

Competition between *Stipa grandis* and *Cleistogenes squarrosa*

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Abstract

Competitive strategy for resources between *Cleistogenes squarrosa* (Trin.) Keng which is a dominant species of grasslands degraded by moderate-heavy grazing, and *Stipa grandis* P. Smirnov, which is a dominant species of ungrazed communities, was studied using a replacement series method in a greenhouse. The knowledge would be helpful in managing grasslands and restoring the degraded *C. squarrosa* grassland. Although there was neither inter- nor intra-specific competition between the two species when no nutrients were added, intra-specific competition of *C. squarrosa* was observed and increased with increased nutrient availability and more sulfur (S) was allocated to the aboveground partition of the plant. Relative competitive ability of *C. squarrosa* was greater than that of *S. grandis* when nutrients were supplied regardless of S. There was no significant difference between shoot and root competition based on dry matter yields. However, root competition was significantly greater than that of shoot based on S uptake under all treatments. A significant interaction was not observed between shoot and root competition. Therefore, nutrients addition benefits the restoration of degraded grassland of *C. squarrosa*, which may not exclude *S. grandis*. Also productivity and forage quality of the community will be increased.

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1. Introduction

Cleistogenes squarrosa (Trin.) Keng is a short, perennial, C₄ bunchgrass, that is similar to blue grama *Bouteloua gracilis* (H.B.K.) Lag. Ex Griffiths in the mixed- and short-grass prairies of North America. Both have the same photosynthetic pathway and are resistant to grazing (Fair et al., 1999; Redmann et al., 1995; Wang and Wang, 2001). In the eastern confines of the *Stipa-Leymus* steppes of the Inner Mongolia, *C. squarrosa* often becomes co-dominants with *Leymus chinensis* (Trin.) Kitagawa and *Stipa* spp. (Chen et al., 2002; Li, 1989). Especially under moderate to heavy grazing where it is frequently a co-dominant species with

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Artemisia frigida Willd. and *Carex duriuscula* C.A. Mey (Wang et al., 2001a; Wang, 1992). Li et al. (1980) also reported that *C. squarrosa* is as part of the *Stipa grandis* P. Smirnov steppe along with *Koeleria cristata* Bertol., *Agropyron cristatum* (L.) Gaertn., *Artemisia* spp. and *Potentilla* spp. It remains active and productive in degraded grasslands because of its C₄ photosynthetic pathway, and grazing compensative mechanism (Chen et al., 2002; Wang and Wang, 2001; Wang et al., 2003a). However, few studies have examined how *C. squarrosa* grassland response to management (Chen et al., 2002). Nor is information available on intra-specific competition. This information is useful for the restoration of degraded steppe of the Inner Mongolia.

Community structure is thought to arise by internal biotic forces (competition) being constrained by abiotic environmental factors and the local history of species invasion into the community (Weiher et al., 1998). The challenge for the community ecologist is therefore to understand which combination of biotic and environmental factors are responsible for determining species co-existence within community (Campbell and Stafford-Smith, 1999). Sulfur (S) is a major plant nutrient and S deficiency has been reported worldwide (Schnug, 1998). S deficiency can impact animal performance (Spears et al., 1985; Tisdale, 1977), particularly sheep are more sensitive to S deficiency than cattle because of their requirement of S for wool production (Qi et al., 1992, 1994). S deficiency is also noted for grasslands in the Inner Mongolia steppe of China (Wang et al., 2001b, 2002a, b, 2003b), there have been few comparative studies of the S nutrition for a range species in either monocultures or mixtures (Wang et al., 2004). S deficiency is often associated with grass dominance (Gilbert and Shaw, 1981; Walker and Adams, 1958a, b); however, it is likely that nitrogen and other nutrients limit the growth of the grass and the responsiveness of the grass to S (Gilbert and Robson, 1984; Walker and Adams, 1958a; Wang et al., 2004). Hence, it is difficult to understand the effect of S on the botanical composition of rangeland plant communities.

Some reports argued that if root and shoot competition interacts in their effects on plant growth, then measuring the strength of one competition form will require their experimental separation (Cahill, 2002a, b). Shoot biomass is not a good proxy of root and total biomass responses when root/shoot allocation is difficult to determine and introduce errors (Cahill, 2002a; Zobel and Zobel, 2002). Therefore, if measurements are inaccurate then methods need to be developed to increase the accuracy of root biomass estimates, not abandon these estimates altogether (Zobel and Zobel, 2002). Different responses of above- and below-ground biomass may result in a situation where even a plant's response to full competition is observable only when root biomass has been taken into account (Cahill, 2002a; Moora and Zobel, 1996; Zobel and Zobel, 2002). The effects of nutrients and S supply on morphological characters (e.g. shoot height, numbers of leaf and tillers, root length, root radius and its surface area, ratio between shoot and root biomass) of *S. grandis* and *C. squarrosa* has been reported (Wang et al., 2004). We found that nutrients supply decreased significantly ratio of root to shoot dry matter (RRS) of *C. squarrosa* regardless of S, but the RRS of *S. grandis* was not affected by nutrients applied, indicating that photosynthesis is more allocated to root in infertility soils than in fertility soils and the competition for nutrient resources may stimulate root production (Wang et al., 2004). In present study we want to determine: (1) the effects of nutrients and S supply on competitive ability and intensity between *S. grandis* and *C. squarrosa*; (2) strategies of *S. grandis* and *C. squarrosa* in competition for S; and (3) whether root and shoot competition interacts in their effects on plant growth or not?

2. Materials and methods

2.1. Soil

A S-deficient top soil (0–20 cm) was collected in August 2000 from the Inner Mongolia Grassland Ecosystem Research Station, Chinese Academy of Sciences of China where is located at 43°37'N, 116°43'E most of which is more than 1000 m above sea level. The soil is a sandy chestnut soil (Chinese classification) and Calcic-orthic Aridisol to US Soil Taxonomy classification systems, respectively, which is the dominate type of soil in the Inner Mongolia Grasslands. Following air-drying at room temperature, the soil was screened through a 2-mm sieve. The chemical composition of the soil is given in Table 1.

Table 1
Chemical characteristics of the basaltic soil used in the study^a

Soil characteristics	Value
Clay content ($< 2 \mu\text{m}$)	8.6%
pH (soil:water 1:5)	7.6
Organic C	8.0 g kg ⁻¹
Total N	1.0 g kg ⁻¹
Free CaCO ₃	0.5 g kg ⁻¹
Ca(H ₂ PO ₄) ₂ -S	7.8 mg kg ⁻¹
P ₂ O ₅ -CAL	2.2 mg kg ⁻¹
Cu (0.43 M HNO ₃)	0.9 mg kg ⁻¹
Zn (0.43 M HNO ₃)	1.1 mg kg ⁻¹
Mn (DTPA)	4.2 mg kg ⁻¹
Water holding capacity (WHC)	0.31

^aAnalyses were performed by laboratories of Institute of Plant Nutrition and Soil Science, FAL, Germany in Braunschweig.

2.2. Pot experiment

The experiment was conducted at the greenhouse of Institute of Plant Nutrition and Soil Science, FAL, Braunschweig of Germany during the 2001 growing season. The equivalent of 0.7 kg oven-dried soil was put into seventy-five 1.4-liter plastic pots, each with a saucer to prevent drainage losses of nutrients. Treatments consisted of two rates of S addition: 0 and 28 mg S pot⁻¹ (denoted as T_1 and T_2) and each was three replications. S was applied as K₂SO₄. All pots received a basal dressing of 140 mg N (NH₄NO₃), 70 mg P (KH₂PO₄), 35 mg Mg (MgCl₂·6H₂O), 7 mg Mn (MnCl₂), 0.7 mg Cu (CuCl₂·2H₂O), 1.4 mg Zn (ZnCl₂) and 0.7 mg B (H₃BO₃). The disproportionate addition of K in different treatments was counter balanced by the addition of proportionate KCl to the pots. These were added to the soil as solutions and mixed thoroughly. The soil moisture content was raised to 70% of WHC by adding deionized water and was maintained approximately at this level by frequently weighing and adding deionized water during experiment. At the same time, blank treatment without any nutrients supply was designed with three replications (denoted as T_0).

Seeds of *S. grandis* and *C. squarrosa* were collected from the *S. grandis* community in September of 2000. Individual seeds were sown in a replacement series at an overall density of four plants per pot. Plants were sown in ratios (*S. grandis*:*C. squarrosa*) of 1:0, 0.75:0.25, 0.5:0.5, 0.25:0.75, 0:1 and put on the corner of 4-cm square. Each pot has four holes. Approximately, three seeds of the same species were sown in each hole in each pot. The plants were thinned to one per hole 3 days after seedling emergence so that individual plants were as homogenous in size as possible after thinning. Seedlings were thinned to leave four uniform plants per pot. The plant density was some 354 plants m⁻² which is greater than what occurs in field conditions in order to shorten the time required for competitive interaction among plants. The greenhouse conditions were kept at approximately 26/18 °C (day/night) with the light/dark times at 16/8 °C h each day. All pots were arranged by randomized block on trolley benches and the positions were rearranged every fortnight.

Shoots were harvested 80 days post emergence at the soil surface and dried to constant weight at 60 °C. Roots were removed by soaking the pots in a container filled with water and gently washed the soil from the roots. The water in the container was screened through a 0.5 mm sieve to avoid the loss of small roots. Roots were also dried to constant weight at 60 °C. Samples were analyzed for total concentrations of S by inductively coupled plasma-atomic emission spectrometry (ICP-AES).

2.3. Relative crowding coefficient

Competition between each species pair was analyzed using the model of de Wit (1960), where O_{ij} is the yield per pot of species *i* grown with species *j* in the proportions *u*: *v*, M_i and M_j are the respective monoculture yields per pot, and k_{ij} and k_{ji} are the respective relative crowding coefficients for one species towards the other.

The de Wit model may be written as described by Hill and Gleeson (1988):

$$O_{ij} = \frac{M_i k_{ij} u}{(k_{ij} - 1)u + 1}; \quad O_{ji} = \frac{M_j k_{ji} v}{(1 - k_{ji})u + k_{ij}}.$$

The relative crowding coefficients are taken as a measure of aggressiveness of one species towards another. Interest centers on the case $k_{ij} \times k_{ji} = 1$, when the species are considered to be excluding each other. When $k_{ij} \times k_{ji} \neq 1$, the species are said to be competing for the same resource. If $k_{ij} = 1$, there is a linear response in biomass yield of species i to the proportion it occupied in the mixture, and similarly for species j if $k_{ji} = 1$.

The relative yield total (RYT), i.e. the sum of the relative yields of species i and j , is given by:

$$(\text{RYT})_{ij} = \frac{O_{ij}}{M_i} + \frac{O_{ji}}{M_j}.$$

Parameters k_{ij} , k_{ji} , M_i and M_j are estimated using the maximum likelihood approach of Machin and Sanderson (1977). Likelihood ratio statistics provide approximate tests for $k_{ij} = 1/k_{ji} = 1$, for $k_{ij} = 1/k_{ji} \neq 1$ and for $k_{ij} \neq 1/k_{ji}$.

2.4. Competitive balance

The relative competitive ability of the components in mixtures is expressed by the “Competitive Balance Index” (C_b), defined as (Wilson, 1988):

$$C_b = \log_e \left(\frac{W_{ab}/W_{ba}}{W_{aa}/W_{bb}} \right),$$

where W is the dry weight per original planted plant; a and b are the two components (species/varieties) investigated; W_{aa} is the weight of component a in monoculture; W_{bb} is the weight of component b in monoculture; W_{ab} is the weight of a growing in association with b; W_{ba} is the weight of b growing in association with a. A C_b value of zero indicates no competition or equal competitive ability. Any other value indicates that one species has a higher competitive ability than the other.

2.5. Interaction between shoot competition and root competition

The appropriate way to combine two C_b values is by addition, so that the predicted C_b for full competition equals shoot C_b plus root C_b . Since the calculation includes logarithmic transformation, this is equivalent to a multiplicative model for the original dry weights. The predicted effect of full competition (estimated by C_b) can then be compared with that actually found. The interaction (I_b) is the actual C_b for full competition less the predicted C_b for full competition. A value of I_b greater than zero indicates positive interaction, a value less than zero indicates negative interaction (Wilson, 1988).

2.6. Statistics

SPSS statistical software was used for the statistical analysis in the study (SPSS, 1998). Analysis of variance (ANOVA) was performed using generalized linear model and curve fitting was used for multinomial regressions. When significant effects of S addition were detected, the one-way ANOVA procedure within SPSS was used. Least significance difference (LSD) between means was declared significant at $p < 0.05$.

3. Results

3.1. Inter- and intra-specific competition

Relative crowding coefficients suggested that there was no inter-competition between *S. grandis* and *C. squarrosa* regardless of whether based on shoot, root, total dry matter yield or S content per pot (product of S concentration and dry matter per pot) under all treatments because of low productivity (Figs. 1–3; Table 2).

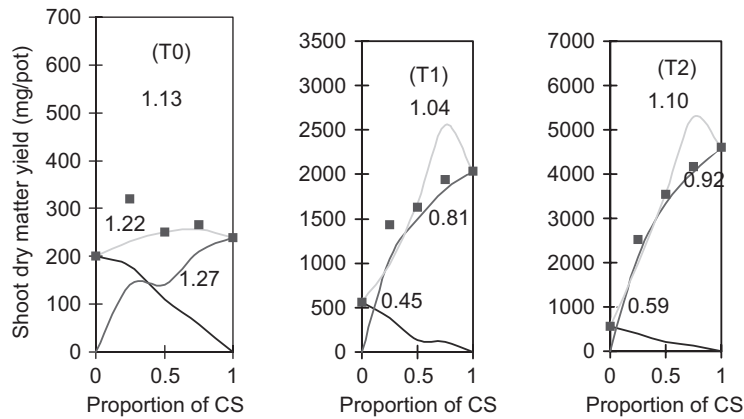


Fig. 1. Replacement diagrams for the *Stipa grandis* (SG)/*Cleistogenes squarrosa* (CS) experiment for shoot dry matter production 80 days after seedling emergence. Relative crowding coefficients measuring the competition power of SG relative to CS (k_{sg}) are given on the left-hand side of each diagram and for CS relative to SG (k_{cs}) on the right-hand side. The relative shoot yield totals ($k_{sg} \times k_{cs}$) are shown at the top of each diagram. Actual data for total combined shoot production from the two species are plotted as (■) to give an indication of how well the model fitted the data.

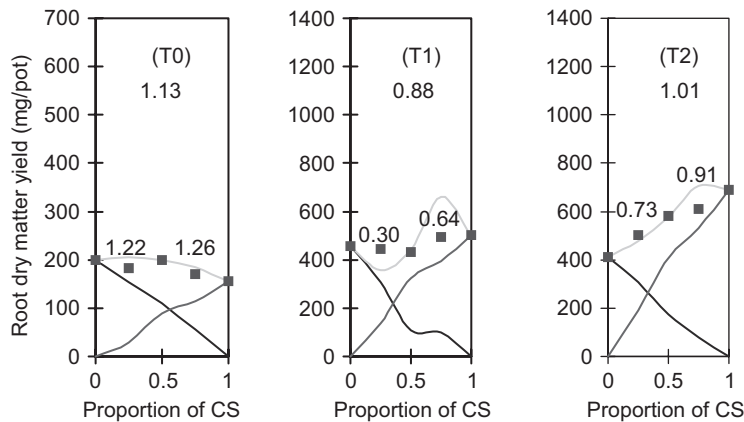


Fig. 2. Replacement diagrams for the *Stipa grandis* (SG)/*Cleistogenes squarrosa* (CS) experiment for root dry matter production 80 days after seedling emergence. Relative crowding coefficients measuring the competition power of SG relative to CS (k_{sg}) are given on the left-hand side of each diagram and for CS relative to SG (k_{cs}) on the right-hand side. The relative root yield totals ($k_{sg} \times k_{cs}$) are shown at the top of each diagram. Actual data for total combined shoot production from the two species are plotted as (■) to give an indication of how well the model fitted the data.

C. squarrosa was slightly dominant under T_0 treatment, and more dominant than *S. grandis* under T_1 and T_2 treatments (as indicated by a higher crowding coefficient, Figs. 1–3). Over-yielding of shoot dry matter ($k \neq 1/k \neq 1$, RYT > 1) occurred for all treatments, indicating that the two species in the mixture were not competing for the same environmental resources. However, under-yielding of root and total dry matter were observed for T_1 treatment, although the model did not appear to fit the data well (Figs. 1–3). Similar results were observed based on S contents per pot (Table 1), but *S. grandis* was slightly dominant in competition for root S uptake and total S uptake over *C. squarrosa* under the T_0 treatment.

The dry weight of *S. grandis* shoots and roots per plant were not significantly affected ($p > 0.05$) by its species proportions for all treatments except the 50% proportion at the T_1 treatment (Fig. 4), indicating that the intra- and inter-specific competition with *S. grandis* was small. However, the shoot dry matter yields of per *C. squarrosa* decreased significantly ($p < 0.05$) when its proportions increased in the mixed treatments for the T_1 and T_2 treatments (Fig. 4). In these cases, it reached the maximum at the 25% proportion of *C. squarrosa*

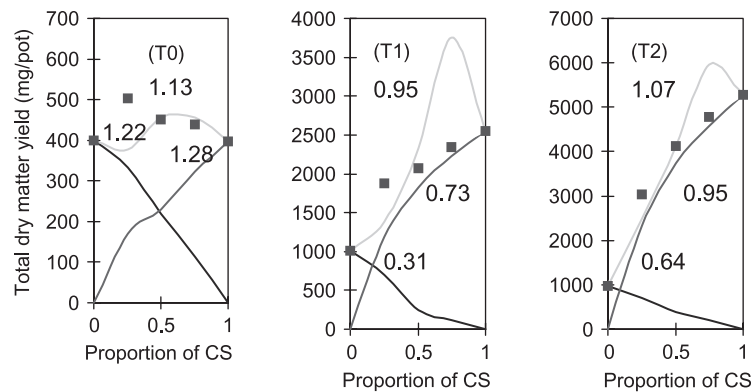


Fig. 3. Replacement diagrams for the *Stipa grandis* (SG)/*Cleistogenes squarrosa* (CS) experiment for total (shoot + root) dry matter production 80 days after seedling emergence. Relative crowding coefficients measuring the competition power of SG relative to CS (k_{sg}) are given on the left-hand side of each diagram and for CS relative to SG (k_{cs}) on the right-hand side. The relative total yields ($k_{sg} \times k_{cs}$) are shown at the top of each diagram. Actual data for total combined shoot production from the two species are plotted as (■) to give an indication of how well the model fitted the data.

Table 2

The fitted model, k_{ij} , k_{ji} , and RYT values, and the biological interpretation for each of the species and its competitor based on sulfur contents per pot

Treatment	Item	Fitted model	k_{ij}	k_{ji}	RYT	Interpretation
T_0	Shoot	$k \neq t \neq 1$	1.1	1.30	1.21	Over yielding
T_1	Shoot	$k \neq t \neq 1$	0.26	0.72	1.11	Over yielding
T_2	Shoot	$k \neq t \neq 1$	0.51	0.97	1.27	Over yielding
T_0	Root	$k \neq t \neq 1$	1.33	1.22	1.07	Over yielding
T_1	Root	$k \neq t \neq 1$	0.24	0.60	0.71	Under yielding
T_2	Root	$k \neq t \neq 1$	0.74	0.91	1.02	Over yielding
T_0	Full (shoot + root)	$k \neq t \neq 1$	1.25	1.18	1.20	Over yielding
T_1	Full (shoot + root)	$k \neq t \neq 1$	0.26	1.02	1.04	Over yielding
T_2	Full (shoot + root)	$k \neq t \neq 1$	0.59	3.61	1.24	Over yielding

Note: i: *Stipa grandis*; j: *Cleistogenes squarrosa*; k: k_{ij} ; t: $1/k_{ji}$.

and was approximately twice that of *C. squarrosa* monoculture, indicating that intra-specific competition was significant ($p < 0.05$) and that an interaction existed between S supply and the species proportions of *C. squarrosa* ($p < 0.05$). However, root dry matter yield of per *C. squarrosa* was not affected by its proportions across all treatments (Fig. 4), indicating that inter- and intra-specific root competition was small under all treatments.

There were no significant differences between mixture proportions and monoculture of *S. grandis* and *C. squarrosa* in shoot, root and total dry matter yields per pot under T_0 treatment; but under T_1 and T_2 treatments, the shoot and total dry matter yields per pot in the mixture proportions were greater than in the monoculture of *S. grandis* and less than in the monoculture of *C. squarrosa* except in the 25% *S. grandis* proportion (Fig. 5). The interactions between S supply and proportion of *C. squarrosa* were observed for dry weight of shoot, root and total per pot, respectively ($p < 0.05$).

3.2. Relative importance of shoot and root competition and interaction between shoot competition and root competition

Root competition had a significantly ($p < 0.05$) greater effect than shoot competition on the S content per pot under all treatments. However, it had a smaller effect than shoot competition based on dry weight per pot,

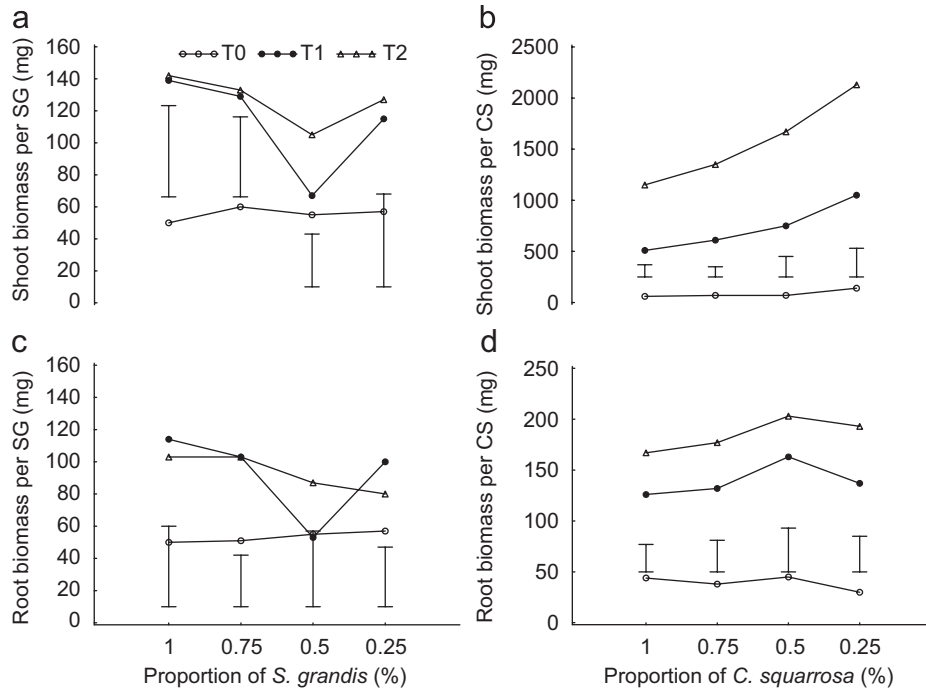


Fig. 4. The effect of nutrients added (T_0 : nothing added; T_1 : all nutrients added except S and T_2 : all nutrients with S) on dry matter yield of shoots and roots per plant. Vertical bars denote least significant differences at $p = 0.05$. SG: *Stipa grandis*. CS: *Cleistogenes squarrosa*.

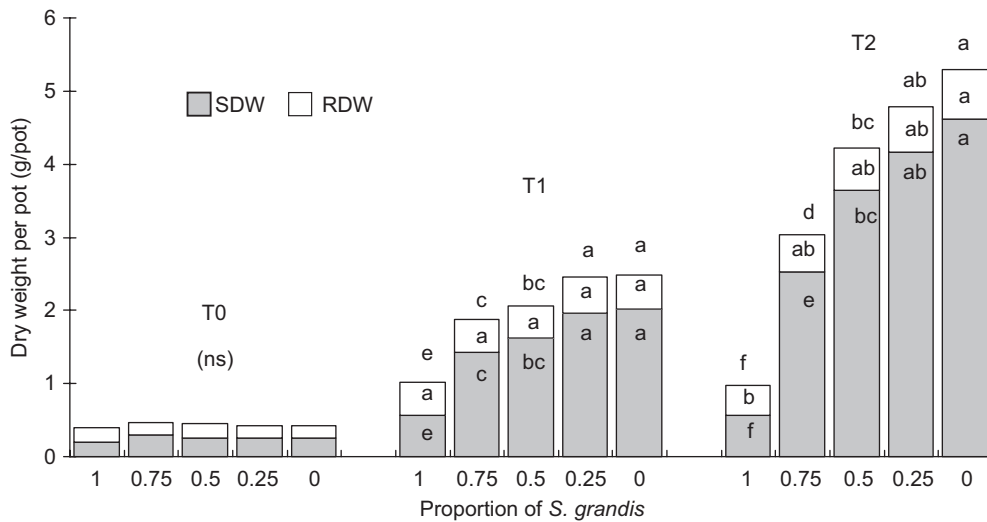


Fig. 5. The dry weight of shoot (SDW), root (RDW) and total (SDW + RDW) of *Stipa grandis*/Cleistogenes squarrosa replacement experiments under different treatments (T_0 , T_1 and T_2). T_0 : nothing added; T_1 : all nutrients added without S; T_2 : all nutrients added with S. Significant differences ($p < 0.05$) in dry weight between replacement series treatments were indicated by different letters in sections of histograms. NS: not significant ($p > 0.05$).

although the difference was not significant (Table 3). There tended to be negative interactions between shoot competition and root competition of both dry weight and S content per pot even though no significant ($p > 0.05$) (Table 4).

Table 3

The relative importance of shoot and root competition in dry weight and S content per pot for *C. squarrosa* as measured by the competitive balance index (C_b)

Item	Treatment	Shoot C_b	Root C_b	Root C_b less shoot C_b
Dry weight per pot	T_0	0.07	0.06	−0.01
	T_1	1.16	0.94	−0.22
	T_2	0.62	0.43	−0.19
S content per pot	T_0	0.20	1.52	1.32*
	T_1	−0.15	1.09	1.24*
	T_2	−0.14	1.43	1.57*

*Significant at 0.05 between root C_b and shoot C_b .

Table 4

The magnitudes of interactions between shoot competitive balance and root competitive balance (I_b)

Item	Treatment	Predicted C_b	Measured C_b	I_b^*
Dry weight per pot	T_0	0.14	0.06	−0.08
	T_1	2.10	1.13	−0.97
	T_2	1.05	0.59	−0.46
S content per pot	T_0	1.72	1.00	−0.72
	T_1	0.94	0.36	−0.58
	T_2	1.29	0.88	−0.41

*No significant ($p > 0.05$) between measured C_b and predicted C_b .

4. Discussion

Competition among species is important in determining species co-existence and the relative abundance of co-occurring species (Warren et al., 2002). Clements et al. (1929) considered that competition occurred for light, soil nutrients and water. *S. grandis* and *C. squarrosa* are two species that co-occur in the Inner Mongolia steppe (Chen et al., 2002; Li, 1989). Our study showed that there were no inter- or intra-specific competitions between *S. grandis* and *C. squarrosa* when nutrients are not added (T_0 treatment) (Fig. 5). Therefore, niche separation may be the mechanism of their co-existence in the natural community. However, *C. squarrosa* had greater competitive abilities than *S. grandis* when nutrients were added (T_1 and T_2 treatments) (Figs. 1–3; Table 2) probably because competition shifts to another resource (T_1 treatment—S deficiency), or because the addition of S did not remove its deficiency (shoot S concentration of *C. squarrosa* was even lower in the T_2 treatment than that of the T_0 treatment (data not shown)). We found that although *C. squarrosa* is called a short-grass, it can grow to 60 cm tall when nutrients and water were available (Wang et al., 2004), which is the same height as *S. grandis* under typical conditions. On the other hand, intra-specific competition of *C. squarrosa* was more intense than inter-specific competition when nutrients were added (Fig. 4). This indicates that intra-specific competition increases with an increase in nutrients availability. It may imply that *C. squarrosa* could not exclude *S. grandis* in the degraded grasslands dominated by *C. squarrosa* if nutrients were supplied. In contrast, it would lose its dominance because of density-dependent effects over time, which would benefit the restoration of degraded grassland of *C. squarrosa*.

Some researchers have recently debated whether we need full separation of above- and below-ground interactions among plants before we can accurately measure the relative importance of root and shoot competition (Cahill, 2002a, b; Wilson, 1988; Zobel and Zobel, 2002). Wilson (1988) reported that in 33 of 47 reported experiments root competition had a greater effect than shoot competition. Our study indicated that the root competition was the same as shoot competition when based on dry matter yield across all treatments. However, root competition was significantly greater ($p < 0.05$) than shoot competition when based on

S content under all treatments (Table 3). In previous debates about shoot and root competition attention was paid to light competition (dry matter yield), rather than competition for resource (e.g. S). There is a large difference between them because the relationship usually is negative between dry matter yield and nutrient concentration in the plant. For example, although increased nutrient supply (with S or without S, T_1 vs. T_2), increased shoot dry matter yield per plant of both species, their S concentration in shoots significantly decreased compared with T_0 treatment (data not shown). Therefore, nutrients without S supply will increase root competition for S which may decrease aboveground net primary productivity and S concentration.

The possibility of an interaction between above- and below-ground has long been considered (Clements et al., 1929; Wilson, 1988; Cahill, 1999). Wilson (1988) found that two-thirds of the cited 47 experiments in the greenhouse showed no interaction, whereas Cahill (1999) found that not only an interaction existed between above- and below-ground competition, but also the form of interaction varied with productivity, switching from no interaction in the unfertilized block to a positive one in the fertilized block. In our study, there were no interactions between above- and below-ground competition regardless of whether based on dry matter yields or S content per pot (Table 4). This shows that the above- and below-ground competition is additive. If we consider the root C_b based on S content per pot as competition for S resource, and shoot C_b as competition for light (Table 3), then we will find that there seems to exist a trade-off in the ability of plants to compete for soil resources and light, and the total strength of competition (shoot C_b of dry weight + root C_b of S content) remain steady (the sum of T_0 , T_1 and T_2 treatments was 1.59, 2.25 and 2.05, respectively) due to a shift from root to shoot competition with increased resource availability and plant productivity. This was consistent with studies by Newman (1973) and Tilman (1988). Therefore, our study shows that shoot biomass may be a sufficient proxy for root and total biomass because the relationship was significantly linear ($p < 0.001$) between shoot and root biomass or S content under all treatments.

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