

MISCELLANEOUS

Effects of Summer Nocturnal Warming on Biomass Production of *Leymus chinensis* in the Songnen Grassland of China: From Bud Bank and Photosynthetic Compensation

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Abstract

Nocturnal warming has various effects on plant biomass production. To understand how biomass production of the dominant grassland species *Leymus chinensis* responds to summer nocturnal warming in the eastern temperate Eurasian steppes, we simulated summer nocturnal warming (+4 °C) using a phytotron system for 100 days operated based on the variation of diurnal temperatures over the past 12 years in the Songnen Grasslands. Our results show summer nocturnal warming significantly increased above-ground biomass production of parent and daughter shoots as well as increased below-ground root and rhizome biomass production; rhizome biomass increased faster than root biomass leading to an increase in the rhizome biomass to root biomass ratio. Nocturnal warming slightly increased the number of daughter shoots per plant, and significantly increased the number of buds in the below-ground bud bank and the number and length of rhizomes per plant. Also, the dark respiratory and net photosynthetic rates, J_{\max} , the rate of triosephosphate utilization and chlorophyll fluorescence parameters (Φ_{PSII} and qP) were significantly higher under nocturnal warming conditions. These findings show that nocturnal warming in this ecosystem improves individual biomass accumulation due to photosynthetic compensation, and may enhance the population density and productivity of *L. chinensis* by increasing bud number in the below-ground bud bank during the early stage of ecological succession for grasslands dominated by *L. chinensis*.

Introduction

Variations in temperature crucially influence plant growth and development and will inevitably induce changes to the morphology of individual plants, and will change population dynamics and even change ecosystem productivity. Current climate change scenarios suggest the greenhouse effect will lead to a projected increase in global surface temperatures of 1.1–6.4 °C by the year 2100 (Easterling et al. 1997, IPCC 2007) and regional surface temperature are predicted to increase 1.2–3.3 °C across China by the year 2100 (Working Group for National Report of Climate Change in China (WGNRCCC 2007)). This warming regime is predicted to cause daily minimum air temperatures to rise more rapidly than maximum air temperature, especially for mid to northern latitudes (IPCC 2007, Lobell

et al. 2007, Zhou et al. 2007). In the Songnen Grassland, temperatures have increased based on the last 50 years of meteorological record from the Songnen Grassland (Xu et al. 2005, Luan et al. 2007). Over the last several decades, a large body of literature has shown that biomass increases, decreases, or exhibits no response to nocturnal warming (Nicholls 1997, Peng et al. 2004, Kelly et al. 2006, Wan et al. 2009, Fang et al. 2010, Prasad et al. 2011). Furthermore, some studies suggest that nocturnal and diurnal warming induce soil drought and cause plant growth to slow down (Herzog and Chai-Arree 2012); however, other studies have shown that nocturnal warming slightly decreased soil water content and did not influence plant growth (Zhang et al. 2010).

Plant growth and biomass accumulation represent the balance between photosynthesis and respiration (Yamagishi

1994, Volder et al. 2004), and an increase or decrease in the rate of photosynthesis might depend on environmental temperature and whether or not temperatures are close to or exceed the optimal temperature for plant growth. Numerous reports have shown that the sensitivity of respiration to warming will eventually surpass that of photosynthesis (Dewar et al. 1999), which could decrease the ratio of the photosynthetic to respiratory rate (McDonald and Paulsen 1997, Atkin and Tjoelker 2003, Wollenweber et al. 2003). However, Turnbull et al. (2002) report that the rate of photosynthesis increases on a day following increased nocturnal temperatures because of greater consumption of leaf carbohydrates by respiration at night. Xu et al. (2004) have shown that the photosynthetic rate of *Leymus chinensis* does not decrease significantly in response to drought when temperatures are between 20 and 26 °C. Meanwhile, some research has demonstrated that warming has no influence on stomatal conductance (G_s) (Llorens et al. 2004, Albert et al. 2011), unless warming induces drought which will decrease stomatal conductance allowing plants to avoid higher transpiration rate. Fluorescence parameters, as one means of detecting plant photosynthesis, are associated with gas exchange and reflect rates of plant growth and biomass accumulation, especially for photosystem II (PSII) which is considered to be the most heat-sensitive component in the photosynthetic apparatus (Berry and Bjorkman 1980). In this study, we use gas exchange and fluorescence parameters to assist in understanding the mechanisms of biomass response to nocturnal warming.

In a perennial-dominated grassland ecosystem, productivity may also be linked to below-ground bud bank dynamics, because the majority of regeneration in perennial grasslands draws on the below-ground bud bank rather than on the seed bank (Barrett and Silander 1992, Benson et al. 2004). The concept of bud banks, first introduced by Harper (1977), was defined as an accumulation of dormant meristems on rhizomes, corms, bulbs, bulbils and tubers in the soil. A growing body of evidence has shown that bud bank could be a main source for regenerating vegetation for many perennial grasses (such as *L. chinensis*), because the germination and establishment of seedlings from seeds occurs only infrequently (Yi et al. 2001, Benson et al. 2004). For now, the importance of a bud bank has been documented in numerous habitats. For example, in mesic remnant grasslands in central North America, almost all above-ground individuals are recruited from the below-ground bud bank rather than the seed bank (Benson and Hartnett 2006). Although a below-ground bud bank is closely linked with above-ground productivity (Knapp and Smith 2001), the key factor which influences above-ground population regeneration is the ability of buds to sprout from clonal structures such as rhizomes and to develop into daughter shoots (Jitka and Leoš 2007).

A considerable amount of research related to bud banks has mainly focused on the tall grass prairie ecosystem (Benson et al. 2004, Choczynska and Johnson 2009, Carter et al. 2012), however, the literature contains few reports related to bud banks in the eastern Eurasian temperate steppes, especially as it relates to global warming. Therefore, the dynamics of below-ground bud banks and the regeneration of above-ground shoots under warming conditions urgently need more attention.

Leymus chinensis is a typical perennial C_3 grass with rhizomatous propagation. It is widely distributed in the eastern region of the Eurasian steppes (including the Russian Baikal), the northern and eastern parts of the People's Republic of Mongolia, the northern and northeastern plain and the Inner Mongolia plateau of China (Wang et al. 2004). This species serves as an economically and ecologically important forage grass in Northern China, which is rich in protein, minerals, carbohydrates and has good palatability. This plant produces thick and long below-ground rhizomes with many adventitious roots at each node and is highly tolerant to arid soil. Currently, the spatial extent of grasslands has decreased by about one third as a result of climate change and associated human disturbance such as overgrazing and inappropriate land use management (Jia et al. 2006), which has reduced grassland productivity. Under global warming scenarios, especially in summer, the key season for the growth and development of *L. chinensis*, it remains unclear how biomass production of *L. chinensis* will respond to summer nocturnal warming and what the causes of that response could be. Therefore, in the present study, we used *L. chinensis* as our study material to examine its response to climate change and simulated summer nocturnal warming (+4 °C) to address the following questions in view of the concept of a bud bank and related photosynthetic compensation: (i) How does summer nocturnal warming impact biomass production in individual *L. chinensis* plants and how does it impact changes and trends in populations? (ii) How do gas exchange and fluorescence parameters of *L. chinensis* respond to nocturnal warming? (iii) Are the effects of nocturnal warming on the below-ground bud bank dynamics consistent with the response of productivity?

Materials and Methods

Plant material and growth conditions

Seeds of *L. chinensis* and soil were obtained from southwest of the Songnen Artificial Grassland Ecosystem Field Station, Institute of Grassland Science, Jilin Province, China (123°44'E, 44°44'N, 167 m a. s. l.). The Songnen Field Station is located in the eastern Eurasian steppes. On June 1, 2012, about 20 seeds were sown in each of 16 plastic pots (inside diameter 19 cm, height 14 cm; 320 seeds in total)

filled with 3.3 kg dry Mollisol which was the main soil types of the Songnen Grassland Ecosystem. The total nitrogen, organic carbon content and pH of the Mollisol soil were 6.8 %, 0.3 % and 8.63 %, respectively. Fifteen days after sowing, the plants were thinned to seven seedlings per pot, selecting uniform and robust seedlings for the nocturnal warming treatment studies. Sixteen pots were used in the warming treatment studies. All plants were placed in an outer room for 60 days and were kept in moist soil during that time, then they were transferred to a phytotron (LT/ACR-2002 Phytotron System; E-Sheng Tech., Beijing, China) of Northeast Normal University for nocturnal warming treatment which commenced 60 days after sowing. In the phytotron, high stress sodium lamps (Philips) with photosynthetically active radiation (PAR) provided light at a rate of $350 \mu\text{mol}^{-2} \text{s}^{-1}$ for 14 h per day. This type of light provided more available light for plant growth by increasing the output of blue light by 30 %. The relative humidity was maintained in a range of 40–60 %. We used a computer to monitor the environmental conditions such as temperature, humidity and light, of the phytotron.

To ensure each plant received equal light conditions, every 3 days the pot positions were randomly changed during the treatment. The pots were irrigated with 240 ml of water every 3 days (equivalent to 8 mm of precipitation, totalling 80 mm every month, equal maintaining the soil water content at 50–60 % of field capacity) based on the precipitation records in *L. chinensis* habitat from June to August for 2000 to 2011 from the Meteorological Bureau of Changling County, Jilin, China (Appendix 1).

Nocturnal warming treatments

Based on the temperature records in *L. chinensis* habitat from June to August for 2000 to 2011 and location described above, the maximum, minimum and average temperature were 28, 18 and 23 °C, respectively (Appendix 2). Therefore, we mimicked the temperature variation of the Songnen Artificial Grassland Ecosystem Field Station as follows (control): 5 : 30–8 : 30, 22 °C; 8 : 30–11 : 30, 25 °C; 11 : 30–14 : 30, 28 °C; 14 : 30–17 : 30, 25 °C; 17 : 30–19 : 30, 22 °C; 19 : 30–5 : 30, 18 °C. Guo *et al.* (2013) showed that the minimum temperature of summer in North China increased at the rate of about 0.4 °C per decade. Therefore, in this experiment, the nocturnal warming treatment was elevated $4 \text{ °C} \pm 0.2 \text{ °C}$ from 19 : 30 to 5 : 30 relative to the control to simulate the temperature in this region by the year 2100.

Clonal parameters and biomass

Plants from four of the 16 pots (each treatment) were randomly destructively sampled after 50 days and again after 100 days of nocturnal warming. Every plant was separated

from soil for examination. Then, we immediately counted the total number of rhizomes and below-ground buds over 1-mm long and corresponding daughter shoots per parent shoot, we also measured total rhizome length from each individual parent shoot. In this research, below-ground buds were defined as rhizome buds which originated from the rhizome and tiller buds which originated at a basal node of a shoot. Finally, plant samples from each pot were divided into the above-ground (parent shoots and daughter shoots) and below-ground (rhizomes and roots) parts, and then dried to a constant weight at 65 °C to obtain dry mass.

In this study, plants developed from seeds were defined as parent shoots and those which resprouted from a bud of a rhizome and basal node of parent shoots were considered daughter shoots.

Gas exchange

Leaf CO₂ exchange parameters were measured with an LI – 6400 gas exchange system (LI – 6400XT; Li-Cor Inc., Lincoln, NE, USA) on 16 of the youngest available fully expanded leaves (four leaves per pot, four pots per treatment) after 50 and 100 days of nocturnal warming (before sampling). Leaf respiratory rates (R_d) were measured at 21 : 30 (at least 2 h after dark and 1 h after reaching the minimum temperature in the phytotron). Net photosynthetic rates (A), G_s , transpiration rate (E) were measured with a LED light source the following day, using a Li-Cor red/blue LED light source and a standard $2 \times 3 \text{ cm}$ chamber. The PAR was set at $350 \mu\text{mol}^{-2} \text{s}^{-1}$ equalling the light of the phytotron and the reference CO₂ concentration was maintained at $380 \mu\text{mol mol}^{-1}$ using CO₂ control modules. Samples were allowed to acclimate for a few minutes until the net photosynthetic rate stabilized and the coefficient of variation was below 0.5.

The assimilation-intercellular CO₂ concentration ($A-C_i$) curve was determined by measuring the response of A to C_i (one leaf per pot, four pots per treatment), and the external CO₂ concentration was set to 13 gradients from 2000 ppm to 50 ppm (400, 300, 200, 100, 50, 400, 400, 600, 800, 1000, 1200, 1500, 2000) at the saturating light level of $1000 \mu\text{mol}^{-2} \text{s}^{-1}$. Leaf temperature was maintained at 25 °C. The Li-Cor auto program ‘ $A-C_i$ curve’ was used (settings: minimum 60 s and maximum 180 s, IRGA matching conducted at each step).

We calculated parameters at which photosynthesis was potentially inhibited from the $A-C_i$ curves using Photosynthesis Assistant software (Photosyn Assistant, Ver. 1.1.2; Dundee Scientific, Dundee, UK) including measures of V_{cmax} , J_{max} and the rate of triosephosphate utilization (TPU). V_{cmax} and J_{max} represented the maximum carboxylation efficiency of ribulose-1,5-diphosphate carboxylase (Rubisco), and the ribulose-1,5-bisphosphate (RuBP) regeneration capacity (Turnbull *et al.* 2002), respectively.

Gas exchange data and chlorophyll fluorescence detection mainly reflect the dark and light reaction stages of photosynthesis, respectively. Thus the application of chlorophyll fluorescence parameters can be used to assist the study of changes in photosynthetic physiology. A LCF fluorescent leaf chamber was used to determine the chlorophyll fluorescence parameters. After putting the prepared and carefully labelled samples into the dark environment for 12 h, we measured minimal fluorescence (F_o), maximal fluorescence (F_m) and variable fluorescence (F) in that sequence under dark conditions. All samples were exposed to the light condition in the growth chamber for 3 h, and then we measured minimum fluorescence (F_o'), maximum fluorescence (F_m') and steady-state fluorescence (F_s) in that sequence. The LED light was set at $350 \mu\text{mol}^{-2} \text{s}^{-1}$ matching the light conditions of the phytotron and the reference CO_2 concentration was maintained at $380 \mu\text{mol mol}^{-1}$ using CO_2 control modules. We calculated F_v/F_m (maximum quantum, $F_v/F_m = (F_m - F_o)/F_m$), Φ_{PSII} (photochemical reaction quantum efficiency, $\Phi_{\text{PSII}} = (F_m' - F_s)/F_m'$), qP (photochemical quenching, $qP = (F_m' - F)/(F_m' - F_o')$), and NPQ (non-chemical quenching coefficient, $\text{NPQ} = F_m/F_m' - 1$). F_v/F_m , Φ_{PSII} , qP and NPQ represented the quantum yield of the PSII reaction centre in an open state, the supply efficiency from photons absorbed by the plant to the PSII reaction centre, the open extent of the PSII reaction centre and the heat dissipation component from light energy which chloroplasts absorbed (Rohacek and Bartak 1999, Maxwell and Johnson 2000), respectively.

Statistical analysis

The clonal parameters and A , G_s , C_i , E , water use efficiency (WUE) were statistically analysed using a mixed effect model with the nocturnal warming treatment as a fixed effect and pots as a random effect. Biomass and the parameters at which photosynthesis was potentially inhibited from the $A-C_i$ curves as well as chlorophyll fluorescence were statistically analyzed using an independent sample t -test. Significance levels reported in the tables and figures were considered significant for $P < 0.05$ (SPSS 13.0; SPSS Inc., Chicago, IL, USA). The number of daughter shoots and buds, the length and number of rhizomes and the measured biomass of plants in this study were counted per plant. All figures were plotted by SIGMAPLOT 11.0 (Systat Software, Inc., San Jose, CA, USA).

Results

Biomass production

Nocturnal warming significantly elevated total biomass of *L. chinensis* (Fig. 1a). The total biomass per plant increased

by 52.9 % and 60 % contrast to the control after 50 and 100 days of nocturnal warming. Biomass of the parent shoots, daughter shoots, roots and rhizomes showed similar trend in total biomass production. Compared with the control, the parent shoot above-ground biomass per plant increased by 60 % and 100 % and the daughter shoot above-ground biomass per plant increased by 44.4 % and 36.4 % after 50 and 100 days of nocturnal warming (Fig. 1c,d), respectively. The below-ground parts of plants in our study were composed of roots and rhizomes. Dry matter of roots and rhizomes increased in successive samples under the nocturnal warming conditions, whereas rhizome biomass increased faster than root biomass (Fig. 1f, g). Therefore, the rhizome biomass to root biomass ratio increased by 73.1 % after 100 days of nocturnal warming (Fig. 1h).

Gas exchange

Nocturnal warming significantly increased the R_d , A , WUE, J_{max} , TPU, Φ_{PSII} and qP and decreased NPQ (Fig. 2 and Table 1). After 50 and 100 days treatment of nocturnal warming, R_d , A and WUE increased significantly by 41.2 % and 25.8 %, by 31.2 % and 36.8 % and by 42 % and 47.8 %, respectively compared with the control (Fig. 2a,b, e). No significant difference was observed for G_s and E after 50 and 100 days of nocturnal warming treatment when compared with the control (Fig. 2c,d).

After 100 days of nocturnal warming treatment, we calculated the potential limiting factor of photosynthesis by calculating parameters of the $A-C_i$ curves and found that J_{max} significantly increased by 33.7 % from $106 \mu\text{mol m}^{-2} \text{s}^{-1}$ to $141.67 \mu\text{mol m}^{-2} \text{s}^{-1}$ compared with the control (Fig. 3b). Also, TPU increased by 32.2 % (Fig. 3c), but there was no obvious effect on V_{cmax} (Fig. 3a). In addition, Φ_{PSII} and qP under nocturnal warming significantly increased by 17.9 % and 14.3 %, respectively, whereas NPQ decreased 37.3 % in contrast to the control (Fig. 3e,f,g).

Overall, nocturnal warming increased the rate of photochemical reactions of *L. chinensis* in the light reaction stage and its capacity to fix C during the dark stage, which implied that nocturnal warming strengthened the photosynthetic capacity of *L. chinensis* during the early stage of ecological succession for grasslands dominated by *L. chinensis*.

Bud bank and clonal growth parameters

Nocturnal warming significantly increased the total bud numbers in the below-ground bud bank and the clonal growth parameters after 100 days of nocturnal warming treatment, but it had little impact on the number of

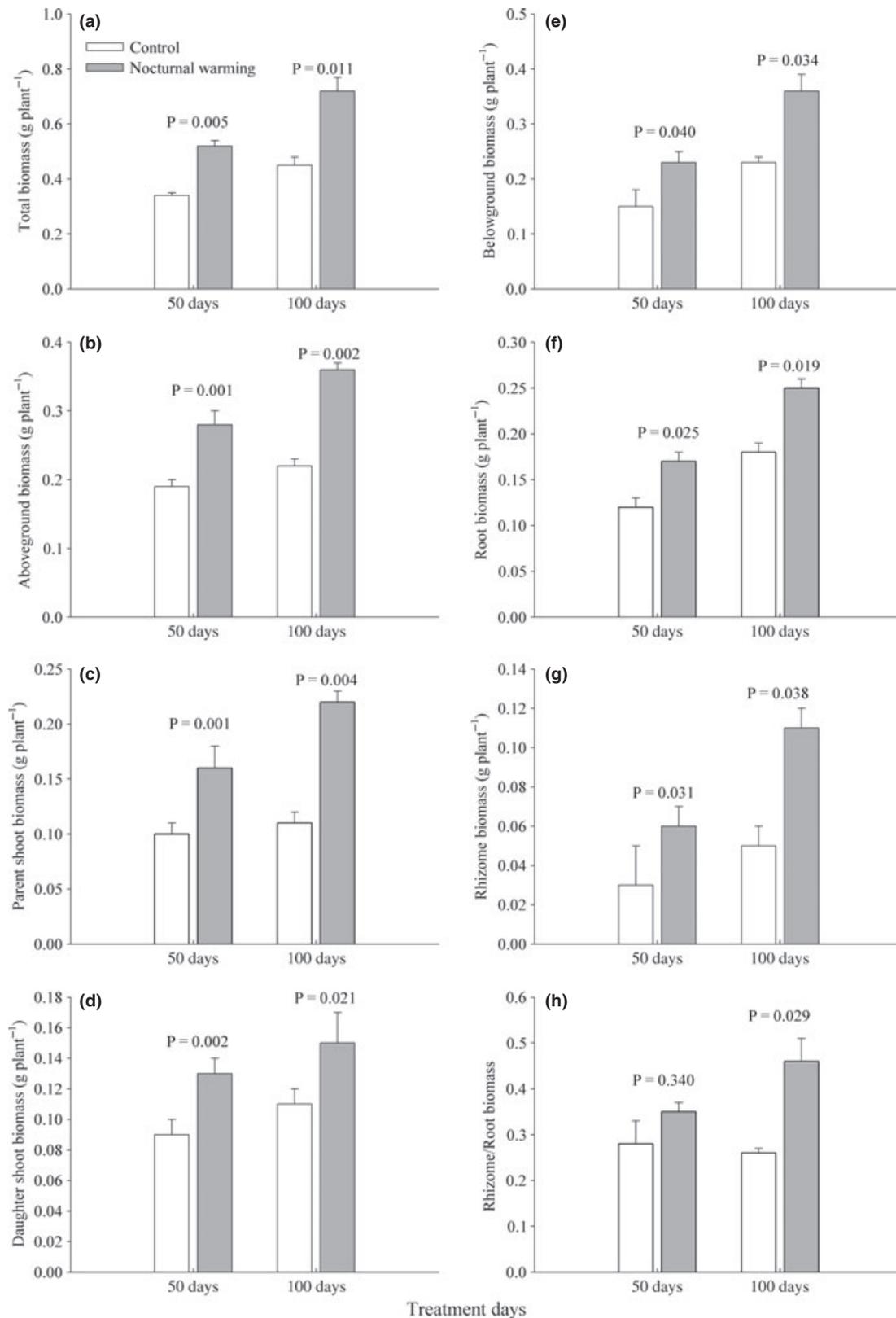


Fig. 1 Biomass production per plant of *Leymus chinensis* under control and nocturnal warming environment. (a) Total biomass, (b) above-ground biomass, (c) parent shoot above-ground biomass, (d) daughter shoot above-ground biomass, (e) below-ground biomass, (f) root biomass, (g) rhizome biomass, (h) ratio of rhizome to root. The biomass was expressed as mean \pm S.E.

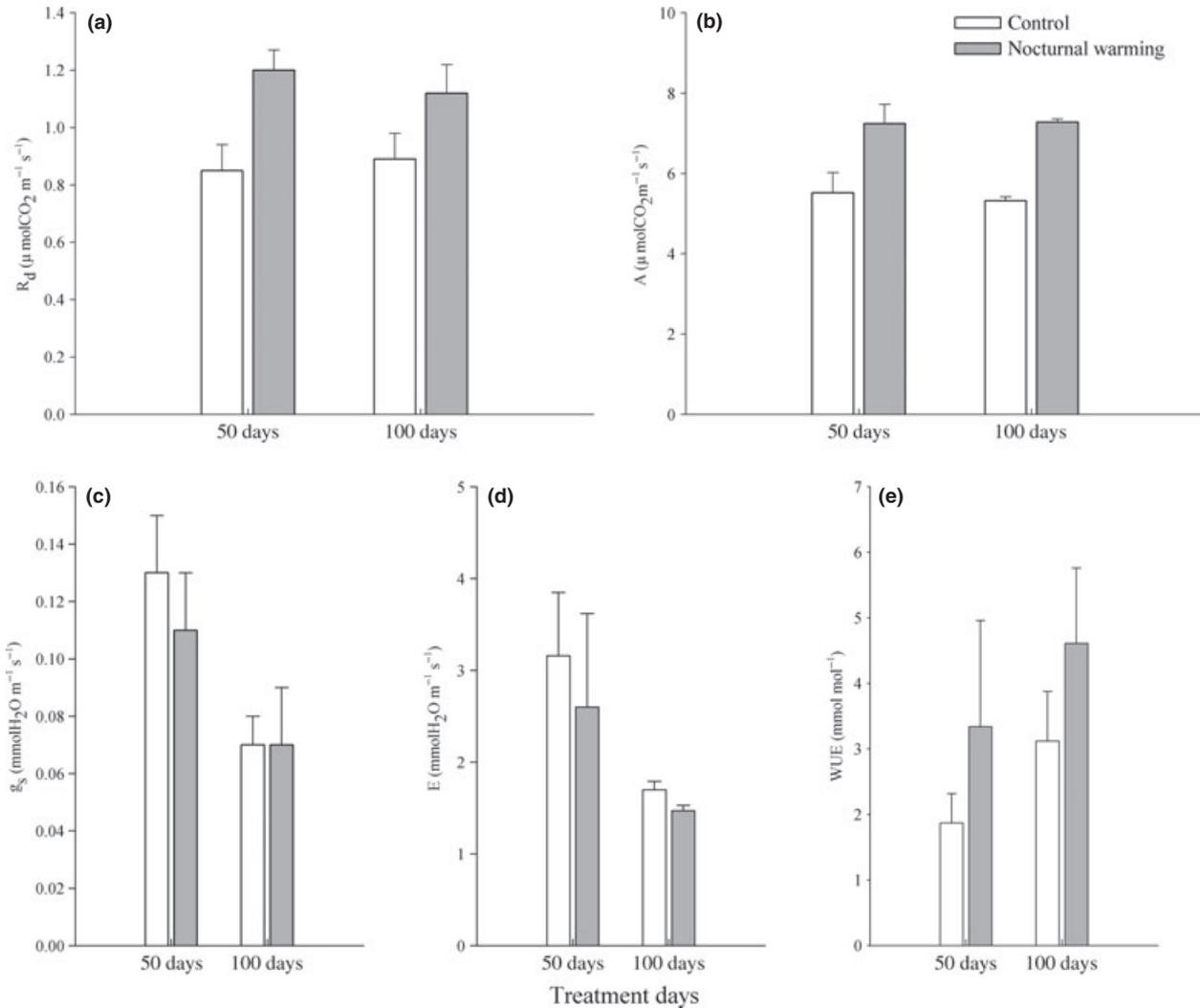


Fig. 2 Gas exchange parameters of *Leymus chinensis* under control and nocturnal warming environment. (a) Dark respiration rate (R_d), (b) net CO_2 assimilation rate (A), (c) stomatal conductance (G_s), (d) transpiration rate (E) and (e) water-use efficiency (WUE). The data were expressed as mean \pm S.E.

Table 1 The value of P for dark respiration rate (R_d), net CO_2 assimilation rate (A), intercellular CO_2 concentration (C_i), stomatal conductance (G_s), transpiration rate (E) and water-use efficiency (WUE) of *Leymus chinensis* under two nocturnal temperature

Treatment	R_d		A		G_s		E		WUE	
Days	50	100	50	100	50	100	50	100	50	100
nw	0.001	0.002	0.001	0.001	0.092	0.310	0.066	0.440	0.001	0.000
b	0.530	0.287	0.067	0.799	0.615	0.209	0.781	0.415	0.924	0.772
nw*b	0.606	0.268	0.216	0.166	0.191	0.507	0.964	0.817	0.890	0.912

nw represented nocturnal warming, b represented pot factor. $P < 0.05$ was considered a statistically significant difference between the control and nocturnal warming environments (bold values).

daughter shoots (Fig. 4; Table 2). After 50 and 100 days of nocturnal warming treatments, the number of buds produced increased by 59.7 % and 93.2 % in contrast to the control (Fig. 4a). Although the above-ground daughter

shoot number did not increase significantly, it had an increasing trend similar to that of the number of buds (Fig. 4b). In addition, after 50 and 100 days treatment of nocturnal warming, rhizome number increased by 57.9 %

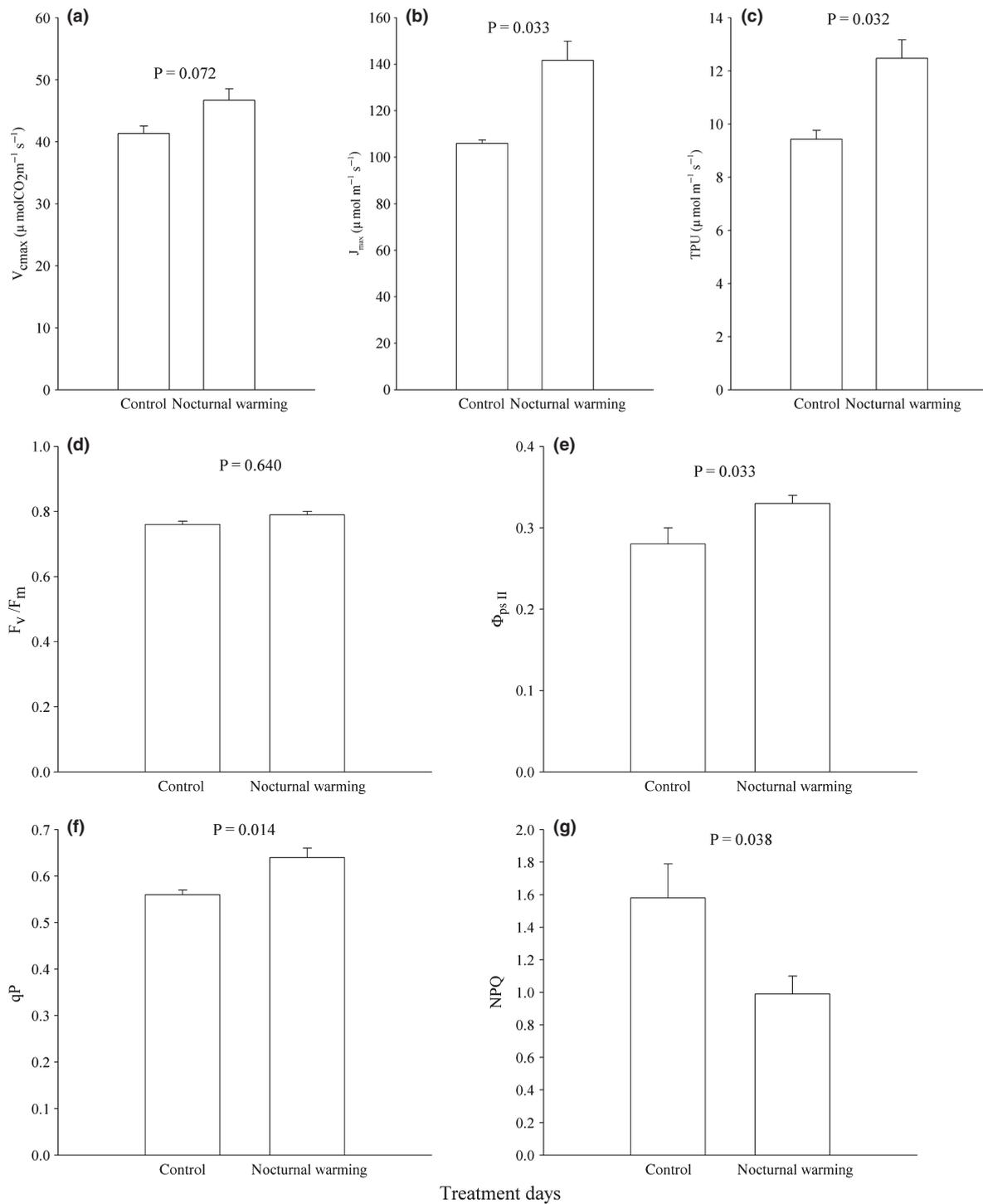


Fig. 3 Photosynthetic parameters derived from A-C₁ curves and chlorophyll fluorescence (F_v/F_m , Φ_{PSII} , qP and NPQ) of *Leymus chinensis* after 100 days under two nocturnal temperature. (a) V_{cmax} , (b) J_{max} , (c) triosephosphate utilization (TPU), (d) F_v/F_m , (e) Φ_{PSII} , (f) qP and (g) NPQ. The data were expressed as mean \pm S.E.

and 52.4 % (Fig. 4c) and rhizome length increased by 97.5 % and 76.2 % compared with the control (Fig. 4d), respectively.

Discussion

Temperature plays a key role in plant growth and development, and it is likely that changing temperatures will also

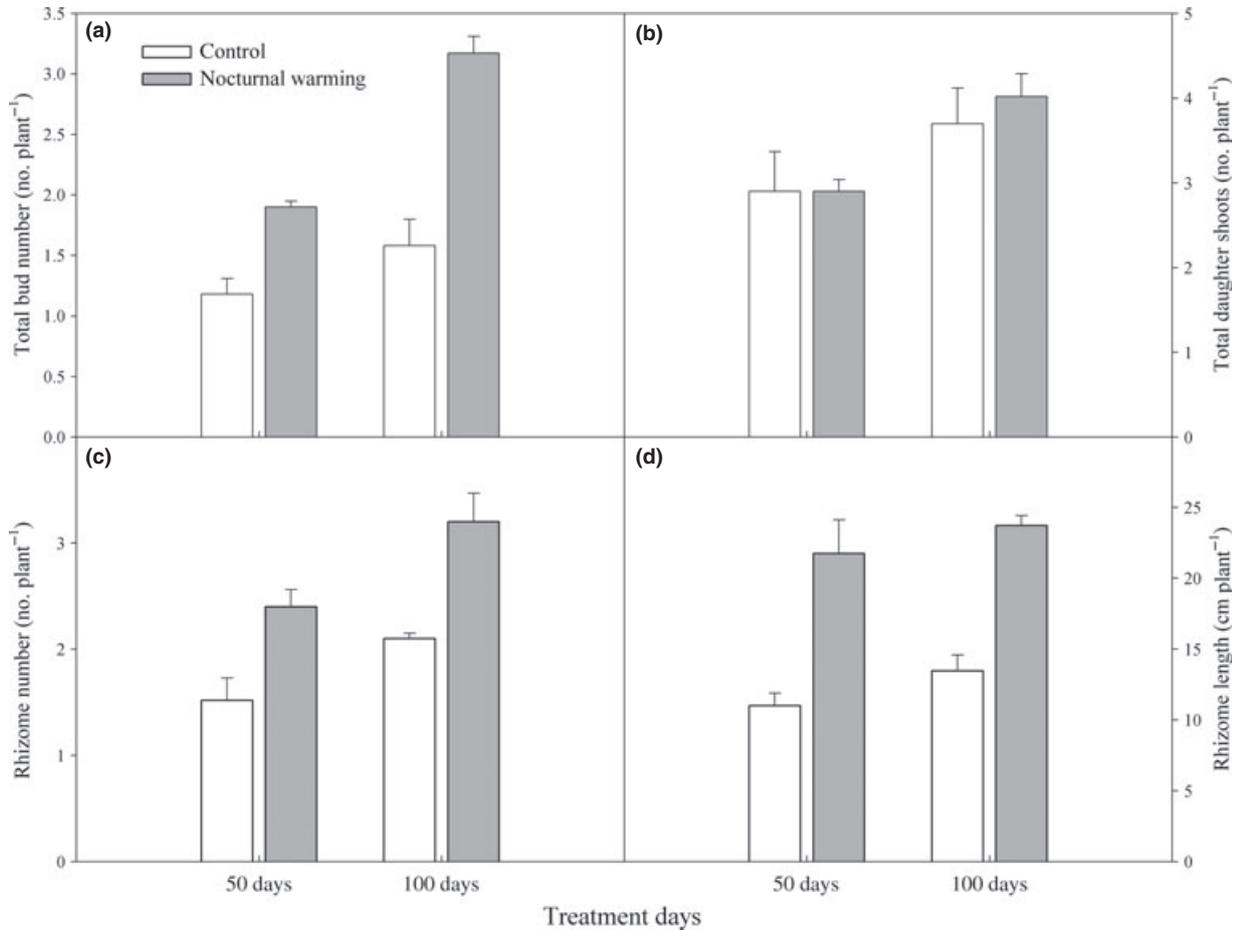


Fig. 4 Bud bank and clonal growth parameters of *Leymus chinensis* under control and nocturnal warming environment. (a) bud number in below-ground bud bank, (b) daughter shoot number, (c) rhizome number and (d) rhizome length. The data were expressed as mean \pm S.E., and counted by per plant.

Table 2 The value of P of bud bank and clonal growth parameters of *Leymus chinensis* under control and nocturnal warming environment

Treatment	Bud number		Daughter shoots		Rhizome number		Rhizome length	
Days	50	100	50	100	50	100	50	100
nw	0.747	0.047	0.758	0.328	0.068	0.004	0.010	0.021
b	0.471	0.313	0.828	0.753	0.115	0.897	0.896	0.225
nw*b	0.519	0.483	0.194	0.607	0.712	0.856	0.924	0.319

nw represents nocturnal warming, *b* represented pot factor. $P < 0.05$ was considered a statistically significant difference between the control and nocturnal warming environments (bold values).

influence plant productivity by clonal growth and so on. Many researchers have shown that nocturnal warming will advance, suppress, or have no influence on plant productivity (Nijs et al. 1996, Dhakhwa and Campbell 1998, Alward et al. 1999, Rustad et al. 2001, Volder et al. 2004, Wan et al. 2005), and increased daily minimum and maximum temperatures have different effects on plant biomass

production (Peng et al. 2004, Lobell 2007). Wang et al. (2007) suggest that in the next 100 years, if the global temperature increases by 2.7–3.9 °C and precipitation increases by 10 %, net primary productivity (NPP) of meadow steppe dominated by *L. chinensis* will increase. In our study, the above-ground biomass of parent and daughter shoots were higher than the control after 50 and

100 days of nocturnal warming treatments, which may imply that summer nocturnal warming promoted biomass production of *L. chinensis* individuals in the early stage of ecological succession for grasslands dominated by *L. chinensis*. The reason for this may be that nocturnal warming promoted depletion of leaf carbohydrates through enhancing the leaf dark respiratory rate and promoting leaf net photosynthetic rate the next day, which contributed to individual biomass accumulation of *L. chinensis* (Figs 2 and 3; Table 1). Our results agree with the findings of Griffin et al. (2002), Turnbull et al. (2002) and Wan et al. (2009). Moreover, consistent with other studies (Zhang et al. 2010), nocturnal warming and daily warming both result in slightly decreased soil water content (data not shown), but this does not cause severe drought and *L. chinensis* is highly tolerant to arid soils. Consequently, warming effects mediated through decreased soil water content is expected to have only minor effects in this study. We also found that nocturnal warming enhanced the ability of *L. chinensis* to absorb and fix C, since J_{\max} and TPU increased significantly under nocturnal warming (Fig. 3b,c), whereas G_s did not change under nocturnal warming conditions (Fig. 2; Table 1), which perhaps happened because the daytime temperature is the same between the control and the nocturnal warming treatment. Consequently, we conclude that the effect of summer nocturnal warming on the photosynthetic rate of *L. chinensis* mainly resulted from promoting the ability of the plants to regenerate RuBP and increased TPU (Turnbull et al. 2002), but did not increase intercellular CO_2 concentration (C_i) caused by G_s . Nocturnal warming increased A and have no influence on E , which led to the increase of WUE. In addition, we found that summer nocturnal warming significantly improved Φ_{PSII} and qP (Fig. 3e,f) by studying the chlorophyll fluorescence parameters which reflected plant change during light reaction phase. This indicates that summer nocturnal warming increased the supply efficiency to the PS II reaction center from photons absorbed by the plant and reduced heat dissipation (Richard and Evelyn 2004).

The below-ground bud bank is the main source of growth that regulates the pattern of above-ground net primary production in grassland ecosystems (Knapp and Smith 2001, Dalgleish and Hartnett 2009), and temperature is a crucial environmental factor affecting bud bank dynamics and the development from buds to daughter shoots (Svejcar 1990). Wang et al. (2010) have studied bud bank dynamics under constant summer warming for 90 days, and their studies show that the number of buds in the below-ground bud bank increased whereas the number of daughter shoots decreased under the warming conditions (Wang et al. 2010). However, nocturnal warming increased both the number of buds and daugh-

ter shoots although it did not cause significant changes in the number of daughter shoots in this study (Fig. 4b; Table 2) perhaps for two reasons. First, buds need time to develop into daughter shoots, and thus the production of daughter shoots lags behind the production of buds. Second, as previously noted, the effect of symmetric and asymmetric warming on the physiological characteristics of plants, as well as on plant productivity, are not exactly consistent (Dhakhwa and Campbell 1998, Volder et al. 2004), so that constant summer warming (diurnal and nocturnal) may have different influences on clonal growth of *L. chinensis*. In addition, as nocturnal warming time increased, not only did the number of rhizomes increase but also the length of rhizomes increased significantly (Fig. 4c,d; Table 2), which implied that the summer nocturnal warming advanced the growth of the clonal organ. Under summer nocturnal warming conditions, plants allocated the majority of below-ground biomass to rhizomes for storage and produced more buds (Fig. 1h). Our results imply that summer nocturnal warming might enhance population density through strengthening the capacity of *L. chinensis* to expand its clones and thus promote above-ground productivity when soil water and fertilizer are not limiting factors and the population density is relatively sparse (≈ 250 plant m^{-2} in this study).

In summary, our findings show that summer nocturnal warming promotes biomass accumulation in *L. chinensis* as a result of net C absorption by photosynthetic compensation and enhanced vegetative propagation. This implies nocturnal warming might be beneficial for the early stage of ecological succession for grasslands dominated by *L. chinensis*. However, our study was a simulated experiment conducted in a phytotron, where it was much easier to control environmental conditions than in a field experiment; also some limiting factors may have existed in this experiment such as low light conditions. Furthermore, future climate change is a multifactorial complex (e.g., warming, elevated CO_2 , N deposition and extreme rainfall events), so a considerable amount of work related to the response strategy of *L. chinensis* to the multifactorial interactions occurring with climate change should be conducted in the future.

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Supporting information

Additional Supporting information may be found in the online version of this article:

Appendix 1 The precipitation in summer (June–August) from 2000 to 2011. The average precipitation monthly was around 80 mm. Data were collected by the Meteorological Bureau of Changling County, China (grown site of *Leymus chinensis*).

Appendix 2 The average maximum, minimum and mean air temperatures in summer (June–August) from 2000 to 2011. Data were collected by the Meteorological Bureau of Changling County, China (grown site of *Leymus chinensis*).