moisture content, resulting in water limitations in these regions (Dermody *et al.* 2007; IPCC 2007). In evaluating the results from the above research, it was predicted that increased temperatures would lead to decreases in seed production and individual seed mass, resulting in constraints on seedling growth in some important grasses in the eastern regions of the temperate Eurasian grassland zone. The objectives of this present study were to determine the effects of increased ambient temperature on seed production, seed mass, seed germinability, and subsequent seedling growth of *Leymus chinensis* (Trin.) Tzvelev.

Materials and methods

Study site

The study site was located at the Grassland Ecosystem Field Station of the Northeast Normal University at Songnen Grassland, China (123°44'E and 44°40'N, 137.8–144.8 m a.s.l.). Long-term (1989–2008) mean annual precipitation is 360 mm, with 70% of the precipitation occurring from June to August. Mean annual temperature is 4.9°C, with the monthly mean temperature ranging from 24.0°C in July to –15.1°C in January. The primary soil type is Mollisols. Between 0 and 25 cm depth, the total N, organic C and pH were measured at $19.6 \pm 1.32 \text{ g kg}^{-1}$, $29.39 \pm 2.96 \text{ g kg}^{-1}$, and 8.64 ± 0.2 , respectively. The measurements were replicated 3 times. The total N concentration was determined by the standard macro-Kjeldahl procedure (2300 Kjtec Analyser Unit, Foss Tecator, Sweden). Soil organic C was measured using the dichromate oxidation method (Nelson and Sommers 1982) and soil pH was measured using a HI98129 acidimeter (Shanghai Thunder Magnetism Instrument Plant).

Species description

Leymus chinensis (Trin.) Tzvel, is widely distributed in the eastern regions of the Eurasian steppe zone, including the northern and eastern parts of the People's Republic of Mongolia, the Songnen plain and the eastern Inner Mongolian plateau in China, and the Russian Baikal region. This species is tolerant to saline-alkali soils, cold extremes, and drought conditions, together with having a high forage value and good palatability for livestock such as cows and sheep (Wang *et al.* 2010a). It sequesters energy resources from early to mid April, and then flowers in late May, with seed maturation occurring from early June to late July. From early August to the end of the growing season, the underground buds emerge and gradually turn into the daughter plants. During this stage, the majority of the daughter plants only grows one to four leaves and exhibits no jointing. The vegetative shoots and daughter shoot leaves die with the arrival of frost in late September or early October, but the daughter shoot will survive the winter and begin growing again the following season. The flowering plant and

vegetative shoots are ~70 cm and 50 cm in height, with three and eight leaves, respectively.

Experimental design

The experimental design was a randomised block design with six replications. Plot size was 3 × 4 m and plots were separated by a 3-m border. The temperature treatments consisted of an ambient temperature treatment and an increased temperature treatment, which was the ambient temperature plus 1.7°C. The increased temperature treatment was achieved by using infrared radiators/heaters (model MS-2420, Kalglo Electronics Inc., Bethlehem, PA, USA) that were on continuously from 23 April 2006. The heaters were suspended 2.25 m above the six increased temperature treatment plots in a north–south orientation. The increased temperature plots had reverse 'V' shields designed to provide uniform radiation for each plot. Each control plot had one 'dummy' heater of identical shape, size and height as the infrared heater in order to simulate the shading effects of the infrared radiator. All heaters under the increased temperature treatments were set at a radiation output of ~1600 W. Ground temperatures and volumetric soil water content (at 0–10 cm depth) were measured with an EM50/R datalogger (EM50/R Decagon Ltd, Washington, USA) from April 2006 to October 2009. Soil moisture sensors and temperature probes were placed in the centre of each plot (three replicates per plot). Soil temperature and volumetric soil water content were recorded at 1-h intervals over the 2006–09 growing seasons.

Seed production and mass classes

In May 2006, a permanent 1 × 1-m quadrat was randomly established in each plot. At the seed maturation stage in 2007, 2008 and 2009, the *L. chinensis* population and its flowering plant density (spike number per square metre) were recorded. To minimise marginal effects, only 20 flowering plants in the centre of each plot were randomly sampled. Then the number of seeds per spike and florets per spike were determined. The filled seeds with glumes were put into a paper bag (100 seeds per bag) and air-dried to determine the thousand-seed weight, while the moisture content was <11%, which was based on the quality grading of the main cultivated grass seeds (Standardisation Administration of China, GB 6142–1985, 1985). The thousand-seed weight was obtained from the weight of 100 seeds multiplied by 10 with three replications. The seeds from six replicates were aggregated and a subsample of 500 seeds was taken in order to obtain individual seed weight. Based on individual seed weight, these seeds were grouped into four mass classes (<2.1, 2.1–2.5, 2.6–3.0, >3.0 mg; seed masses ranging from 2.50–2.54 and 2.55–2.60 mg were calculated in the 2.1–2.5 and 2.6–3.0 mg classes, respectively) for germination testing. The seed number per square metre was calculated from the number of flowering plants per square metre multiplied by the seed number per plant.

Germination test

After harvest in each experimental year, germination tests were undertaken in growth chambers (HPG-400, Harbin, China) with a 30/20°C 8/16-h light/dark cycle. The light

source was Sylvania cool white fluorescent lamps ($200 \mu\text{mol}^{-2} \text{S}^{-1}$, 400–700 nm). The 20 seeds (with three replications) were sterilised using 5% potassium permanganate solution for 10 min (Xu and Zhou 2006), then washed and germinated with distilled water at 1700 hours each day in Petri dishes (11 cm diameter) containing two layers of filter paper (Whatman No. 3). Germination success was recorded daily for 20 days. The germinated seeds were then left to grow on the filter paper for 15 days to determine seedling shoot biomass (SSB) and seedling root biomass (SRB).

The germination rate (GR) was estimated using a modified Timson index: germination velocity = $\sum G/t$, where G is the percentage of germinated seeds per day and t is the total germination period (Khan and Ungar 1984). Potential seed germination (the proportion of seeds that will germinate) per square metre was calculated using: $(SG) = \sum_i^4 TS \times RF \times GS$, where TS is the total number of seeds per square metre; RF is the proportion of each mass class and GS is the germination success (%).

Data analysis

All statistical analyses were performed using SPSS 13.0 (SPSS, Chicago, IL, USA). Independent sample t -tests were used to investigate the differences between control and warming treatments in each growing season. The effects of the warming (W), experimental year (inter-annual variability) and their interaction on seed production, together with germination and seedling growth were analysed using the General Linear Model. In the combined analysis, the warming treatment and experimental years were considered as fixed factors, and the block (difference between experiment plots) was considered a random factor.

Results

Variations in monthly temperature and precipitation

Monthly precipitation and air temperature data from July 2006 to July 2009 are shown in Fig. 1. In comparison to the long-term (1989–2009) seasonal temperature data, the winter temperature in 2006 and spring 2007 was higher (by 3.9 and 1.3°C, respectively), but there was no difference in temperature between spring and autumn. Seasonal precipitation changed considerably from 2007 to 2009 compared with the long-term (1989–2009) seasonal precipitation. Spring precipitation in 2007 was lower (by 33.9 mm) but higher in 2008 and 2009 (by 26.1 and 23.2 mm, respectively) and summer precipitation was higher than the long-term average (by 23.7 mm) in 2008, but lower in 2007 and 2009 (by 72.1 and 61.7 mm, respectively). Autumn and winter precipitation showed no difference between 2006, 2007 and 2008, but was lower than the long-term mean precipitation.

Soil microclimate

The increased temperature significantly elevated soil temperature and reduced soil moisture ($P < 0.05$). Mean ground temperature increased by 1.72°C in 2007, 1.71°C in 2008, and 1.72°C in 2009, compared with the ambient temperatures. Volumetric soil water content at 0–10 cm depth fluctuated greatly over the growing season (Fig. 2). In contrast to the control, increases in the ambient temperature decreased the seasonal mean volumetric soil water content by 2.3% in 2007, 2.8% in 2008, and 2.8% (v/v) in 2009 ($P < 0.05$).

Seed production

The mean number of flowering plant was 24% lower in the increased temperature treatment across the 3 years (Table 1).

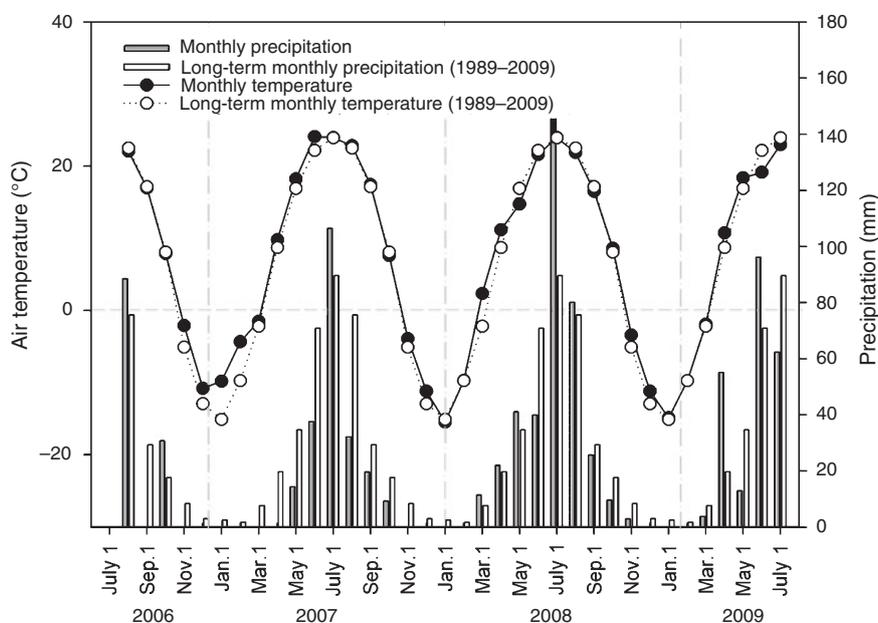


Fig. 1. Average monthly air temperature and daily precipitation during August 2006 to August 2009. Data were from the eddy tower adjacent (~200 m) to the experimental plots. Long-term (1989–2009) weather data were from the Ecosystem Field Station of the Institute of Grassland Science at the Northeast Normal University in south-west Songnen grassland, Jilin Province, China (123°44'E and 44°40'N).

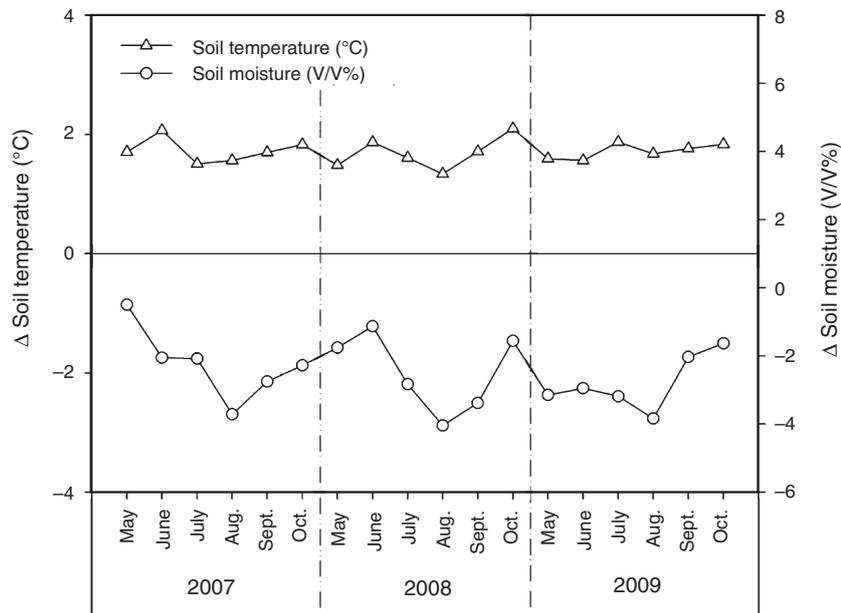


Fig. 2. Changes in soil monthly mean temperature (soil surface) and moisture (at 10 cm depth) under the increased temperature treatment from the August 2006 to August 2009 growing season.

There were significant differences between increased temperature and experimental year ($P < 0.05$) (Table 2). The increased temperature treatment had no effect on population density (Table 1). Combined ANOVA showed that population density was significantly affected by experimental year ($P < 0.05$) (Table 2). Increasing the ambient temperature significantly increased seed number per plant, floret number per plant, and seed weight ($P < 0.05$) by an average of 18.1, 16.8 and 10.8%, in 2007, 2008 and 2009, respectively ($P < 0.05$) (Table 1). These three traits were significantly influenced by increased temperature only (Table 2). Increasing temperature marginally decreased seed number per square metre by 5.9% in 2007 and 7.1% in 2008 whereas it significantly decreased seed number per square metre by 18.1% in 2009 ($P < 0.05$) (Table 1). Analysis of two-way ANOVA result showed that the seed number per square metre was significantly influenced by increasing temperature and experimental year ($P < 0.05$) (Table 2).

Seed mass frequency distribution

The mean proportion of seeds weighing less than 2.1, 2.1–2.5, 2.6–3.0 mg and more than 3.0 mg was 33.5, 27.5, 21.5, and

17.5%, respectively, across the three successive experimental years in the control treatment and was 27.5, 24.5, 21.5, and 25.5%, respectively, in the increased temperature plots. There was a substantial alteration in the seed mass frequency distribution, with the increased temperature plot having fewer light weight seeds (<2.1, 2.1–2.5 mg) than the control plots, and a greater proportion of heavy weight seeds (2.6–3.0, >3.0 mg) (Fig. 3). In 2008, the proportion of seeds weighing less than 2.1 mg was reduced by 6.5%, while seeds weighing more than 3.0 mg increased by 12.5%. The decrease in the proportion of light weight seeds and the increase in the proportions of heavy weight seeds were both significant in each experimental year ($P < 0.05$) (Fig. 3).

Seed germination success and rate

Across the 3 successive experimental years, the GS of seeds weighing less than 2.1 mg and from 2.1 to 2.5 mg significantly decreased by 23.0 and 6.8%, respectively ($P < 0.05$) (Fig. 4a). Analysis of the two-way ANOVA results showed that the GS of the lighter weight seeds was significantly influenced by increasing temperature and experimental year (Table 2).

Table 1. No. of flowering plants per m², seed and floret no. per plant, thousand-seed weight, and seed no. per m² of *Leymus chinensis* collected from the control (CK) plots and increased temperature (IT) plots

The data are expressed as mean \pm s.e. for six replications

	2007		2008		2009	
	CK	IT	CK	IT	CK	IT
Flowering plant no. (per m ²)	82.0 \pm 4.5	66.0 \pm 3.7	79.0 \pm 3.2	61.3 \pm 3.9	72.2 \pm 6.0	50.4 \pm 4.5
Population density no. (per m ²)	680.7 \pm 57.8	682.3 \pm 34.3	573.0 \pm 32.4	565.0 \pm 26.2	564.0 \pm 44.1	550.0 \pm 33.1
Seed no. per plant	14.0 \pm 1.8	16.4 \pm 2.5	14.2 \pm 1.4	17.0 \pm 1.8	13.3 \pm 1.5	15.6 \pm 1.8
Floret no. per plant	48.5 \pm 3.6	54.7 \pm 4.1	52.9 \pm 3.5	67.5 \pm 2.1	55.7 \pm 4.5	61.2 \pm 4.7
Thousand-seed weight (g)	2.1 \pm 0.1	2.3 \pm 0.1	2.2 \pm 0.1	2.5 \pm 0.1	2.2 \pm 0.1	2.4 \pm 0.1
Seed no. (per m ²)	1150.4 \pm 42.8	1082.4 \pm 64.0	1121.8 \pm 68.3	1042.1 \pm 57.7	960.3 \pm 34.7	786.2 \pm 62.7

Table 2. ANOVA results (*F*-values and *P*-values at 0.05 probability level) for each reproductive trait from the control (CK) plots and increased temperature (IT) plots for across 2007, 2008, and 2009

The combined ANOVA results for germination success, germination rate, seedling shoot biomass, seedling root biomass, and seedling root:shoot ratio from 2.6 to 3.0, >3.0 mg class are not shown in the Table 2 because there were no significant differences for these classes between the control plots and the increased temperature plots. Bold text indicates that the significant values were less than 0.05 ($P < 0.05$). PG = potential germination per m²; GS = germination success (%); GR = germination rate; SSB = seedling shoot biomass (g); SRB = seedling root biomass (g)

Dependent trait	Year (Y)		Increasing temperature (IT)		Y × IT	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Flowering plant no. (per m ²)	7.567	0.002	46.673	0.000	0.434	0.652
Population density no. (per m ²)	9.438	0.002	0.011	0.918	0.225	0.800
Seed no. per plant	0.285	0.754	4.300	0.047	0.132	0.877
Floret no. per plant	2.609	0.09	8.351	0.007	0.899	0.418
Thousand-seed weight (g)	6.299	0.085	36.385	0.000	0.541	0.588
Seed no. (per m ²)	11.051	0.009	5.810	0.022	0.380	0.687
PG no. (m ²)	15.840	0.000	21.281	0.000	1.029	0.037
GS (<2.1 mg)	6.618	0.012	108.088	0.000	2.206	0.153
GS (2.1–2.5 mg)	3.462	0.065	6.254	0.029	0.385	0.689
GR (<2.1 mg)	6.422	0.013	62.809	0.000	1.582	0.246
GR (2.1–2.5 mg)	4.695	0.031	46.972	0.000	1.704	0.223
SSB (<2.1 mg)	4.510	0.035	9.064	0.011	0.687	0.522
SSB (2.1–2.5 mg)	7.687	0.007	10.955	0.006	0.774	0.483
SRB (<2.1 mg)	0.198	0.823	8.570	0.013	0.944	0.416
SRB (2.1–2.5 mg)	0.321	0.731	31.595	0.000	4.238	0.041
Root:shoot ratio (<2.1 mg)	7.771	0.007	7.384	0.014	7.742	0.008
Root:shoot ratio (2.1–2.5 mg)	14.984	0.001	12.769	0.004	18.769	0.000

However, neither increasing temperature nor experimental year significantly influenced the GS of heavy weight seeds.

The results for seed GR changes were similar to the GS results (Fig. 4b). Increased temperature substantially decreased the GR of seeds weighing less than 2.1 mg and from the 2.1–2.5 mg by an average of 49.3 and 38.8%, respectively. These rates were significantly influenced by increased temperature and experimental year ($P < 0.05$) (Table 2).

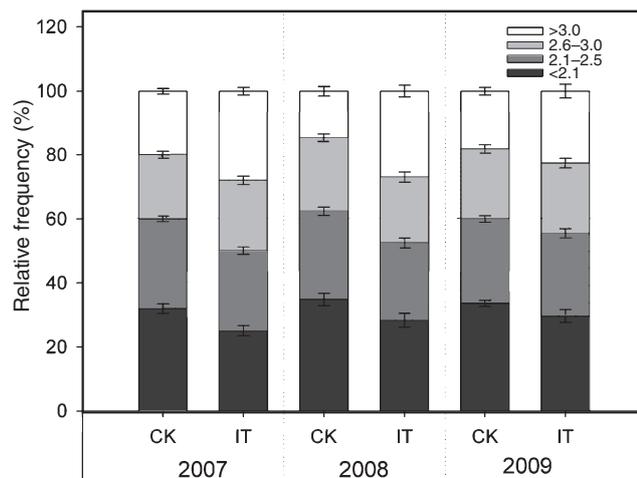


Fig. 3. Mass (mg) frequency distribution data for *Leymus chinensis* seeds were collected from control (CK) plots and increased temperature (IT) plots during the summers of 2007, 2008 and 2009. The data are expressed as mean \pm s.e. for three replications.

However, the GR of heavy weight seeds was not affected by these two main factors and their interaction.

Potential germination

Increasing ambient temperature decreased the potential germination (PG, proportion of seeds that will germinate) per square metre by 11.7, 24.9 and 29.5% in 2007, 2008 and 2009, respectively (Fig. 5). A significant reduction was found in 2008 and 2009 ($P < 0.05$). Combined ANOVA showed that PG was significantly affected by increased temperature and experimental year ($P < 0.05$) (Table 2).

Seedlings growth

Across the 3 experimental years, increased temperature reduced the mean SSB of seeds weighing less than 2.1 mg and from 2.1 to 2.5 mg by 16.3 and 18.6%, respectively, and reduced the mean SRB by 25.9 and 37.5%, respectively. For each year, increasing temperature had a significant effect on SSB, except for the 2.1–2.5-mg class in 2007 and less than the 2.1-mg class in 2008 ($P < 0.05$) (Fig. 6). The mean root:shoot ratio of seeds weighing less than 2.1 mg and from 2.1 to 2.5 mg was reduced by 18.8 and 34.7%, respectively. The SSB and root:shoot ratio were significantly affected by increased temperature and experimental year, but SRB was significantly influenced only by increased temperature (Table 2).

The mean seedling shoot and root biomass of heavy weight seeds (2.6–3.0, more than 3.0 mg) from the increased temperature plots was slightly higher than the control plots across the three years, but there was no significant difference

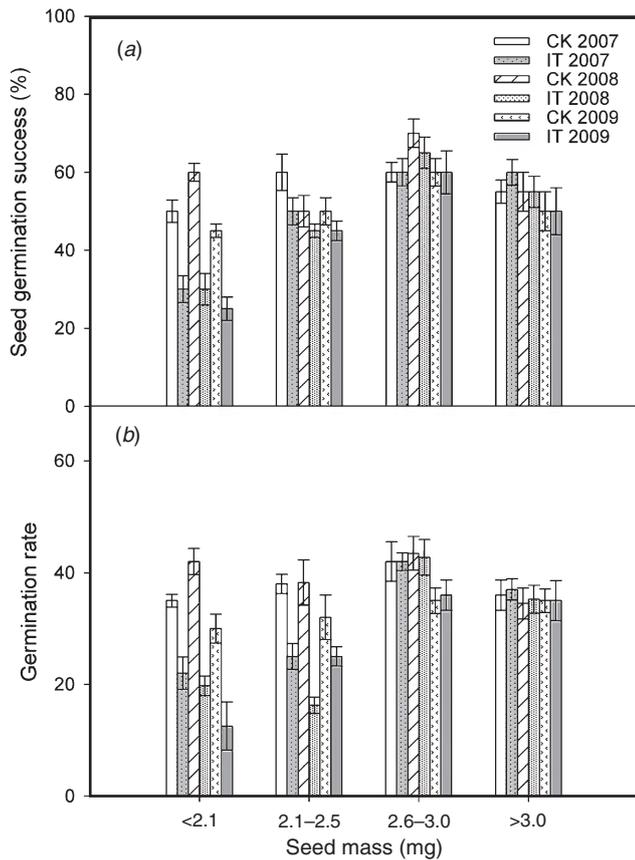


Fig. 4. Mean germination success and germination rate of *Leymus chinensis* seeds from increased temperature (IT) and the control (CK) plots. The data are expressed as mean \pm s.e. for three replications.

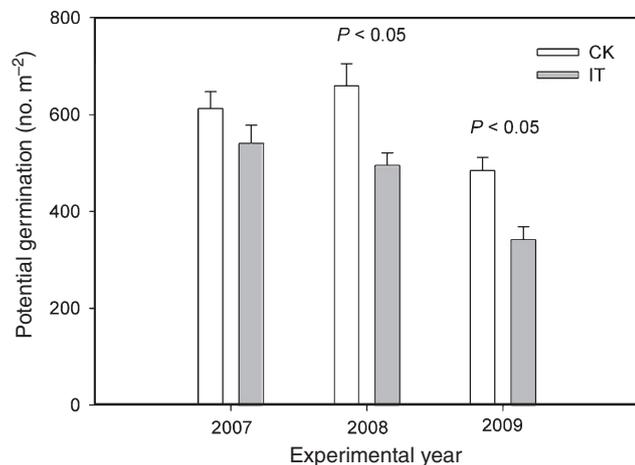


Fig. 5. Potential germination number for *Leymus chinensis* in the control (CK) plots and the increased temperature (IT) plots. The data are expressed as mean \pm s.e. for six replications.

between the control and the increased temperature treatments. Neither increased temperature nor experimental year had any significant effect on seedling shoot or root biomass.

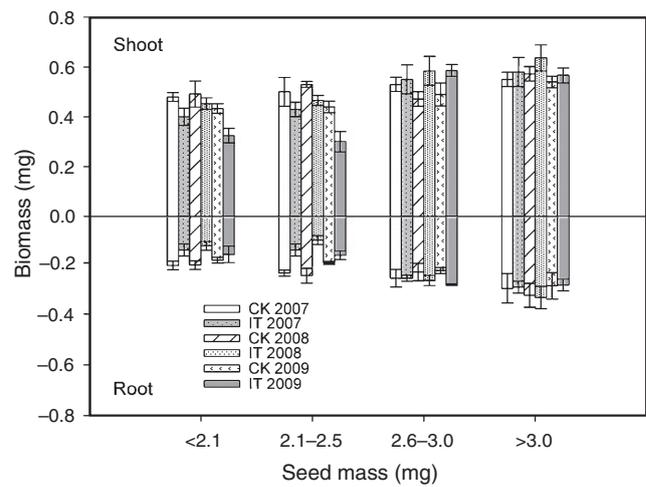


Fig. 6. Seedling biomass of *Leymus chinensis* grown for 15 days in a common incubator. Seeds were collected from the control (CK) plots and the increased temperature (IT) plots during July 2007–09. The data are expressed as mean \pm s.e. for three replications.

Discussion

Leymus chinensis seed yield, which is determined by the number of flowering plants per unit area, seed number per flowering plant and seed weight, depends primarily on the number of flowering plants (Wang et al. 2010b). Studies have indicated that the number of flowering plants is determined by the daughter shoot number, which is positively correlated with the autumn precipitation in the previous year (Yang et al. 2000; Zhang et al. 2009; Wang et al. 2010b). In this study, the reduction in the number of flowering plants was ~20% (Table 1); simultaneously, the reduction in autumn soil moisture, by increasing the soil temperature, was ~3% (Fig. 2). The results suggest that decreased soil moisture due to soil warming resulted in a decrease in flowering plant density. The inter-annual variability had a significant effect on the number of flowering plant because of the large variation in precipitation over the 3 experimental years (Fig. 1).

Reports of elevated temperature enhancing seed production in high-latitude and arctic regions are linked to the thawing of frozen soils, which leads to an advance in plant growth and an acceleration of leaf emergence and unfolding in plants (Wookey et al. 1994, 1995; Molau and Shaver 1997; Dunne et al. 2003; Post et al. 2008; Klady et al. 2011). The increased temperature impacts on floret and seed number per plant were correlated with accelerated leaf emergence and unfolding in this study, because the increased temperature reduced the impact of low spring temperate limits to a certain extent. Additionally, lower densities of flowering plants provide the remaining reproductive shoots greater access to photoassimilate via reduced competitiveness among spikes, which was what probably led to the observed increase in seed number per plant (Wang et al. 2010b).

The increase in thousand-seed weight was due to the increased proportion of heavy weight seed (2.6–3.0, more than 3.0 mg). Generally, the critical determinant period of

individual seed mass is the grain filling stage and this is decided by several important factors, such as temperature, moisture and nutrient availability (Acreche and Slafer 2006). The summer upper thermal limit is generally considered as one of the most important factors in temperate semi-arid regions (Sherry *et al.* 2007). Increasing temperature constrains the photoassimilate transport to seeds and changes seed structure (Vong and Murata 1977; Wallwork *et al.* 1998), leading to a reduction in seed mass (Hovenden *et al.* 2008). The grain filling stage of *L. chinensis* is from mid June to late July, when air temperature and rainfall are at their highest. In this experiment, elevating the temperature by 1.7°C did not constrain seed development. This indicates that the negative effect of increasing temperature does not always occur during hot summers in semi-arid regions. These results are different from the results by Hovenden *et al.* (2008), who found that warming reduced the seed mass in a dominant Australian grass, *A. caespitosa*. This difference in results was caused by the differences in environmental factors, such as temperature and rainfall between two experimental regions. The above results clearly indicate that the effects of warming on seed production was changed with variation in precipitations, which are consistent with the general performance of grassland productivity under varying rates of precipitation (O'Connor *et al.* 2001).

Seed mass is a strong determinant of seed GS, seedling establishment and plant growth (Stanton 1984). The influence of seed mass on subsequent seedling development usually persists for many months (Howe and Richter 1982). Previous studies suggested that the reduction in seed GS due to warming was not only related to seed mass, but also related to the changes in chemical composition and epigenetic effects in the parental plants (Hovenden *et al.* 2008). This explanation may also apply to the reduction in GS and GR of the light weight seeds (<2.1, 2.1–2.5 mg) recorded in this study. Additionally, the individual seed mass distribution range was from 0.7 to 4.6 mg in the increased temperature treatment, and from 1.2 to 4.0 mg in the control. The relatively increase in very light weight seeds was another important reason for reduced GS and rate because these seeds may have suffered from reduced viability. The reductions in seedling shoot and root biomass from light weight seeds in the increased temperature plots were caused by the lower GR because of seeds with a high GR require a short germination time and have a long growth period.

Due to accelerated shoot growth and leaf unfolding in heavy weight seeds (Howe and Richter 1982), GS and seedling growth is usually greater than for light weight seeds (Silvertown 1981; Hendrix 1984). In increased temperature and soil water deficits environments, light weight seeds cannot meet the nutrient demands of germination and seedling survival. Therefore, plants substantially increase the proportion of heavy weight seeds in order to compensate for the adverse influence of the warmer environment, which may represent a potential adaptation to global climate warming. However, degraded grassland renewal depends on large numbers of viable seeds and the reduction in potential seed germination number per unit area by global warming could negatively affect future new grassland establishment.

Conclusions

The conclusions from this study are: (i) increasing ambient temperature reduced mean seed number per square metre and PG; (ii) increasing temperature resulted in decreased proportion of light weight seeds but increased the proportion of heavy weight seeds, leading to an increased thousand-seed weight; and (iii) the GS, GR, and seedling shoot and root biomass of light weight seeds were reduced by increased temperature but the same effects were not observed in heavy weight seeds. A reduction in the PG seed number by increased temperature may imply that climate warming will constrain new grassland establishment depending on the viability implications for seeds under further global climate warming. These results can also provide some important clues to the growth and survival of other rhizomatous, perennial grass faced with further continued global warming.

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