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Responses of two dominant plant species to drought stress and defoliation in the Inner Mongolia Steppe of China

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Abstract There has been a dramatic shift in dominance from *Stipa grandis* communities to *S. krylovii* communities in the Inner Mongolia steppe of China, in recent decades due to climate change and human activity. We examined the growth and carbohydrate allocation pattern of *S. grandis* and *S. krylovii* under controlled conditions. The experimental approach involved a drought stress treatment and a simulated defoliation (clipping) treatment of both species. Growth (above ground biomass and root biomass) and carbon allocation (concentration of leaf total phenolics and pool of total non-structural carbohydrate) variables were evaluated at the end of the experiment. Responses to drought stress differed significantly between *S. grandis* and *S. krylovii*. For *S. krylovii*, growth and the pool of total non-structural carbohydrate were more negatively affected by drought stress, whereas concentration of total phenolics was positively affected. Drought stress reinforced responses to defoliation, and drought stress × defoliation interaction was significant for all of the variables. There was a distinct defoliation response level for growth after drought stress between the two species. For aboveground biomass, both species responded positively to drought stress, which changed from responses equivalence to *S. krylovii* being superior; for root biomass, the two species responded oppositely to drought stress, which changed from *S. grandis* being superior to *S. krylovii* being superior. There was a weak and reverse defoliation response level for the carbon allocation pattern after drought stress between the two species, with *S. krylovii* changing from superior in defense to superior in storage. These results suggested that *S. grandis* utilized an avoidance strategy (investment in defense compounds) and *S. krylovii* utilized a tolerance strategy (investment in storage for regrowth) in response to defoliation under drought stress, supporting the idea that stress-tolerant species may become the new dominant species because of their ability to re-grow after disturbance. This provided a possible explanation for the replacement of *S. grandis* communities from the view point of adaptive strategy.

Keywords Dominant species · Defoliation · Drought stress · Tolerance strategy · Avoidance strategy

Abbreviations

C_p	Concentration of total phenolics
TNC	Total nonstructural carbohydrates
C_TNC	Concentration of total nonstructural carbohydrates
P_TNC	Pool of total nonstructural carbohydrates

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Introduction

Both climate change and human activity have significant effects on natural processes of terrestrial ecosystems. Climate change is a major force for community shifts, especially in arid and semi-arid areas (Brown et al. 1997; Yang et al. 2011). Moreover, human activity is a major force shaping the composition and structure of plant communities throughout the world (Garnier et al. 2007; Kohyani et al. 2009; Wan et al. 2011). For example, human activities caused sandy desertification to expand in northern China, where the total desertification area exceeded 350,000 km^2 by the mid-1990s (Tao and Wei 1999). In fact, the effects of climate change and human activity always interact in natural environments—thus the effect of human activity may be much more serious under conditions of climate change (Distel et al. 1996; Loeser et al. 2007). Responding to a combination of various intensities of stress and disturbance, plants have evolved toward particular strategies expressed in distinctive combinations of biological characteristics (Grime 2002; Kühner and Kleyer 2008; Sonnier et al. 2010). Research on adaptive strategies utilized by plants in response to climate change and human activity has drawn much attention from community and restoration ecologists (Walther et al. 2002; Cleland et al. 2007; Cingolani et al. 2005).

Plant species can be divided into those sensitive to physical damage (i.e., are unprotected and unable to regrow) and those that are resistant. Resistant species include plants utilizing avoidance strategies (e.g., defense) and plants utilizing tolerance strategies (Briske 1986; Belsky et al. 1993; Zheng et al. 2010, 2011). The preference of either avoidance or tolerance strategy can be explained by species' net photosynthesis production allocation patterns. Species utilizing avoidance prefer investment of net photosynthetic production in defense compounds (e.g., total phenolics) to deter herbivores, while species utilizing tolerance prefer investment in storage compounds (e.g., total nonstructural carbohydrates; TNC), and species using tolerance strategy do not prevent disturbance but compensate for damage (Archer and Tieszen 1986; Imaji and Seiwa 2010).

In response to recent climate change and human activity, *Stipa grandis* communities were replaced by *S. krylovii* communities in the Inner Mongolia steppe of China. *S. grandis* and *S. krylovii* are two dominant species in the Inner Mongolia steppe, a semi-arid area in northern China *S. grandis* occupies relatively moist and fertile habitats, whereas *S. krylovii* occupies dry and infertile habitats. Many empirical studies have shown that dominant species determine the structure and composition of the community and maintain community productivity (Walther et al. 2002; Smith and Knapp 2003; Beierkuhnlein et al. 2011), so study of dominant species could partially explain the community replacement phenomenon. Previous studies of the replacement of the *S. grandis* community by the *S. krylovii* community have focused on comparison between *S. grandis* and *S. krylovii* for nitrogen (N) economy, leaf traits, and karyotypes in natural habitats (Wu et al. 2009; Yuan et al. 2005, 2006; Jia et al. 2010). Few studies have explained their differential responses to climate change (e.g., drought stress) and human activity (e.g., grazing)—except for adaptive responses to polyethylene glycol-induced osmotic stress in a common garden experiment between the two species (Wang et al. 2005). In the present study, we examined the growth (including aboveground biomass and root biomass) and carbohydrate allocation pattern (including C_p and P_{TNC}) of *S. grandis* and *S. krylovii* under treatments of defoliation and drought stress in controlled conditions. Specifically, we expected that (1) *S. krylovii* would perform better than *S. grandis* in response to drought stress and defoliation, and this would indicate growth superiority shift from *S. grandis* to *S. krylovii*; and (2) *S. grandis* would utilize avoidance strategy, and *S. krylovii* would utilize tolerance strategies in response to defoliation under drought stress, which would further result in the growth superiority shift between the two species.

Materials and methods

Species

S. grandis and *S. krylovii*, two perennial C$_3$ tussock grasses, are the most widely distributed grasses and dominate the landscape of the vast semi-arid area of the Inner Mongolia steppe, China. Both species start to expand their leaves in mid-May, and their aboveground parts die completely from autumn to next early spring. *S. grandis* can grow to almost 1 m tall at the peak time of the growing season (late August), whereas *S. krylovii* is slightly shorter. *S. grandis* is the dominant species of the steppe in central Asia, and the *S. grandis* community is the main climatic climax of the typical temperate steppe area. The *S. krylovii* community is on the west side of *S. grandis* community and is the zonal formation of the typical steppe and part of desert steppe.

Experimental design

The experiment was carried out at the experimental site of Nankai University (39.10° N, 117.16° E) in Tianjin, China. The mean annual precipitation and temperature were 550–680 mm and 12.3 °C, respectively, with most rainfall during summer and highest temperatures in July and early August. In addition, photosynthetically available radiation varied between 600 and 1,800 μmol m^{-2} s^{-1}.

Seeds were collected from communities dominated by *S. grandis* and *S. krylovii* in the Inner Mongolia steppe in autumn 2007. The seeds were sown in plastic pots that were filled with vermiculite on January 20, 2010. Seedlings were watered to ensure optimum growing conditions, thus avoiding serious mortality. On June 12, 2010, 60 healthy seedlings (mean tiller number of 8.53 ± 0.43 and 8.98 ± 0.47 per plant for *S. grandis* and *S. krylovii*, respectively) were chosen from each species and planted with one seedling per pot (20 × 21 cm). Soil fertility in the pots was similar and soil organic matter, availability of N, and phosphorus were 40, 3, and 0.6 g kg^{-1}, respectively. All plots were placed in a shed outdoors with a transparent ceiling to allow sunlight, but not rainfall, to pass through.

We used a three-way factorial design with species and two environmental treatments which included two levels of drought stress (i.e., no drought and drought stress) and two levels of defoliation (i.e., no defoliation and defoliation twice). No-drought (normally watered) plants received 300 mL water every 3 days, while plants under drought stress received 75 mL water every 5 days. Defoliation was simulated by clipping the aboveground parts with scissors to a height of 5 cm, and clipping was performed at the end of July and at the end of August, 2010. Clipped biomass was not added to the final aboveground biomass. Each treatment was performed with 15 replicates, and all pots were randomly positioned. During the experiment, shading, fertility stress, and light stress were avoided, and regular weeding and insect control were conducted. The experiment ran for 143 days and was terminated on December 6, 2010.

Measurements and data analysis

On December 5, 2010, 4–5 green leaves per plant were clipped and freeze-dried for determination of total phenolics. On December 6, 2010, each plant was excavated and washed carefully, and then transported to the laboratory in a polyethylene box with ice in it. In the laboratory, plants were separated into roots, green leaves, and brown leaves; then the respective biomass was recorded after 0.5 h at 105 °C and then 72 h at 80 °C in an oven. The dried roots were used for determination of TNC.

The total phenolic concentration of leaves (C_p) was determined by visible spectrophotometry (Waterman and Mole 1994), and C_p was used to evaluate a plant's investment in defense. The concentration of total TNC (C_{TNC}) in roots was determined using an enzymatic hydrolysis method with the modification of substituting Teles' reagent with dinitrosalicylic acid (Silveira et al. 1978). Underground organs are the major storage region for carbohydrate reserves (White 1973), so the pool of TNC in roots (P_{TNC}) was used to evaluate plant investment in storage. In the present study, P_{TNC} was a product of C_{TNC} and dry root biomass.

Similar to Suding et al. (2003), we quantified the effect of each treatment (drought or defoliation) with a natural-log-transformed response ratio: $\ln RR_{tolerance} = \ln(\text{Performance}_{\text{stress condition}}/\text{Performance}_{\text{non-stress condition}})$. $\ln RR_{Dr}$ and $\ln RR_{De}$ indicated the effect of drought stress and defoliation, respectively. Values of lnRR are symmetric around 0, so that positive values indicate a positive effect of the treatment and negative values indicate a negative effect.

Response to drought stress and defoliation between the two species was analyzed using one-way ANOVA. Response to drought stress was assessed by comparing the $\ln RR_{Dr}$ of all variables without defoliation, and response to defoliation was assessed by comparing all variables with and without drought stress, respectively. The overall effect of drought stress and defoliation was analyzed using general linear models (GLM), with $\ln RR_{De}$ as dependent variables, and drought stress and species as fixed factors. A significant main effect of species indicated a distinct response level to defoliation. A significant interaction between species and drought indicated a change of response level between no-drought and drought treatments. A significant main effect of drought stress indicated a difference in response between no-drought and drought stress. All statistical analyses were conducted using SPSS 16.0 for Windows (SPSS Inc., Chicago, IL).

Results

All variables were negatively affected by defoliation and drought stress except for C_p. There was an significant interaction between defoliation and drought stress for all variables, and this interaction had different effects between the two species for all the variables except for P_{TNC}. Aboveground biomass and carbon-based compounds were significantly different between the two species (Table 1).

The $\ln RR_{Dr}$ of *S. grandis* and that of *S. krylovii* were negative for aboveground biomass, root biomass and P_{TNC}, indicating that water was an important limiting resource for both species (Fig. 1). However, *S. grandis* and *S. krylovii* differed significantly in their responses to drought stress ($P < 0.05$). The growth (aboveground biomass and root biomass) and the P_{TNC} of *S. krylovii* were much more negatively affected than those of *S. grandis* by drought stress. The C_p of *S. grandis* was negatively affected by drought stress, while that of *S. krylovii* was positively affected by drought stress.

The $\ln RR_{De}$ of *S. grandis* and *S. krylovii* differed for no-drought and drought treatments, indicating the importance of defoliation for growth of both species and the interaction between drought stress and defoliation (Figs. 2, 3). Root biomass of *S. krylovii* was more negatively affected by defoliation, and its investment in defense (C_p) was facilitated by defoliation under no-drought treatment. Growth of *S. krylovii* was positively affected by defoliation, and its investment in defense (C_p) was negatively affected by defoliation under drought stress. In contrast, growth of *S. grandis* was negatively affected by defoliation, and its investment in defense was facilitated by defoliation under drought stress.

Drought stress had significant effects on $\ln RR_{De}$ of *S. grandis* and *S. krylovii* for both growth and carbon allocation patterns (Table 2; Fig. 4). When each species was exposed to a normal water regime and a drought-stress regime, there was a distinct response level between the two species biomass production, which changed from response equivalence (aboveground biomass) or *S. grandis* being superior (root biomass) to *S. krylovii* being superior; a weak level was formed for the $\ln RR_{De}$ of C_p, changing from *S. krylovii* being superior to *S. grandis* being superior. Response of P_{TNC} to defoliation showed a reverse pattern (Fig. 4).

Discussion

The interaction of drought stress with grazing has been widely studied, and drought stress was thought to reinforce the negative effect of grazing (Heitschmidt et al. 1999, 2005; Teague et al. 2004). Loeser et al. (2007) proposed that episodic drought interacted with grazing, leading to infrequent but biologically important shifts in plant communities. The present study showed that drought stress reinforced species'

Table 1 Results (*F* statistics and *P* value) of the general linear model testing for effect of defoliation, drought, species, and their interactions on different growth variables (aboveground and root biomass) and carbon-based compounds (C_p and P_{TNC}) for *S. grandis* and *S. krylovii* (*De* defoliation, *Dr* drought and *Sp* species)

Experimental parameters	Aboveground biomass		Root biomass		C_p		P_{TNC}	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Defoliation	38.320	0.000	30.460	0.000	0.008	0.928	5.943	0.019
Drought	55.367	0.000	18.907	0.000	0.224	0.638	5.489	0.024
Species	8.478	0.005	0.827	0.366	10.536	0.002	6.194	0.017
De × Dr	36.242	0.000	30.599	0.000	6.912	0.012	7.366	0.010
De × Sp	1.464	0.229	0.050	0.823	1.128	0.295	4.424	0.042
Dr × Sp	3.719	0.057	3.510	0.064	3.396	0.073	1.388	0.246
De × Dr × Sp	5.434	0.022	11.377	0.001	16.815	0.000	0.092	0.763

Fig. 1 Results of ANOVA for the response ratio of *S. grandis* and *S. krylovii* to the drought treatment ($\ln RR_{Dr}$) calculated from **a** aboveground biomass, **b** root biomass, **c** C_p , and **d** P_{TNC} (data are means and SE)

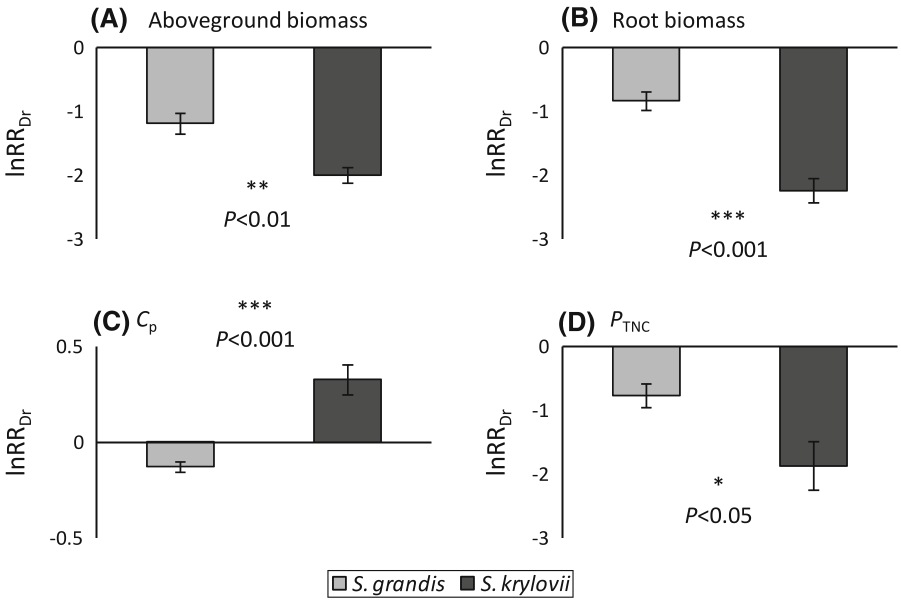
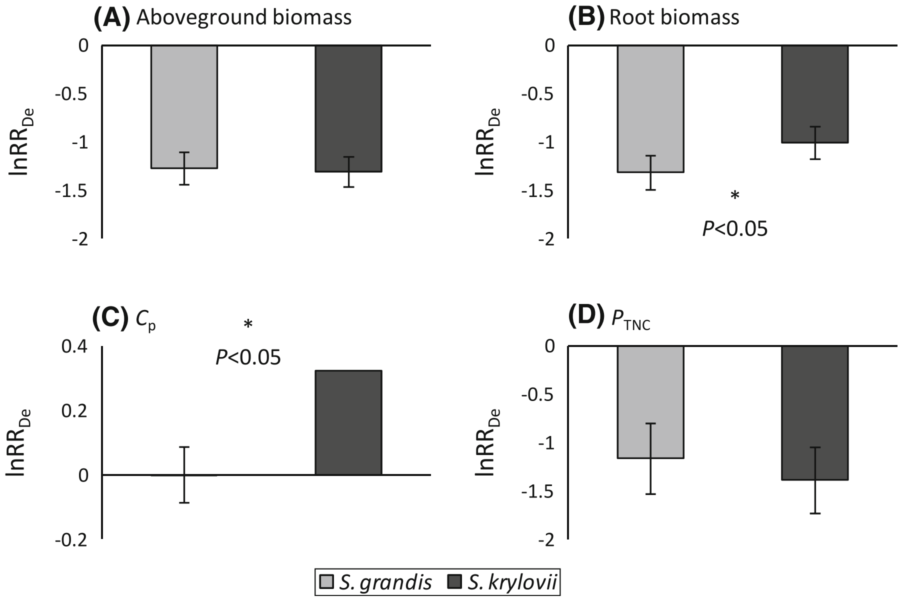


Fig. 2 Results of ANOVA for the response ratio of *S. grandis* and *S. krylovii* to the defoliation treatment ($\ln RR_{De}$) under no drought treatment calculated from **a** aboveground biomass, **b** root biomass, **c** C_p, and **d** P_{TNC} (data are means and SE)



responses to defoliation. Responses to drought stress or defoliation in relatively moist areas did not change the growth superiority of *S. grandis* (Figs. 1, 2); however, the defoliation response level changed, and *S. krylovii* showed superior growth when each species was exposed to a normal water regime and a drought stress regime (Table 2; Figs. 3, 4). This indicated that different response strategies to disturbance were used by *S. grandis* and *S. krylovii*. Good regrowth ability after damage implies utilization of tolerance strategies of a species and is widely defined as compensatory growth (Strauss and Agrawal 1999; Fornoni 2011). Compensatory growth could lessen the effect of damage and is an alternative or supplement to plant defenses, enabling the plant to tolerate disturbance (Meijden et al. 1988; Lehtila and Syrjanen 1995). The superior growth response ratio ($\ln RR_{De}$) of *S. krylovii* indicated its utilization of a tolerance strategy.

In arid and semi-arid areas, species' tolerance to climate change and human activity plays an important

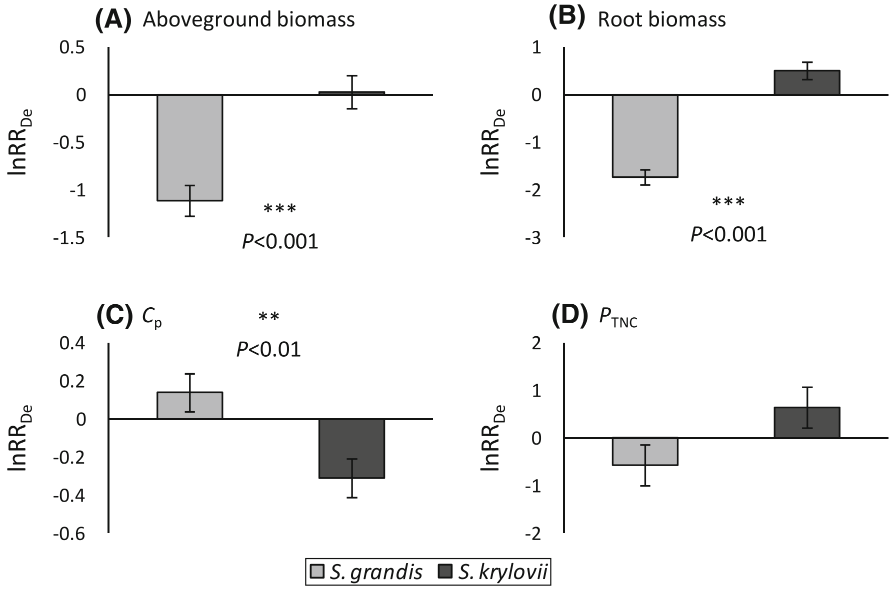


Fig. 3 Results of ANOVA for the response ratio of *S. grandis* and *S. krylovii* to the defoliation treatment (lnRR$_{De}$) under drought treatment calculated from **a** aboveground biomass, **b** root biomass, **c** C_p, and **d** P_{TNC} (data are means and SE)

Table 2 Results (*F* statistics and *P* value) of general linear model testing for the response ratio of *S. grandis* and *S. krylovii* to defoliation (lnRR$_{De}$) calculated from aboveground biomass, root biomass, C_p and P_{TNC}

Source of variation	lnRR$_{De}$, from aboveground biomass		lnRR$_{De}$, from Root biomass		lnRR$_{De}$, from C_p		lnRR$_{De}$, from P_{TNC}	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Drought	20.578	0.000	54.917	0.000	7.180	0.014	11.094	0.003
Species	11.307	0.001	10.123	0.002	0.469	0.501	1.592	0.221
Dr × Sp	12.837	0.001	31.475	0.000	17.372	0.000	3.331	0.082

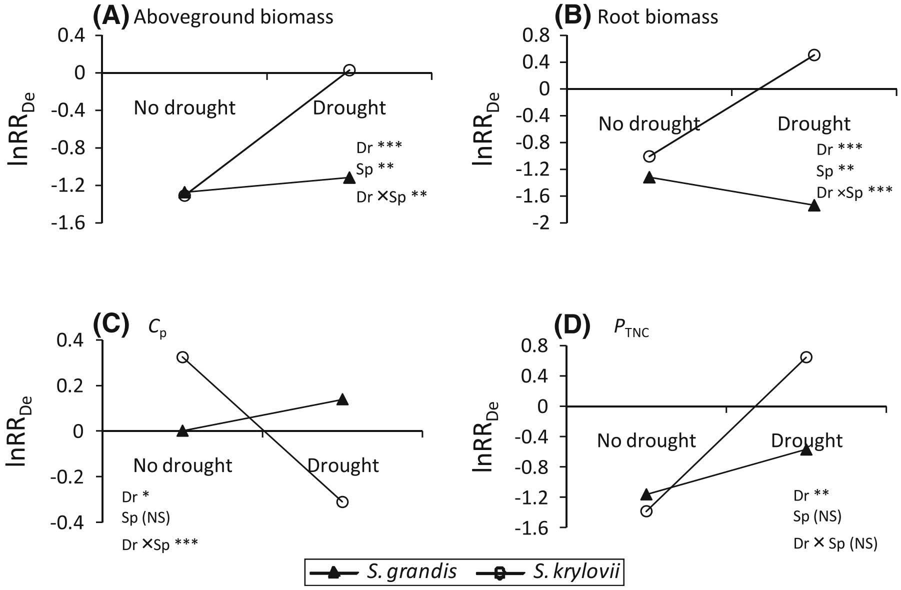


Fig. 4 Results of general linear model testing for the response ratio of *S. grandis* and *S. krylovii* to defoliation (lnRR$_{De}$) calculated from aboveground biomass, root biomass, C_p and P_{TNC}

role in plant distribution and abundance (Crawley 1990; Burt-Smith et al. 2003; Del-Val and Crawley 2005; Williamson and Wardle 2007). Previous studies have shown that species dominant in drier and nutrient-poor sites were generally more stress tolerant than species dominant in mesic and fertile environments (Mahmoud and Grime 1976; Wilson and Keddy 1986). In the present study, we showed that *S. krylovii* was stress tolerant and that its tolerance to defoliation ensured its dominance in response to climate change and human activity. Consistent with our conclusion, Corcket et al. (2003) found that survival of dominant species from a relatively drier habitat (*Bromus erectus*) was not affected by drought stress, while the survival of dominant species from a relatively moister habitat (*Brachypodium pinnatum*) was significantly decreased in response to drought stress.

We observed a trade-off between defense and tolerance investment. Concentration of defense compounds in leaves usually indicates plant quality for herbivores and pathogens (Koricheva 1999) and is useful in evaluating a plant's defense ability against herbivores (Imaji and Seiwa 2010). Carbon storage plays a particularly important role in plant regrowth after a period of inactivity or in recovery after disturbance (Chapin et al. 1990; Heilmeier and Monson 1994), and TNC level provides an estimate of the amount of energy available for plant growth (Marquis et al. 1997). In response to defoliation, *S. grandis* increased investment in defense compounds and decreased investment in storage; however, *S. krylovii* showed the opposite preference of investment when each species was exposed to a normally watered treatment and a drought stress treatment (Fig. 4). Increased tolerance of a plant involves a pre-existing high level of carbon storage in roots for allocation to aboveground reproduction (Strauss and Agrawal 1999). Considering the significant difference in regrowth between the two species, relatively higher investment in TNC was acceptable for *S. krylovii* after defoliation under drought stress. The biased allocation of net photosynthesis production by species can be explained by optimal growth strategy (i.e., carbon acquisition strategy) in relation to the relative resource availability of habitats (Coley et al. 1985). Species originating from relatively mesic zones are thought to have higher growth advantages (e.g., higher resource acquisition ability and higher aboveground production) than species originating from relatively xeric zones (Grime 2002; Corcket et al. 2003). In the present study, different strategies between *S. grandis* and *S. krylovii* were related to their primary habitats. *S. grandis* is found in a relatively moist and fertile habitat, and use of a defense strategy enabled it to avoid herbivores, grow quickly and get a dominant position. The habitat of *S. krylovii* is relatively dry and infertile, so the use of a tolerance strategy ensured its ability to survive and recover from damage or poor conditions. Other researchers showed similar results. For example, Imaji and Seiwa (2010) found that shade-intolerant *Castanea* sp. preferentially invested more carbon in growth rather than defense because severe competition occurred for light in gaps. While shade-tolerant *Quercus* sp. preferentially invested more carbon in defense than in storage because damage from herbivores and pathogens was common in its habitat.

Climate change and human activity are the main driving forces of replacement between the *S. grandis* and *S. krylovii* communities. Compared with avoidance strategy, utilization of tolerance strategy in response to defoliation under drought stress facilitated growth of *S. krylovii*. Considering the importance of the dominant species to community structure, different response strategies to defoliation under drought stress partially determined the dominant position of *S. krylovii* in the degraded *S. grandis* communities. Studies on replacement phenomenon showed that the identity of the dominant species resulted in differences in productivity between disturbed and undisturbed areas (Altesor et al. 2005; Castro and Freitas 2009). However, the *S. grandis* steppe displayed better productivity and higher quality than the area occupied by *S. krylovii*. Therefore, bearing in mind the dry conditions of the Inner Mongolia steppe and the fact that the communities dominated by *S. grandis* do not support extensive grazing during drought while *S. krylovii* is rather robust to grazing during drought, to protect the *S. grandis* communities from being replaced by *S. krylovii* communities which are less productive and lower in quality for forage, grazing pressure should be maintained at a reasonable intensity in the former ecosystem.

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