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Germination ecology of Central Asian *Stipa* spp: differences among species, seed provenances, and the importance of field studies

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Abstract *Stipa*-species are wide-spread in Central Asia, but sexual reproduction in the dry steppes is rare. To facilitate conservation and restoration of these important rangelands, we studied germination characteristics of three common Mongolian *Stipa*-species under field- and lab conditions. Seeds of *Stipa krylovii*, *Stipa gobica* and *Stipa glareosa* were sown at the study site in Southern Mongolia over two consecutive years during which period tests were carried out to ascertain whether competition or herbivory are the main constraints of seedling establishment. In addition, we tested germination and seed viability in the laboratory under two different temperature regimes (20/10°C and 8/4°C), as well as the effect of cold-stratification. The lab experiments also included *S. krylovii* seeds originating from three climatically different provenances. None of the three *Stipa*-species seedlings emerged during the first 2 years of the field study. However, after an unusually intense rain event in the third year, 3% of *S. krylovii*, 0.6% of *S. glareosa* and 0.1% of *S. gobica* seeds germinated in the study plots. The factors 'sowing-year' and 'vegetation' significantly affected seedling emergence, whereas grazing had no effect at all. Under laboratory conditions a high percentage of viable seeds of *S. gobica* and *S. glareosa* germinated at both incubation temperatures, and cold-stratification had no effect on germination or viability. Germination of *S. krylovii* seeds required warmer temperatures and cold-stratification had a positive effect. Such evidence for dormancy was more pronounced in seeds from the moister, northern provenances. Germination of *Stipa*-species in the field is rare and only possible under exceptionally moist conditions. Conservation should thus concentrate on steppe conservation rather than on restoration. Where artificial reseeding is necessary, differences among species and also among different seed provenances should be taken into account.

Keywords Dormancy · Mongolia · Restoration · Seed viability · Steppe · Stratification

Introduction

There is an ongoing discussion as to whether pastures in southern Mongolia are degraded or not, but degradation certainly is less severe than in the adjacent parts of the Chinese Gobi (Sneath 1998), where extensive restoration schemes have been initiated that involved aerial seeding of pioneer species (Qi 1998; Zheng et al. 2003). Grazing in Mongolia is nonetheless intense, and there is evidence of increasing degradation, at least in northern and central regions (Hilbig and Opp 2005; Miklayeva et al. 2005; Sasaki et al. 2005). The

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restoration of degraded Central Asian steppes has been hampered due to the fact that natural sexual reproduction is rare in most of the dominant perennial species (Lavrenko and Karamysheva 1993). This lack of reproduction may either be due to ubiquitous grazing (Retzer et al. 2006), or to harsh climate.

Germination studies are important for gaining information on the effects of seed storage, pretreatments, the optimal conditions for seed germination and the influence of seed provenance, all of which are crucial for conservation and restoration programmes. Results of lab studies are indispensable, but are of limited practical relevance where they are not validated by results obtained from field studies. Moreover, germination is only one stage in the life cycle, and only a small fraction of seedlings will actually establish under field conditions due to the influence of competition and grazing. Eventhough the above-ground vegetation cover is low in arid environments, belowground biomass is usually denser in order to ensure sufficient water and nutrient uptake (Clark and Woodmansee 1992; Casper and Jackson 1997). Thus, establishment might be dependant on disturbances and gaps, where the root-competition is reduced. In Mongolia at least modest grazing is omnipresent, even in protected areas, and is a possible factor in the creation of such gaps, however, it can also harm plants due to biomass reduction (van Staalduinen and Anten 2005). Surrounding vegetation on the other hand can also facilitate establishment by providing safe sites (Holmgren et al. 1997).

Stipa-species are especially relevant to restoration studies because they represent an exceptionally large proportion of the Eurasian zonal vegetation (Lavrenko and Karamysheva 1993). Several studies on reproduction of *Stipa*-species have been undertaken in order to elucidate the influence of, e.g. phenology (especially flowering characteristics; Brown 1952; Ponomarev 1961), the effect of the hygroscopic awn (Ghermandi 1995; Schöning et al. 2004), dispersal efficiency (Haase et al. 1995; Hensen and Müller 1997), and dormancy and germination (e.g. Fulbright et al. 1983; White and Van Auken 1996; Gasque and Garcia-Fayos 2003; Boeken et al. 2004). Most of these studies are from western Eurasia, while Central Asian *Stipa*-species have mainly been studied in terms of ecophysiology (Yuan et al. 2006; Cheng et al. 2007) and genetic structure (Wang et al. 2006). Data on germination ecology are still limited but suggest that *Stipa* spp. differ from other Central Asian species (Wesche et al. 2006). Differences among seed provenances have not been tested at all, and are also ignored in restoration schemes carried out with other Central Asian plant species. However, species with a wide distribution range often show differences in germination characteristics depending on seed provenance (e.g. Keller and Kollmann 1999; Fenner and Thompson 2005), thus, especially for *Stipa krylovii* with a distribution range covering different climatic zones, some differences could be expected.

In the present study, we investigated germination and establishment of three *Stipa*-species typical of the dry southern Mongolian mountain steppes and semi-deserts (*S. krylovii, Stipa gobica, Stipa glareosa*; Wesche et al. 2005a; von Wehrden et al. 2006) in their natural environment and in the lab; and we also analysed longevity of caryopses (hereafter referred to as seeds) in the field and after dry storage. Specifically, we addressed the following questions: Are *Stipa* seeds able to survive the harsh Mongolian winter in the soil? Is their establishment constrained by herbivore pressure or by competition? What are the optimum temperatures for germination, and does cold-stratification influence germination? Do different seed provenances of *S. krylovii* differ in their temperature requirements or effects of cold-stratification on germination?

Material and methods

Study species and sites

S. krylovii Roshev. (*Stipa* section—*Leiostipa*, Poaceae) is distributed in Mongolia, China, Kazakhstan and Russia. In Mongolia (Gubanov 1996; Wu and Raven 2006), it inhabits a wide macroclimatic gradient from the central Mongolian meadow steppes to the southern dry mountain steppes. Its phenology is highly dependant on rainfall. In an average year, flowers pollinate in July and seeds mature in August; with southern populations starting their reproductive cycle earlier than the northern populations (Ronnenberg, unpublished data). Moreover individuals in northern, moister populations grow higher and more vigorously. The distribution range of *S. gobica* Roshev. (section—*Stipa*) is restricted to the dry mountain steppes and semi-deserts of southern Mongolia and northern China (Wu and Raven 2006). Flowering usually takes place in June; seed dispersal in July. *S. glareosa* P. Smirn. (section—*Stipa*) occupies the driest sites of the three species. Its distribution range includes Middle Asia with Kazakhstan, Afghanistan, Kyrgyzstan, but also Siberia, Mongolia and China (Wu and Raven 2006). Flowering and seed dispersal are usually completed by the end of June. At dry sites, populations of all three species, but especially *S. glareosa* and *S. gobica*, form relatively low inflorescences, attaining 25–35 cm in height. They are typical bunchgrasses (caespitose hemicryptophytes) and clonal spread is restricted to the immediate vicinity due to forced separation of tufts, making them highly dependant on sexual reproduction.

The main site for seed collecting and field studies was the Dund Saykhan mountain range situated in the Gobi Gurvan Saykhan National Park, southern Mongolia (Fig. 1) at an altitude of 2,300 m asl. (N 43°36.76; E 103°46.36). This region receives an estimated 180 mm mean annual precipitation, with 160 mm falling in the summer months (Table 1). The vegetation period usually begins in May or June with the onset of the summer rains and ceases at the end of September with dropping temperatures. Mean winter temperatures are around –9.9°C; mean summer temperatures are 10.9°C. Soils are degraded chestnut soils with a water retaining capacity of 12–25% by weight (Ronnenberg, unpublished data).

The two other sites (Fig. 1) were chosen with respect to the presence of *S. krylovii*-dominated vegetation, geographical position and mean annual precipitation. The "Khangay sampling site" is located at the western edge of the Khangay mountains (N 45°55.42; E 102°46.37) at 1,700 m asl. It receives some 255 mm mean annual precipitation (Table 1) and has a mean winter temperature of –8.9°C and a mean summer temperature of 10.9°C. The dominant soil-types are chestnut soils with a water-retaining capacity of 14–20% by weight. The "Khentey sampling site" is situated in the westernmost outposts of the Khentey mountains (N 48°15.43; E 106°33.23) at an altitude of 1,500 m asl. Here, *S. krylovii* is a dominant species of the plains and south-facing slopes. On the moister, northerly exposures and at higher elevations, *Larix sibirica* forests and other more humidity-demanding communities replace the steppes (Hilbig et al. 2004). Mean winter temperatures are lower than at the two other sites (Table 1), while mean annual precipitation is slightly higher (270 mm). Soils are chernozems with a water-retaining capacity of often more than 40% by weight. Thus, even though mean precipitation is almost equal to the Khangay site, we assume that the water stress experienced by the plants is more severe at the latter site, because soils dry up much faster after rainfall. Differences in winter temperatures should be of limited importance as pollination and seed maturation of *S. krylovii* are finished before temperatures drop.

Methods

Seeds of the three *Stipa*-species were collected in 2003, 2004 and 2005 in the Gobi Gurvan Saykhan National Park. *S. gobica* and *S. krylovii* were collected in the mountain ranges and the upper pediments of the Dund Saykhan (N 43°36.76; E 103°46.36). Inflorescences were rare due to the omnipresent livestock grazing. Thus, most seeds were collected from safe sites such as livestock-exclosures or on hardly accessible rocks. Inflorescences of both species were completely cleistogamous in 2005. In the moister years of 2003 and 2004 some flowers opened for pollination, but the ratio was not quantified. *S. glareosa* inflorescences were also very rare and were mainly found on the lower

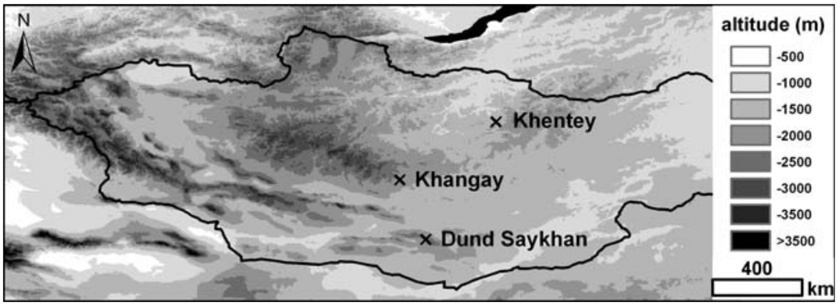

Fig. 1 Topographical map of Mongolia showing the three sampling sites (Draft: Henrik von Wehrden)

Table 1 Key-characteristics of the climate in the three study regions (mean values, extrapolated data, Hijmans et al. 2005; summer: April–September, winter: October–March)

	Precipitation (mm)		Temperature (°C)		
	Annual total	Summer total	Annual mean	Winter mean	Summer mean
Dund Saykhan	180	160	0.9	–9.9	10.9
Khangay	255	220	1.6	–8.9	10.9
Khentey	270	250	–2.0	–17.7	10.6

piedmont region at a small oasis (Bayan Bag; N 43°29.40 E 103°42.9). The plants grew in the surroundings of vegetable gardens, which were regularly watered, but no further amelioration or fertilization measures were applied. Thus, the site was presumably favoured in respect to moisture availability; here, most inflorescences apparently flowered chasmogamously. In 2005, *S. krylovii* seeds were also collected in the two moister regions of Khangay and Khentey for use in the lab study.

Winter survival and seedling occurrence in the field

In 2003 and 2004, three batches containing 50 seeds of *S. krylovii* and 50 seeds of *S. glareosa* were wrapped in nylon socks and buried at the Dund Saykhan field station at a soil depth of 5 cm (the number of collected *S. gobica* seeds was too low to carry out this experiment). At the beginning of the following vegetation period (2004 and 2005) seeds were excavated and viability was tested with a TTC test (Baskin and Baskin 2001) directly in the field.

In the same years (2003 and 2004), and from the same batches of seeds, we started a sowing experiment to test whether competition or herbivory are the main constraints for seedling establishment. In a block-design (five replicates), we divided each plot into four 0.15 m^2 sections which were subjected to the following treatments: (a) above- and below-ground vegetation removed, sub-plot covered by a grazing cage; (b) above- and below-ground vegetation removed, without cage; (c) original vegetation maintained and covered by a cage; (d) original vegetation maintained, without cage (control). For *S. krylovii* and *S. glareosa,* we sowed 100 seeds at a depth of approx. 0.5 cm on each subplot, for *S. gobica*—due to the lack of seeds—we could only use 50 seeds each. Seeds of all three species were sown directly after seed maturation of *S. krylovii* in the middle of August in both years. We prepared separate sub-plots for each species and each year. In the years 2004 and 2005, we monitored the plots every 7–10 days from the middle of June to the end of August. In 2006, we only checked plots at the end of August.

In August 2005, 50 freshly collected seeds of all three study species were put in Petri dishes (5 replicates) and exposed to ambient temperature- and light conditions (mean measured air temperatures at that time were 19°C/day and 15°C/night), but were kept constantly moist with water from the nearest well. After 20 days the test was terminated and ungerminated seeds were subjected to a TTC-test. Germination of all three species did not differ from results obtained some 6 months later in the lab at 20/10°C for 20 days (U-test, $P > 0.6$). Thus, dry storage had no influence on germination and results from the lab-study (described below) should be comparable to germination under ambient temperature and light conditions.

Effects of temperature and cold-stratification

In January 2006, 35 seeds per Petri-dish (6 replicates) were incubated for 54 days on filter paper moistened with deionised water. Two different temperature-regimes were applied (20/10°C and 8/4°C, each at 12 h warm white light/12 h darkness). For cold-stratification, another batch of Petri dishes was wrapped in tinfoil to prevent germination and stored in a cold climate chamber (8/4°C). Because in situ temperatures rise and drop quickly in spring and autumn, stratification was terminated after 10 days; the tin-foil was removed and the dishes were incubated in the same way as an unstratified control-group (20/10°C). Dishes were checked three times a week and germinated seeds were removed.

All tests were terminated after 54 days and were followed by TTC viability-tests. Germination was expressed in reference to the presumed number of viable seeds (i.e. excluding those that were unviable according to final TTC-tests, see Baskin and Baskin 2001). In November 2006, the viability of seeds (3 × 20) stored in the lab at about 20°C was reassessed. Again, mean seed viability did not differ from the test carried out in August 2005 (U-test; $P > 0.3$ for all three species, see above).

Statistics

In the sowing experiment, the factors 'cage' and 'vegetation' were crossed and year of sowing and block were integrated as random factors in a multifactorial ANOVA. Analyses were conducted separately for *S. krylovii* and *S. glareosa* with raw numbers of the germinated seedlings in 2006. Seedling numbers in *S. gobica* were too low to conduct any meaningful calculations.

Germination data from Petri dishes were expressed as percentages of viable seeds to facilitate comparison between species and regions (see recommendations by Baskin and Baskin 2001). Data were arcsine square-root transformed and separate Two-Way ANOVAs were calculated to assess the effects of temperature, stratification and provenance (only *S. krylovii*) on germination of the species. Subsequent Tukey post-hoc tests revealed potential differences between species and provenances. The results of the viability tests were analysed in the same manner. All statistics were carried out with SPSS 12.0 (SPSSInc. 2003).

Results

Winter survival and seedling occurrence in the field

All buried seeds of *S. glareosa* and 90.8% of *S. krylovii* seeds lost their viability between 2003 and 2004 (Table 2). Survival of seeds collected in 2004 was slightly higher, because in 2005, 29% and 45% respectively were still viable.

In the first 3 years, none of the seeds sown in 2003 or 2004 produced seedlings on the establishment-plots. However, after two days of exceptionally heavy rain in 2006 (36 mm and 20 mm), seedlings of all three study species started to emerge. At the end of August, a total of 4 seedlings of *S. krylovii* appeared, equalling 0.2% of those sown in 2003, while 62 of those sown in 2004 emerged (3.1%; Table 3). The factors 'year' and 'vegetation' had a significant effect on emergence ($P = 0.026$; $P = 0.006$; Table 4a), whereas the effects of 'block', 'cage' and 'cage × vegetation' were not significant ($P > 0.2$). Seedling emergences of *S. glareosa* were 0.1% and 0.55% respectively; and the factors 'vegetation' and 'year' had significant ($P = 0.023$), or marginally significant effects ($P = 0.059$; Table 4b). Seed germination rates of *S. gobica* were 0.0% (2003) and 0.1% (2004).

Effects of temperature and cold stratification

At 20/10°C both *S. glareosa* and *S. gobica* started to germinate on the fifth day of incubation, and 90% germination was reached after 10 and 15 days respectively. *S. krylovii* germinated slower starting after 10 days and reaching 90% after 34 days of incubation. At 8/4°C, germination was considerably delayed in all study species (Fig. 2a), and none of the species reached 90% germination within 54 days.

Temperature had a significant effect on total germination ($P < 0.001$). All three species germinated to higher percentages at 20/10°C (Fig. 2a), but effects were more pronounced in *S. krylovii* ('species × temperature' interaction $P < 0.001$). The species terms were highly significant in tests of both total germination and seed viability ($P < 0.001$). Overall seed viability was also affected by germination at different temperatures ($P = 0.023$), and incubation under cold conditions decreased viability in *S. krylovii* and *S. glareosa*, while the effect was the opposite in *S. gobica* (interaction term $P < 0.001$; Fig. 3a).

Cold-stratification had no effect on seed viability ($P = 0.336$, Table 5b) in any of the species (interaction $P = 0.807$; Fig. 3b), but it accelerated germination (Fig. 2b). Final germination was only raised in *S. krylovii*, whereas *S. gobica* and *S. glareosa* germinated to almost 100% regardless of the stratification (Fig. 2b). Accordingly, we found a significant interaction between the factors 'stratification × species' ($P = 0.035$; Table 5b).

Seed provenance of *S. krylovii* ($P < 0.001$) had a strong effect, both on germination and on seed

Table 2 Viability of seeds collected in 2003 and 2004 'before' burying, and their loss in viability 'after' 1 year in the soil (mean and standard deviation, $n = 3 \times 50$ for each species)

	2003			2004		
	% before	% after	% loss	% before	% after	% loss
Stipa krylovii	51 ± 15.1	4.7 ± 4.6	90.8	75 ± 13.1	45 ± 2.6	40.0
Stipa glareosa	56 ± 9.4	0	100.0	61 ± 5.3	29 ± 6.3	52.5

Table 3 Number of seedlings encountered in August 2006 on the experimental plots sown in 2003 and 2004; with the treatments: nCnV—no cage, no vegetation; CnV—cage, no vegetation; nCV—no cage but vegetation; CV—cage and vegetation present

Treatment	Year of sowing	*S. krylovii*	*S. gobica*	*S. glareosa*
∑nCnV	2003	2	0	0
∑CnV		2	0	2
∑nCV		0	0	0
∑CV		0	0	0
∑nCnV	2004	33	1	5
∑CnV		19	0	5
∑nCV		5	0	1
∑CV		5	0	0
Total	2003	4	0	2
Total	2004	62	1	11

viability in both treatments (Table 5c). At 8/4°C, only one seed from each region emerged (Fig. 4a). However, at 20/10°C moderately high germination rates were reached in all three provenances (Fig. 4a). Temperatures affected final germination, but effects differed between the Dund Saykhan and the two moister provenances ('provenance × temperature' interaction, $P < 0.001$; Table 5c). The response of seed viability differed among provenances (interaction term $P = 0.005$): Viability was low after cold incubation for seeds collected in Dund Saykhan and Khentey, while there was no influence on seed viability of those collected in Khangay (Fig. 5a).

Assessed over all provenances, cold-stratification again did not affect seed viability ($P = 0.140$; Table 5d, Fig. 5b), but did improve final germination. This effect was stronger in seeds from the northern provenances ('species × provenance' interaction $P = 0.031$; Table 5d). Seedling emergence for the southern provenances started earlier than for the Khentey provenance (Fig. 4b). Stratification increased germination in seeds from the Khentey and Khangay regions by more than 20% (absolute), while this increase was only 6% for seeds from the Dund Saykhan.

Discussion

Our study proves that sexual reproduction of *Stipa*-species is rare in southern Mongolia, but nonetheless possible under certain conditions. In the years 2003, 2004 and 2005 we did not observe a single seedling, neither in the natural steppe nor in any of the plots artificially sown in 2003 and 2004. However, at the

Table 4 ANOVA-table of the establishment experiment showing the effect of the factors 'cage—i.e. grazing exclusion', 'vegetation—i.e. removal of the above- and belowground vegetation', 'year of sowing (2003 and 2004)' and the 'block' on seedling occurrence of *Stipa krylovii* (a) and *S. glareosa* (b)

Source	df	Mean sum of squares	F	*P*	df	Mean sum of squares	F	*P*
(a) *S. krylovii*					(b) *S. glareosa*			
Cage	1	4.900	0.508	0.481	1	0.025	0.047	0.829
Vegetation	1	52.900	5.486	0.026	1	3.025	5.744	0.023
Cage × vegetation	1	4.900	0.508	0.481	1	0.225	0.427	0.518
Year	1	84.100	8.721	0.006	1	2.025	3.845	0.059
Block	4	14.338	1.487	0.23	4	0.288	0.546	0.703
Error	31	9.644			31	0.527		

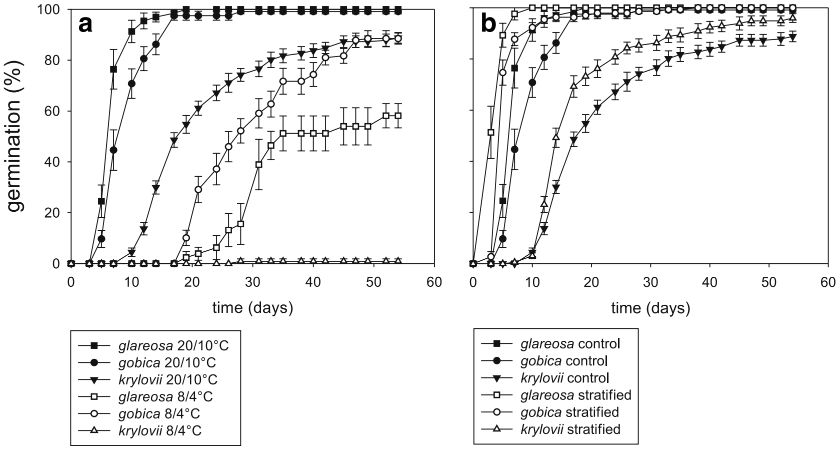

Fig. 2 Germination of three *Stipa*-species at 20/10°C and 8/4°C (**a**); and behaviour of cold-stratified seeds incubated at 20/10°C (**b**). All three species germinated significantly differently at $P < 0.001$ (Tukey-test) in the temperature treatment; but after moist chilling, only *S. krylovii* differed significantly (Tukey-test $P < 0.001$) from both *S. gobica* and *S. glareosa*

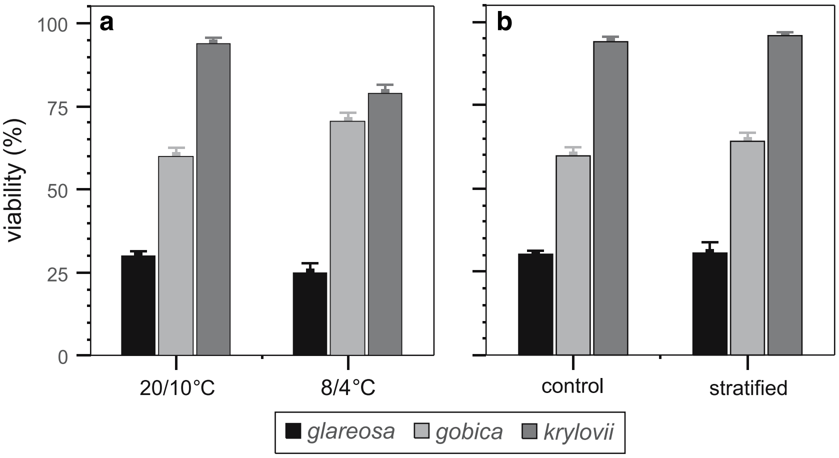

Fig. 3 Overall seed viability of three *Stipa*-species following the end of the germination experiment at 20/10°C and 8/4°C (**a**); and behaviour of cold-stratified seeds incubated at 20/10°C (**b**). In both experiments, seed viability was significantly different for all three species (Tukey-test $P < 0.001$)

end of August 2006, a total number of 66 seedlings of *S. krylovii* and 13 of *S. glareosa* were recorded; four and two of which, respectively, originated from seeds sown in 2003. Thus, some seeds survive a minimum of up to 3 years in the soil. In contrast, *S. gobica* produced only one seedling of a seed sown in 2004. Data for *S. gobica* are not sufficient to draw definite conclusions, but point to an, at most, short-term persistent soil seed bank; which has been described for other grass species before (Thompson et al. 1993).

A number of grass species with awns are capable of becoming readily anchored and germinating quickly at the soil surface (Peart 1984). Regarding *S. speciosa*, Ghermandi (1995) demonstrated that the hygroscopic awn effectively drills the seed into the ground leading to accelerated germination. Thus, the morphology of *Stipa*-seeds seems to be optimised for fast germination, as opposed to building up a long-term persistent soil seed bank. However, Zhan et al. (2007) describe the presence of *S. krylovii* in the soil seed banks of Inner Mongolian (northern Chinese) grasslands. Our data imply the presence of a rather short-term persistent seed bank, indicated by the low ratio of seeds surviving the winter in the soil (5–45% of *S. krylovii* seeds and 0-29% of *S. glareosa* seeds). These values are slightly higher than that, but are still comparable to results obtained for *S. tenacissima* in south-eastern Spain (Gasque and Garcia-Fayos 2003).

Seedling emergence was significantly higher on plots where above- and below-ground vegetation had been removed. Thus, lack of competition seems to favour emergence during the early stages of the life cycle. This, is in line with other studies from semi-arid regions where below-ground competition had a pronounced effect on seedling establishment

Table 5 ANOVA-tables of the germination experiments showing the effects of the study species (a, b; *Stipa glareosa, S. gobica, S. krylovii*), different temperatures (a, c; 20/10°C and 8/4°C), seed provenances of *S. krylovii* (c, d; Khentey, Khangay, Dund Saykhan) and cold stratification (b, d; control, moist chilling) on germination and seed viability

Source	Germination				Viability			
	df	Mean of squares	F	*P*	df	Mean of squares	F	*P*
(a) Species & temperature-effects								
Species	2	1.869	305.64	<0.001	2	1.362	206.48	<0.001
Temperature	1	4.707	769.68	<0.001	1	0.038	5.79	0.023
Species × temp.	2	0.704	115.11	<0.001	2	0.101	15.26	<0.001
Error	30	0.006			30	0.007		
Sum	36				36			
(b) Species & stratification-effects								
Species	2	0.206	40.00	<0.001	2	1.869	250.12	<0.001
Stratification	1	0.037	7.21	0.012	1	0.007	0.96	0.336
Species × strat.	2	0.019	3.74	0.035	2	0.002	0.22	0.807
Error	30	0.005			30	0.007		
Sum	36				36			
(c) Provenances & temperature-effects								
Provenances	2	0.119	13.44	<0.001	2	0.317	26.30	<0.001
Temperature	1	9.172	1037.27	<0.001	1	0.194	16.05	<0.001
Prov. × temp.	2	0.109	12.33	<0.001	2	0.077	6.36	0.005
Error	30	0.009			30	0.012		
Sum	36				36			
(d) Provenances & stratification-effects								
Povenances	2	0.356	40.75	<0.001	2	0.386	33.55	<0.001
Stratification	1	0.649	74.27	<0.001	1	0.026	2.30	0.140
Prov. × strat.	2	0.034	3.89	0.031	2	0.002	0.14	0.869
Error	30	0.009			30	0.011		
Sum	36				36			

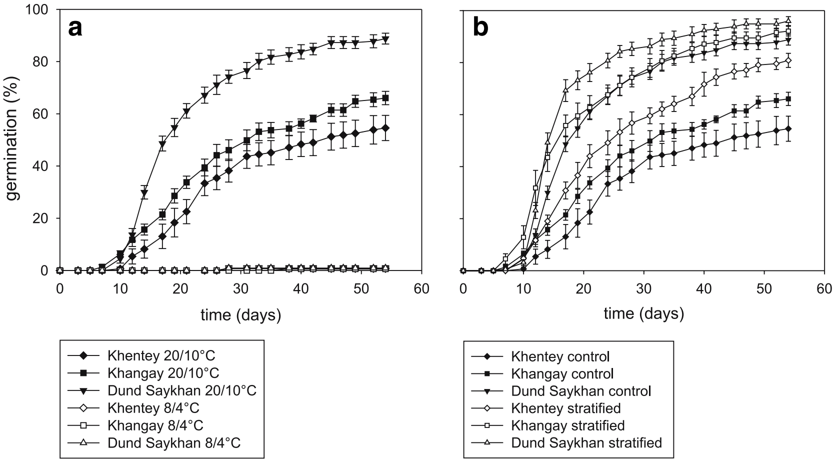

Fig. 4 Germination of *S. krylovii* from three different regions at 20/10°C and 8/4°C (**a**), and behaviour of cold-stratified seeds incubated at 20/10°C (**b**). Germination of seeds from the Dund Saykhan differs significantly from the other two regions at different temperatures (Tukey-test $P < 0.01$)

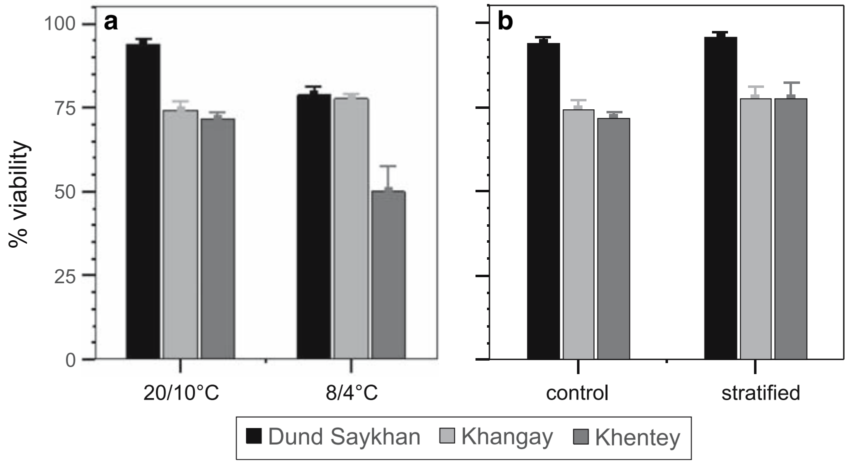

Fig. 5 Overall seed viability of *S. krylovii* from three different regions after the end of the germination experiment at 20/10°C and 8/4°C (**a**); and behaviour of cold-stratified seeds incubated at 20/10°C (**b**). All three regions differ significantly at a level of $P < 0.01$ for the temperature treatment (**a**); and the Dund Saykhan differs at $P < 0.001$ for the stratification treatment (**b**)

(McPherson 1993; Casper and Jackson 1997). More surprisingly, in the Dund Saykhan, herbivore exclusion exerted no influence. This could theoretically be an artefact, as spring and early summer 2006 were very dry, and herders had, by then, left the area. As a result, grazing pressure by livestock had been unusually low. However, wild ungulates were still there and small mammals were abundant. In 2005, we could actually prove a negative effect of herbivores on the establishment of *Ulmus pumila* and *S. glareosa* seedlings in an establishment experiment on irrigated plots (Chuluunkhuyag Oyundari, unpubl. master thesis).

Of all three study species, *S. krylovii* showed the highest probability of surviving in the soil over the winter. Its seeds usually mature relatively late in the summer, whereas the seeds of the other two species ripen in June–July. Especially *S. glareosa* seeds, which disperse by the end of June, could germinate before the summer actually starts. This corresponds well to the germination characteristics of the three species. At higher temperatures, which are typical for the summer months, *S. gobica* and *S. glareosa* germinate readily. Almost 100% of the seeds of *S. gobica* and *S. glareosa* had germinated at 20/10°C after approximately 2 weeks, indicating that germination in the field may well be completed in the summer of dispersal. *S. krylovii* germinated much slower and radicle emergence continued until the test was terminated after 54 days. Extending the experiment further seemed to be of limited practical relevance due to the dry conditions prevailing at the site after the summer rains stopped in autumn. At 8/4°C, *S. krylovii* was almost completely incapable of germination, whereas the two species from the section *Stipa* finally germinated. Thus, *S. krylovii* is unlikely to germinate in late summer or autumn. Likewise for the other species, the capability of germinating under cold conditions will be of limited importance. By that time autumn temperatures are down to 8/4°C, low moisture levels in the field most probably enforce seed quiescence. This has been described for other perennials of dry Central Asian steppes before (Huang and Gutterman 2003; Zheng et al. 2004; Wesche et al. 2006; Ronnenberg et al. 2007).

In all three geographical regions, *S. krylovii* seeds disperse at a time when the chance of moisture levels being relatively high is likely. Thus, there is a theoretical risk that some seeds will germinate just before the winter, exposing the young seedlings to harsh climatic conditions. However, germination characteristics seem to prevent this. At least some rain is necessary for the hygroscopic mechanism of the awn to operate (Ghermandi 1995), so seed burial is likely to be less effective under dry conditions. Moreover, germination of *S. krylovii* is a slow process—not all seeds germinate after a single rain event, and increasingly colder temperatures render germination in late summer or autumn impossible. Finally, *S. krylovii* showed some evidence of dormancy and the ratio of dormant to non-dormant seeds was higher in the moister northern populations, where the risk of untimely germination is higher.

After we terminated the experiment, 10% from the Dund Saykhan and around 40% (corrected numbers) from the northern regions had not germinated.

Although the difference is rather small, this result is remarkable as dormancy is typical of temperate grasslands, including North American prairies (Baskin and Baskin 2001), but rare in the Central Asian semi-deserts (Wesche et al. 2006). The fact that the macroclimate is more mesic in the northern regions suggests that *S. krylovii* undergoes a change in its germination strategy, which parallels with the macroclimatic gradient. It remains to be tested whether dormancy is indeed more common in the moister meadow steppes of central and northern Mongolia than in the dryer southern regions. Moreover, whether differences in germination characteristics originate from maternal or genetic causes is an unsolved question.

The present study demonstrates that temperature is an important factor for germination. We did not experimentally assess the importance of other potential triggers, but field observations suggest that the amount of rain and length of the period of increased soil humidity are also decisive. We have recorded summer precipitation since 2001 and, until 2006, never had totals of more than 20 mm on a single event. On July 17th 2006, a rainfall event yielding more than 36 mm moistened the soil deeply and triggered emergence. In the following 10 days another 39 mm fell, preventing the soil from drying out. Thus, exceptionally heavy rains seem to trigger germination, which has also been described for other dryland regions (Ackerman 1979; Bowers 1994, 1996; Gutterman and Gozlan 1998).

At a value of about 90%, overall seed viability of *S. krylovii* was relatively high in 2005. Seed viability in both *S. gobica* (60%) and *S. glareosa* (30%) was clearly lower. These values are, for all three species, comparable to the seed viability of freshly harvested seeds assessed in 2005 (confer Ronnenberg et al. 2006). Hence the actual magnitude of the effect seems to reflect annual fluctuations more than a response to germination treatments. Surprisingly, seed viability of *S. krylovii* was highest in the driest habitat. This is in line with observations by Ronnenberg et al. (2006), who revealed a general trend of decreasing seed viability in *S. krylovii* with increasing water availability. A possible mechanism lies in the flowering pattern: The ratio of chasmogamous to cleistogamous flowers in *Stipa*-species is known to increase with higher soil moisture content (Brown 1952; Ponomarev 1961), and seed viability was reported to be lower in chasmogamous seeds of *Stipa leucotricha* compared to cleistogamous seeds (Call and Spoonts 1989). This remains to be tested, but we suspect that the low seed viability of *S. glareosa* seeds was related to the relatively moist situations at the sampling site (oasis, see above), which presumably caused flowers to open.

Implications for management and conservation

Sexual reproduction of the *Stipa*-species is apparently constrained by several factors. The harsh climate is certainly a major aspect, which renders *Stipa*-steppes in southern Mongolia vulnerable in the sense that recovery of degraded stages would presumably be difficult and slow. It is known for the shrub *Juniperus sabina* growing in the higher mountain ranges in the study area (Wesche et al. 2005b) that sexual recruitment is practically impossible under current conditions. Nonetheless, stands are able to persist over extended periods of time by vegetative growth. Given their life form, *Stipa*-species should also be able to survive unfavourable periods and reproduce only in more favourable years. This is supported by Lavrenko and Karamysheva (1993), who reported that sexual reproduction of *S. gobica* takes place in time spans of 7–10 years.

There is little doubt that sexual reproduction of *Stipa*-species is also limited by the low number of seeds. In average years, both shoots and inflorescences are almost completely grazed (Wesche et al. 2007; Wesche et al. in prep.). Moreover, *S. krylovii* seeds are known to decrease in weight and number with increasing grazing pressure (Li et al. 1997; Bai et al. 1999). However, despite high grazing pressure in Northern China, viable seeds were still found in soil samples of *S. glareosa* (Ren et al. 2002), as well as *S. krylovii* (Zhan et al. 2007).

At present, southern Mongolian *Stipa* plant communities are not explicitly threatened, but continued intensive grazing may result in a lack of sexual reproduction (Wesche et al. in prep.). Thus, at least temporary exclusion of herbivores (mainly livestock) would be an option to support natural seed production. For actual reseeding programmes of *S. krylovii*, we recommend storing seeds at room temperature and stratifying them for a few weeks under dark, cold and moist conditions. Obviously it would be advisable, albeit perhaps unfeasible, to sow the seeds after heavy rain. For the other two species, no special treatments are required. They may be sown directly after maturation without any treatment, although it would also be possible to store them at room temperature for a year or even longer. We have demonstrated that provenances of *S. krylovii* from moister, northern regions are more suitably adapted for the prevention of potentially fatal autumn germination. Taking seed provenance into account and the consequent use of local seeds are aspects that have not received much attention in current restoration schemes, but should be considered in future.

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