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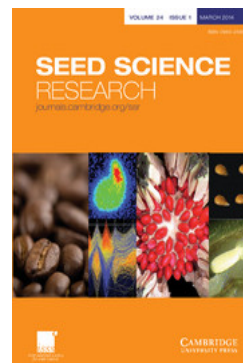
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Germination of fresh and frost-treated seeds from dry Central Asian steppes

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Abstract

We tested the germination of fresh and frost-treated seeds of 26 species of southern Mongolian mountain and desert steppes, covering the major growth forms of woody and herbaceous perennials and short-lived species in the region. In the field, germination depends on rains that are largely restricted to the summer months between June and August. Thus, germination tests were performed at alternating conditions of 10°C in darkness and 20°C in light (12h/12h), which correspond to temperatures at the study site in early and late summer. Seeds of both woody and herbaceous perennials germinated well under the chosen conditions and apparently did not require stratification or scarification. In contrast, germination of annual species was mostly below 30%, while seed viability was equally high in all three growth forms. Winter conditions, simulated by freezing dried seeds at –18°C, hardly changed seed germination in the perennial species, but several short-lived species responded with increased germination. Short-lived species are not abundant in the real vegetation, which is governed by perennials. Thus, we conclude that the important species in Mongolian mountain steppes germinate readily without a dormancy-breaking treatment. A review of the available literature revealed that a complete lack of dormancy, or presence of only conditional dormancy, is also widely described for other species of Central Asian deserts and steppes, which is in contrast to data from North American prairies.

Keywords: China, climate, dormancy, germination, Mongolia, steppe

Introduction

As seed dormancy is one of the main strategies ensuring suitable timing of germination with respect to favourable climatic conditions, relationships between dormancy and *in situ* climatic conditions are still a major focus in seed ecology (Fenner and Thompson, 2005). The importance of various types of dormancy and non-dormancy differs among seed-bearing plants from the major climatic regions of the globe (Baskin and Baskin, 1998): while species with non-dormant seeds dominate in the tropics, physiological dormancy appears to be common in mid-latitude steppes or woodlands. In the latter, seeds often require a period of cold stratification or warm stratification/after-ripening that prevents them from germinating directly after dispersal in summer and autumn, thus avoiding high seedling mortality under the relatively harsh winter conditions. Physiological dormancy is apparently also widespread throughout the cold deserts of the northern hemisphere.

The amount of available information on germination strategies varies widely for each of the major geographical regions. Seed germination is well studied for hot deserts (e.g. Gutterman, 1993), but data on cold drylands are much more limited. Most studies come from North America, while information on Eurasian deserts and semi-deserts is less readily available. Seeds of species from western and Middle Eurasia have been studied extensively, although most data were published in Russian (summarized by Nikolaeva *et al.*, 1985; Nikolaeva, 2001; Baskin and Baskin, 2004). Some information was gathered during the restoration of desertified Middle Asian grasslands, e.g. Kazakhstan (Babaev, 1999; Tursunov *et al.*, 1999), but until recently, little data were available for the Central Asian drylands of Mongolia and northern China. This has changed tremendously in the past few years, with large-scale land restoration projects being initiated in desertified steppes of northern China (e.g. Katoh *et al.*, 1998; Zhang *et al.*, 2005), triggering research on germination characteristics of species

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commonly used for artificial sowing in restoration projects. However, as steppes in China are heavily degraded, most research has concentrated on species of the earlier successional stages suitable for stabilizing bare soils, e.g. *Artemisia sphaerocephala* (Huang and Gutterman, 2000; Zheng *et al.*, 2004c; Nie and Zheng, 2005), or on species of saline soils (Tobe *et al.*, 2000a, b, 2002). In contrast, only a few true grassland species have been tested, e.g. *Leymus chinensis* (Liu *et al.*, 2004). Information on population ecology and germination of species growing in (Outer) Mongolian grasslands and deserts is still very limited (Lavrenko and Karamysheva, 1993), although pastures there are still comparatively intact (Sneath, 1998).

The vegetation of mid-latitude prairies and desert grasslands in North America is physiognomically similar to that of Central Asia. Baskin and Baskin (1998) summarized the information available and concluded that about 10% of grassland species produce non-dormant seeds, and the incidence of non-dormancy was virtually zero in cold deserts. In both types of drylands, physiological dormancy is the prevailing germination strategy (Baskin and Baskin, 1998). Hardly any data for Central Asia were available for this review; however, differences in elevations and climate provide enough grounds to expect differences in germination strategies. Central Asian steppes and deserts are usually situated at comparatively high elevations; almost 85% of the Mongolian terrain lies above 1000 m above sea level (asl) (Barthel, 1990). Seasonal temperature fluctuations are less extreme in North America, and thermal conditions allow for a longer growth period. In consequence, limits of total annual precipitation on short-grass steppes (300–550 mm) (Lauenroth and Milchunas, 1992) and desert grasslands (230–600 mm) (Schmutz *et al.*, 1992) are much higher than in Central Asia, where 250 mm of precipitation is sufficient to sustain coniferous forests in the surroundings of Ulaan Baatar (Hilbig, 1995). Moreover, the timing of precipitation differs among regions of different longitudes: while winter rain is common in parts of North America and Middle Asia, Central Asian drylands receive almost exclusively summer rains.

Recent studies from the cold deserts of northern China have reported effective germination of fresh seeds without any apparent sign of dormancy (e.g. Liu *et al.*, 2003; Zhu *et al.*, 2004; Tobe *et al.*, 2005). However, as these publications focus mainly on pioneer species, the aim of our study was to provide the first data on germination strategies of southern Mongolian steppe species, most of which had not been tested before. Tests were performed under conditions resembling those seasons when germination is likely to occur in the field, as these are of particular relevance for artificial sowing in possible restoration schemes. With reference to Baskin and Baskin (1998), we asked three questions: (1) Do seeds of Central Asian drylands really require dormancy-breaking treatments for germination? (2) Are there differences among major plant growth forms with respect to germination strategies? (3) If germination is delayed after dispersal, are seeds able to survive the harsh frost conditions during winter? We place our findings in a broader context, and include a short review of the recently published literature on seed germination of Central Asian dryland species.

Material and methods

Study area

The seeds for our study were collected in the surroundings of a semi-permanent research camp on the southern slopes of the Dund Saykhan (approximately 43°36'W, 103°48'E, 2300 m asl), the central range of the 'Gobi Gurvan Saykhan National Park' (southern Mongolia). Here, (semi-)deserts with scattered shrubs (*Chenopodiaceae*, *Tamaricaceae*) dominate in the intermontane basins, while desert steppes with *Stipa glareosa* reach up to 2000 m asl (Wesche *et al.*, 2005b). The upper pediments between 2000 and 2300 m asl are covered by montane desert steppes with *Stipa gobica*, while the steep mountain habitats between 2300 and 2600 m asl are composed of mountain steppes with *Stipa krylovii*. Sampling covered the two latter altitudinal belts; Table 1 summarizes the dominant species in the respective vegetation types.

Table 1. Survey of the most important vascular plant species (all perennials) in the two altitudinal belts, 2000–2300 and 2300–2600 m above sea level, in the eastern Gobi Gurvan Saykhan National Park

Zone		
Mountain steppe	Shrubs	<i>Artemisia frigida</i> , <i>A. santolinifolia</i> , <i>Juniperus sabina</i> , <i>Lonicera microphylla</i>
	Herbaceous species	<i>Agropyron cristatum</i> , <i>Allium prostratum</i> , <i>Arenaria meyeri</i> , <i>Heteropappus altaicus</i> , <i>Oxytropis pumila</i> , <i>Stipa krylovii</i>
Montane desert steppe	Shrubs	<i>Artemisia frigida</i> , <i>A. santolinifolia</i> , <i>Caragana leucophloea</i> , <i>Eurotia ceratoides</i>
	Herbaceous species	<i>Achnatherum inebrians</i> , <i>Agropyron cristatum</i> , <i>Allium polyrrhizum</i> , <i>Arenaria meyeri</i> , <i>Cleistogenes squarrosa</i> , <i>Ptilotrichum canescens</i> , <i>Stipa gobica</i>

Table 2. Long-term climatic conditions at Bayandalay station (1570 m above sea level, 1966–1999, National Meteorological Service of Mongolia)

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Annual mean
Temperature													
Mean (°C)	-16.5	-11.8	-3.2	7.2	15.5	21.1	22.8	20.2	14.5	5.0	-6.6	-13.6	4.5
SD	2.5	3.4	2.6	2.2	1.7	1.4	1.5	1.9	3.1	2.0	3.1	3.4	
Precipitation													
Mean total (mm)	1.7	1.6	2.3	3.0	8.5	14.0	36.4	27.9	12.4	4.2	1.3	1.0	114
SD	1.9	2.3	2.4	3.2	16.1	10.1	22.5	23.0	21.8	3.9	2.0	1.0	

Winters in Mongolia are dry and very cold; temperatures in spring rise rapidly, and rains start when temperatures are already relatively high. Long-term meteorological data are available from the governmental weather station Bayandalay, situated c. 25 km south-west of the study region at 1570 m asl. The regional climate is highly continental and arid throughout the larger part of the year (Table 2). Mean temperatures drop to -16.5°C in winter, but remain above 0°C from April to October and reach $>20^{\circ}\text{C}$ in summer months. The zonal desert steppes receive an average of 114 mm precipitation per year (Table 2), of which 89% falls between April and September, and 68.5% between June and September. Winter precipitation is rare, and any snow that does fall usually evaporates without being absorbed by the soil. Onset of plant growth is usually delayed by dry conditions until May/early June. The interannual

variability in precipitation is great; the mean standard deviation is highest in August, at 23 mm (Table 2).

There are no governmental weather stations above 2000 m asl, and records kept at the research camp are incomplete (Fig. 1). Here, mean winter temperatures dropped to -15.5°C in February 2002, and absolute minimum temperatures were as low as -27°C . In contrast, summer conditions were more or less constantly warm (mean August temperatures of 18.7°C in 2001, 16.7°C in 2002, 13.2°C in 2003). Mean daytime temperatures range between 17 and 22°C in summer; mean night-time temperatures are between 10 and 16°C . Mean monthly minima are around $12\text{--}13^{\circ}\text{C}$ in July and $6\text{--}11^{\circ}\text{C}$ in August; mean maxima are $22\text{--}24^{\circ}\text{C}$ and $18\text{--}21^{\circ}\text{C}$, respectively (Fig. 1). Thus, temperatures are lower overall than in Bayandalay, while precipitation is higher. Rain amounts are rather unpredictable even in the mountains, as totals

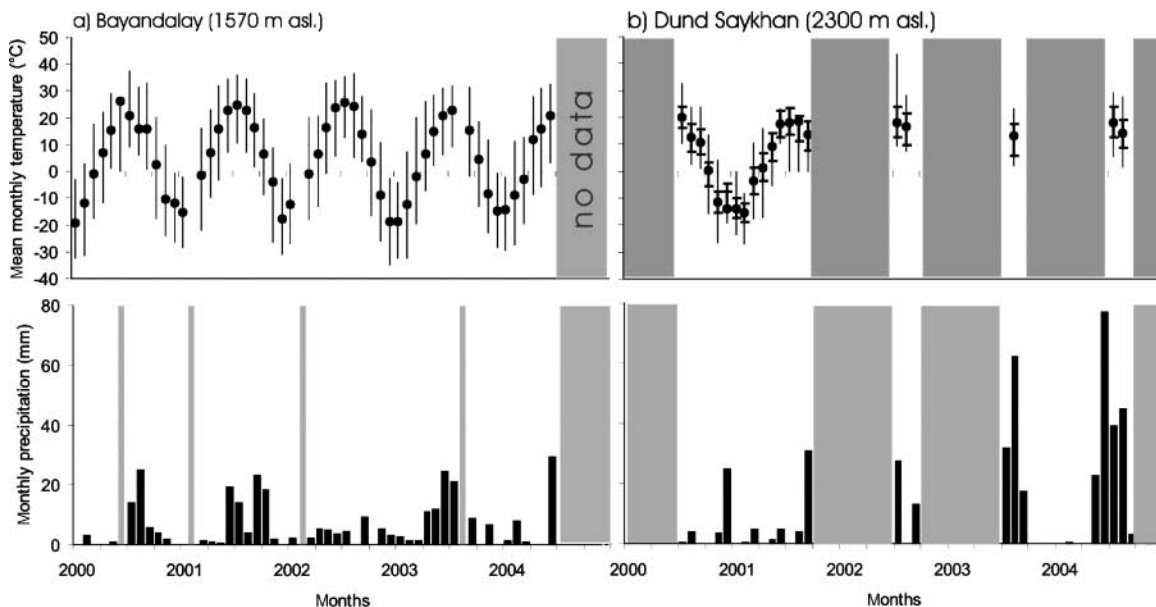


Figure 1. Climate conditions during the study period. Upper diagrams give mean monthly temperatures and absolute temperature range (minimum, maximum). For the Dund Saykhan station, values for mean minimum and maximum temperature were available; these are indicated by horizontal error lines. The lower figures indicate the monthly precipitation totals (Bayandalay: National Meteorological Service; Dund Saykhan camp: authors' measurements).

were 74 mm in 2001/2002 (compared to 48 mm in Bayandalay during the same period, Fig. 1), 211 mm in 2003/2004 and 125 mm in 2004/2005.

Data collection and analyses

Our study covered 26 species common in desert steppes and mountain steppes of the Gobi Altay region (Table 3); most of these have a Central to Middle Asian distribution range. The dominant life forms are perennial hemicryptophytes, both in the actual vegetation and in our data set. We also studied a range of woody perennials, plus several short-lived species, that are only found on small mammal burrows and in dry river beds. Seed production is generally limited and very irregular, because of high interannual variability of rains and impact of herbivores. Seeds were collected over a period of 3 years (2001–2003), whenever sufficient numbers were available. Most seeds were collected in dry montane steppes between 2200 and 2450 m asl (Table 3). Only ripe seeds were

taken, and always after natural dispersal had already begun. Collecting covered at least 10 plants per species; however, in several species many more individuals had to be sampled to obtain a sufficient number for germination analyses. Seeds were stored in cotton bags at ambient temperatures. Dormancy tests were performed within 3 weeks after collection; when transport to the lab was delayed, initial dormancy tests were performed directly in the field under ambient conditions (values for August, see above and Fig. 1). As results did not differ from those obtained from subsequent lab studies, data described in the results section always refer to germination under lab conditions.

In the lab, batches of 50 seeds ($n = 4$) were put on filter paper in standard Petri dishes and were kept permanently moist with de-ionized water. An initial screening of a subset of the species showed that germination was usually high at temperatures between 10 and 32°C, while germination was somewhat lowered at alternating temperatures of 4/8°C (Table 4). As

Table 3. List of species tested, arranged by growth form and Raunkiaer life form. Overall distribution and dispersal time (in months, '5' = May, '6' = June, etc.) are also indicated. The right-hand column gives the elevation where seeds were collected (m above sea level)

Species	Life form	Distribution	Dispersal Elev.
Woody perennials			
<i>Artemisia frigida</i>	Chamaephyte	Circum-polar, Eurasian steppes ¹	9–10 2300
<i>Artemisia santolinifolia</i>	Chamaephyte	Southern Siberia, Mongolia, eastern Asia ^{1,2}	7–10 2300
<i>Caragana leucophloea</i>	Microphanerophyte	Central Asia ¹	7–9 2200
<i>Eurotia ceratoides</i>	Microphanerophyte	Eurasian steppes and semi-deserts ²	9–10 2300
<i>Ulmus pumila</i>	Phanerophyte	Sub-oceanic to sub-continental regions of eastern Asia ²	5–6 1600
Herbaceous perennials			
<i>Achnatherum inebrians</i>	Hemicryptophyte	Mongolia, northern China ³	8–9 2350
<i>Agropyron cristatum</i>	Hemicryptophyte	Eurasian steppes and semi-deserts ^{1,2}	7–9 2350
<i>Arenaria meyeri</i>	Hemicryptophyte	Mongolian and northern Chinese steppes and semi-deserts ¹	7–9 2350
<i>Galitzkya macrocarpa</i>	Hemicryptophyte	Endemic to the Gobi Altay ⁴	7–9 2450
<i>Halerpestes sarmentosa</i>	Hemicryptophyte	Middle and Central Asia ⁵	8–9 2200
<i>Papaver saichanensis</i>	Hemicryptophyte	Endemic to the Gobi Altay ⁴	7–9 2450
<i>Potentilla ikonnikovii</i>	Hemicryptophyte	Endemic to the Gobi Altay ⁴	7–9 2400
<i>Saussurea saichanense</i>	Hemicryptophyte	Endemic to Mongolian mountains ⁴	8–9 2400
<i>Stipa glareosa</i>	Hemicryptophyte	Middle and Central Asia, Gobi ⁶	7–8 2100
<i>S. gobica</i>	Hemicryptophyte	Middle and Central Asia ³	7–8 2200
<i>S. krylovii</i>	Hemicryptophyte	Eurasian steppes ¹	8 2300
<i>Allium polyrrhizum</i>	Geophyte	Middle and Central Asia ⁷	9–10 2400
<i>Rheum undulatum</i>	Geophyte	Subcontinental eastern Asia to Central Asian mountains ¹	8–9 2400
Short-lived species			
<i>Androsace maxima</i>	Therophyte (1–2 years)	Eurasia, western Asia ¹	7–9 2350
<i>Axyris hybrida</i>	Therophyte	Central Asian highlands ¹	8–10 2300
<i>Chenopodium album s.l.</i>	Therophyte	Eurasia, now cosmopolitan ^{1,6}	8–10 2300
<i>Chenopodium vulvaria</i>	Therophyte	Western Eurasia, Central Asia ⁸	8–10 2300
<i>Corispermum mongolicum</i>	Therophyte	W-Siberian, Central Asia ⁹	8–10 2000
<i>Isatis costata</i>	Therophyte (1–2 years)	Highlands of Central and Middle Asia ¹⁰	8–9 2350
<i>Pedicularis abrotanifolia</i>	Therophyte (1–2 years)	Steppes of western Siberia, Middle and Central Asia ¹¹	8–9 2400
<i>Salsola collina</i>	Therophyte	Eurasian steppes and semi-deserts ¹	8–10 2300

¹Hilbig *et al.* (2004); ²Hilbig and Knapp (1983); ³Tzvelev (2001); ⁴Wesche *et al.* (2005a); ⁵Flora of China Editorial Committee (2001a); ⁶Hilbig *et al.* (1999); ⁷Flora of China Editorial Committee (2000); ⁸Meusel *et al.* (1965); ⁹Flora of China Editorial Committee (2003); ¹⁰Flora of China Editorial Committee (2001b); ¹¹Flora of China Editorial Committee (1998).

Table 4. Effect of temperature regime on final germination of fresh seeds for 9 species tested in initial screenings (mean values after 4 weeks). Germination values are expressed relative to the overall number of viable seeds

Species	% final germination at			Source
	4/8°C	10/20°C	32°C	
<i>Artemisia frigida</i>	48	99	100	Pietsch unpubl. ¹
<i>Artemisia santolinifolia</i>	58	100	100	Ronnenberg (2005)
<i>Agropyron cristatum</i>	44	98	100	Pietsch unpubl. ¹
<i>Arenaria meyeri</i>	23	98	100	Pietsch unpubl. ¹
<i>Galitzkya macrocarpa</i>	81	100	100	Undrakh unpubl. ²
<i>Papaver saichanensis</i>	0	100	100	Undrakh unpubl. ²
<i>Potentilla ikonnikovii</i>	0	100	100	Wesche and Undrakh (2003)
<i>Saussurea saichanense</i>	62	100	100	Undrakh unpubl. ²
<i>Allium polyrrhizum</i>	75	57	68	Pietsch unpubl. ¹

¹Pietsch, M. (2005) Population ecology of five keystone species of southern Mongolian mountain steppes. Unpublished diploma thesis, University of Halle-Wittenberg.

²Undrakh, R. (2002) Population biological analyses of rare montane plants from the south-eastern Gobi Altai. Unpublished report to the German Academic Exchange Service, Halle.

seed material was scarce, the samples of seeds were incubated at only one alternating temperature and light regime of 12 h 10°C/darkness, and 12 h 20°C/warm white light, corresponding to study site conditions in August or in May/June. All species were tested under the same conditions using the same equipment. After germination ceased (always within 4 weeks), viabilities of the remaining ungerminated seeds were tested with a tetrazolium staining procedure. In 22 species, sufficient seeds were available to perform an additional frost-treatment experiment. To test whether seeds were able to survive the winter, they were dried over a hygroscopic chemical (CuSO₄) for 2 d. Seeds were then frozen at –18°C for a period of 6 weeks, and afterwards treated in the same way as described previously for the fresh seeds.

Percentage germination was calculated with respect to the potentially viable seeds, i.e. the number of seeds germinated plus those remaining viable that did not germinate during the experiment. Expressed in this way, percent germination is strongly influenced by overall viability, which is also reported, as are the data on raw germination. However, statistical analysis was based on values corrected for viability; tests concentrated on differences among major groups of growth forms, i.e. woody perennials, herbaceous perennials and herbaceous short-lived species (including true annuals and biennials). We used parametric repeated-measures analysis of variance (ANOVA) with frost treatment as the intra-subject factor, and growth form as the inter-subject factor. Percentages were arc-sin square-root transformed prior to analysis, but values in Fig. 2 and Tables 4 and 5 refer to untransformed data.

In order to compare the results of our dataset, we searched for studies on Central Asian plants in several major journals with a focus on germination studies, and in a standard literature database (ISI Web of Knowledge™) covering the past 5 years.

Results

Fresh seeds

In the majority of species, fresh seeds germinated well under the chosen conditions (Table 5), but germination differed among major growth forms (Table 6a). Germination of woody and herbaceous perennials was equally high (>90%, Fig. 2a), while germination of short-lived species was generally <40%. The exception was the annual *Salsola collina*, fresh seeds of which germinated effectively (Table 5). Differences between annuals and both groups of perennials were significant (Fig. 2a).

Overall seed viability in both annual and perennial species tended to be high at a mean of >80% (Fig. 2b). The principal exceptions were the three *Stipa* species and *Ulmus pumila* (Table 5). Differences among growth forms were not significant (Table 6b) and did not explain the differences found in viability-corrected germination.

Frost-treated seeds

After freezing, germination still differed among life forms, albeit to a less pronounced extent (Fig. 2a). Germination of woody, as well as herbaceous, perennials hardly changed after freezing. Exceptions

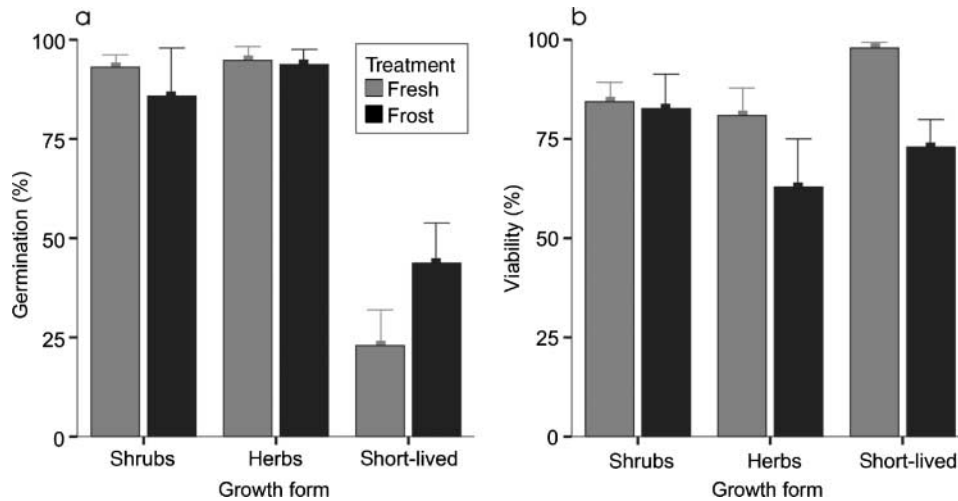


Figure 2. Summary of germination characteristics for the three major groups of growth forms. Columns give mean values; error bars indicate one standard error. (a) Germination of fresh and frost-treated seeds; (b) viability of fresh and frost-treated seeds.

Table 5. Average germination of fresh and frost-treated seeds under standard conditions of alternating light (12h dark/12h light) and temperature regime (10/20°C). Germination percentages are expressed on a total seed basis (raw), and as values corrected (corr.) for the total number of viable seeds. Viability was based on the number of germinated seeds plus non-germinated tetrazolium-positive seeds

Species	Fresh seeds				Frost-treated seeds					
	Germination (%)		SD	Viability (%)		Germination (%)		Viability (%)		
	raw	corr.		SD	raw	corr.	SD	SD		
Woody perennials										
<i>At. frigida</i>	94	99	2	95	4	97	100	0	97	4
<i>At. santolinifolia</i>	92	100	0	92	1	95	100	0	95	3
<i>Ca. leucophloea</i>	76	94	7	80	4	53	91	3	58	9
<i>Eu. ceratoides</i>	76	87	5	87	4	99	100	0	99	1
<i>Ul. pumila</i>	56	84	13	67	5	24	37	3	64	7
Herbaceous perennials										
<i>Ac. inebrians</i>	97	97	1	99	1	95	100	0	95	3
<i>Ag. cristatum</i>	68	98	3	70	4	68	99	1	68	8
<i>Ar. meyeri</i>	92	98	2	93	3	100	100	0	100	0
<i>Ga. macrocarpa</i>	100	100	0	100	0					
<i>Ha. sarmentosa</i>	85	100	0	85	15	87	96	4	90	5
<i>Pa. saichanensis</i>	100	100	0	100	0					
<i>Po. ikonnikovii</i>	100	100	0	100	0					
<i>Sa. saichanense</i>	100	100	0	100	0					
<i>St. glareosa</i>	63	100	0	63	7	22	100	0	22	3
<i>St. gobica</i>	18	100	0	18	4	25	100	0	25	13
<i>St. krylovii</i>	69	92	7	75	12	2	67	47	3	1
<i>Al. polyrrhizum</i>	32	57	13	56	6	58	83	8	70	7
<i>Rh. undulatum</i>	84	91	5	93	6	90	99	1	91	5
Short-lived species										
<i>An. maxima</i>	26	26	5	100	0	32	43	8	74	10
<i>Ax. hybrida</i>	3	3	3	98	3	31	31	11	99	2
<i>Ch. album s.l.</i>	9	10	5	97	3	20	33	6	62	10
<i>Ch. vulvaria</i>	20	22	5	91	8	18	32	11	55	8
<i>Co. mongolicum</i>	4	4	4	100	0	2	3	1	53	9
<i>Is. costata</i>	6	6	7	100	0	23	45	6	51	8
<i>Pe. abrotanifolia</i>	32	32	5	99	1	59	63	9	93	2
<i>Sa. collina</i>	79	80	7	99	2	94	100	0	94	4

Table 6. Repeated-measures ANOVA for the effect of freezing on species of Mongolian steppes, split by growth form (woody perennials, herbaceous perennials, short-lived species; general linear model, germination is based on corrected values in Table 5). (a) Effect on germination; (b) effect on viability

	(a) Germination				(b) Viability			
	Sum of Squares (Type III)	df	F	P	Sum of Squares (Type III)	df	F	P
Model: Freezing effect								
Frost treatment	0.101	1	4.109	0.057	0.280	1	6.278	0.021
Frost × Growth form	0.179	2	3.658	0.045	0.333	2	3.732	0.043
Error term	0.466	19			0.847	19		
Model: Growth form								
Constant	50.892	1	339.572	<0.001	54.795	1	397.083	<0.001
Growth form	6.113	2	20.396	<0.001	0.598	2	2.168	0.142
Error term	2.848	19			2.622	19		

were *Ulmus pumila* and *Stipa krylovii* with decreasing germination, and *Allium polyrrhizum* with slightly increasing germination after freezing (Table 5). The effect of the frost treatment was stronger for short-lived species (Fig. 2a). The increase in germination was pronounced in *Axyris hybrida*, *Chenopodium album*, *Isatis costata* and *Pedicularis abrotanifolia*; this effect was apparent in raw and corrected figures for germination and thus independent of changes in viability (Table 5). The ANOVA confirmed these inferences (Table 6a). The overall effect of frost treatment was marginally significant (Table 6a), but a weakly significant interaction term indicated that species of different growth forms tended to respond differently.

The freezing effect on viability was weakly significant (Table 6b), and there was an interaction between freezing effect and growth form. Viability decreased slightly due to freezing in many short-lived and some perennial herbs, but was hardly affected in the woody perennials (Fig. 2b).

Discussion

Importance of seed dormancy

Fresh seeds of 19 out of the 26 species tested germinated readily under the chosen conditions. Values for final germination were >80%; among perennials, only *Stipa gobica* was characterized by low raw germination percentages (related to low viability). Given that tests were performed under temperatures reflecting conditions in early or late summer, untreated seeds of most perennials should be able to germinate readily when sufficient moisture becomes available. Among annuals, only seeds of *Salsola collina* germinated at high percentages. Our methods did not allow differentiation between conditional dormancy and non-dormancy, but requirements of stratification or scarification were apparently not as common as

expected for a cold, arid environment. Short-lived species may show some type of dormancy, but as they are negligible in terms of general vegetation cover (Hilbig, 1995; Wesche *et al.*, 2005b), we therefore conclude that non-dormancy, or at most conditional dormancy, is the prevailing strategy in Mongolian dry steppe vegetation.

Our results are in contrast to knowledge gained from germination studies in North American mid-latitude steppes and cold deserts, where physiological dormancy is generally common (Baskin and Baskin, 1998), including perennial species that also dominate in North America (Lauenroth and Milchunas, 1992). Compared to Central Asia, the seasonality of the climate is less pronounced in North America, and the levels of precipitation are higher overall. Moreover, prairies are situated on lower elevations, whereas most of Central Asia is upland. Comparable data for montane sites are sparse; although physiological dormancy appears to be the single dominant strategy, about one-third of montane species are known to show non-dormancy (Baskin and Baskin, 1998). Thus, part of the differences when compared to North America may be related directly to the special abiotic conditions in the cold montane drylands of Central Asia.

These results support findings of recent studies performed mainly in northern China (summarized in Table 7). Although the data are heterogeneous, general patterns are nonetheless quite clear. Most studies report optimum germination at a temperature range between 10 and 25°C, and at osmotic potentials between 0 and 1 MPa. Most species germinated well in light (Table 7), implying that the conditions chosen in our study are suitable for most species. Evidence of dormancy was not always tested explicitly; many studies were performed with seeds that had been stored for an indefinite time at dry and moderately cold temperatures (usually 4°C, e.g. Zheng *et al.*, 2004c, 2005b; Tobe *et al.*, 2005). In these cases species almost

Table 7. Summary of germination characteristics of 39 Central Asian species, arranged by growth forms according to 25 published literature sources ('+' yes/possible; '-' no/impossible; '?' possible but not certain). Germination under field conditions and dispersal: '1, 2, 3, etc.' = January, February, March, etc. Germination temperature: 'opt', optimum temperature, usually tested in 5°C intervals. Dormancy: 'PD', physiological dormancy; 'PY', physical dormancy; 'ND', non-dormant. Tolerance to osmotic stress: 'opt', germination not or hardly suppressed

Species	Dispersal in the field	Germination temperature	Seed longevity	Dark germination	Light germination	Tolerance drought stress	Dormancy
Woody perennials							
<i>Ammopiptanthus nanus</i>		30°C opt ¹	>7 months ¹	+ ¹	+ ¹	Opt: 10–30% soil moisture ¹	PY + ¹
<i>Artemisia ordosica</i>	5–7 ^{2,3}	5 < opt < 30°C ²		- ² ; + ^{4,5}	+ ^{2,5} ; - ⁴	-0.4 MPa salt, -0.8 MPa ^{2,5}	ND? (PD - ?) ²
<i>Artemisia sphaerocephala</i>	9 ⁶	10 < opt < 30°C ^{4,6,7}		- ⁶ ; + ³ ; + under sand ^{4,7}	+ ⁶ ; + / - ⁴ ; - ³	Opt: 2–20% soil moisture, 0–10 mM salt ⁶ , 0–0.8 MPa ⁸	ND? (PY - ?) / PD - ? ^{4,6,7}
<i>Atraphaxis bracteata</i>		10 < opt < 25°C ⁹				Opt < -0.1 MPa ⁹	PD + ? / PY? + ? ⁹
<i>Calligonum</i> spp.	7–9 ¹⁰					Sensitive to desiccation	PD? + ¹⁰
<i>Caragana intermedia</i>	5–6 ⁴	10/20°C ⁴		+ ⁴	+ ⁴		ND? (PY - ?) / PD - ? ⁴
<i>Caragana microphylla</i>	10–11 ¹¹	5 < opt < 20°C ¹¹		poor ¹¹	+ ¹¹		ND ¹¹
<i>Caragana korshinskii</i>	8–9 ¹²	10 < opt < 35°C ¹²		+ under sand ⁷ ; + ^{4,11} ; - ³	+ ^{4,11} ; - ³	Opt < -1 MPa ⁹ ; -0.6 MPa ¹²	ND? (PY - ?) / PD - ? ^{4,7,9,12} , ND ¹¹
<i>Haloxylon ammodendron</i>	10–11 ^{13,14}	From 4 on ¹³	<10 months ^{13,15}	+ ^{4,7}	+ ¹³	Opt < -1.3 / 3 MPa ^{5,14,15} ; + / - < -0.2 M NaCl ^{13,15}	ND? (PY - ?) / PD - ? ^{4,7}
<i>Hedysarum fruticosum</i>	5–6 ⁴	5 < opt < 30°C ^{4,9}		+ ^{4,7}	+ ⁴		ND ¹¹
<i>Hedysarum laeve</i>	10–11 ¹¹	5 < opt < 20°C ¹¹		+ ³ ; - ¹¹	- ³ ; + ¹¹		ND? (PY - ?) / PD - ? ⁹
<i>Hedysarum scoparium</i>	5–10 ⁹	10 < opt < 35°C ⁹		+ ⁵		Opt < -1.4 MPa / -0.8 MPa NaCl ^{5,9}	ND? (PY - ?) / PD - ? ⁹
<i>Kalidium caspicum</i>	11 ¹⁶	5 < opt < 35°C ^{16,17}	>12 months ¹⁶	+ ^{16,17}	- ¹⁶	Opt -1 MPa ¹⁶ ; depending on cation ⁷	ND ^{16,17}
<i>Lespedeza davurica</i>	5–10 ⁹	10 < opt < 30°C ⁹				Opt < -1 MPa ⁹	ND? (PY - ?) / PD - ? ⁹
<i>Zygophyllum xanthoxylon</i>	5–6, 9–10 ⁹	10 < opt < 25°C ⁹		+ ⁴	+ ⁴	Opt < -0.4 MPa ⁹	ND? (PY - ?) / PD - ? ⁹
Herbaceous perennials							
<i>Astragalus adsurgens</i> (introduced to China)	5–6 ⁴	10/20°C ⁴		+ ⁴	+ ⁴		ND ¹⁸
<i>Cleistogenes squarrosa</i>		Only 16°C tested, + ¹⁸					ND ¹⁸
<i>Elymus dahuricus</i>		Only 16°C tested, + ¹⁸					ND ¹⁸

Table 7. Continued

Species	Dispersal in the field	Germination in the field	Germination temperature	Seed longevity	Dark germination	Light germination	Tolerance drought stress	Dormancy
<i>Glycyrrhiza uralensis</i>	5–6 ⁴		10/20°C ⁴		+ ⁴	+ ⁴		ND? (PY – ?/ PD – ?) ⁴ +? ¹⁸
<i>Hemiarthra compressa</i>	8–9 ¹⁹		Only 16°C tested, + ¹⁸ Well at 22°C ¹⁹	> 3 years ¹⁹	+ ¹⁹			PD + after- ripening ¹⁹
<i>Leymus chinensis</i>	8–9 ²⁰		Opt 25–30°C ²⁰		+ ²⁰	+ / – ²⁰		PD + cold stratification, ²⁰ scarification ²⁰
<i>Leymus racemosus</i>	4–6 ²⁰				+ ²⁰			ND? (PY – ?/ PD – ?) ⁷
<i>Medicago sativa</i> (introduced to China)	5–6 ^{7,4}		15/25°C ⁷		+ ^{4,7}	+ ⁴		ND ¹⁸
<i>Phragmites communis</i>	9–11 ²¹		Only 16°C tested, + ¹⁸ 15 < opt < 35°C ²¹		+ after stratification ²¹	+ ²¹		PD+ (cold- stratification, scarification) ²¹
<i>Panicum polyanthemum</i>	8–9 ²²	Late spring? ^{4,22}	10 < opt < 30°C ^{4,7,22,23} ; low < 25°C ²⁰	< 6 years ²³	+ ^{4,5,7,20,23} ; + under sand ^{7,24}	– ^{4,20} + / – ^{22,23}	Opt < (–0.8 MPa; –(0.8 MPa NaCl) ^{5,23}	ND ^{23,25} ND? (PY – ?/ PD – ?) ^{4,7,22}
<i>Aristida adscensionis</i>			10–40°C ²³	> 7 years ²³	+ ^{5,23}	+ ²³	Opt < –1.0 MPa; –0.8 MPa NaCl ^{5,23}	ND ²³
<i>Arundinella hirta</i>			Only 16°C tested, + ¹⁸	< 6 years ²³	+ ^{5,23}	+ ²³	Opt < –1.6 MPa; –1.6 MPa NaCl ^{5,23}	ND ¹⁸ ND ²³
<i>Bassia dasycarpa</i>			5–35°C ²³					ND ¹⁸
<i>Chloris virgata</i>			Only 16°C tested, + ¹⁸					ND ¹⁸
<i>Digitaria ciliaris</i>			Only 16°C tested, + ¹⁸					ND ¹⁸
<i>Echinochloa hispidula</i>			Only 16°C tested, + ¹⁸					ND ¹⁸
<i>Enneapogon borealis</i>			Only 16°C tested, + ¹⁸					ND ¹⁸
<i>Eragrostis pilosa</i>			Only 16°C tested, + ¹⁸					ND ¹⁸
<i>Pennisetum alopecuroides</i>			Only 16°C tested, + ¹⁸					ND ¹⁸
<i>Setaria glauca</i>			Only 16°C tested, + ¹⁸					ND ¹⁸
<i>Setaria viridis</i>			Only 16°C tested, + ¹⁸					ND ¹⁸
<i>Spodiopogon sibiricus</i>			Only 16°C tested, + ¹⁸					+? ¹⁸
<i>Tragus berteronianus</i>			Only 16°C tested, + ¹⁸					ND ¹⁸ + ¹⁸

¹Yang et al. (2004); ²Huang and Gutterman (2000); ³Nie and Zheng (2005); ⁴Zheng et al. (2004c); ⁵Tobe et al. (1999); ⁶Huang and Gutterman (1999); ⁷Zheng et al. (2005a); ⁸Zheng et al. (2005b); ⁹Tobe et al. (2001); ¹⁰Ren and Tao (2003); ¹¹Zhu et al. (2004); ¹²Zheng et al. (2004a); ¹³Huang et al. (2003); ¹⁴Tobe et al. (2004); ¹⁵Tobe et al. (2000a); ¹⁶Tobe et al. (2000b); ¹⁷Tobe et al. (2002); ¹⁸Liu et al. (2003); ¹⁹Liu et al. (2004); ²⁰Huang et al. (2004a); ²¹Huang et al. (2004b); ²²Zheng et al. (2004b); ²³Zheng et al. (2005); ²⁴Bai et al. (2004); ²⁵Wang et al. (1998).

always germinated well, but dry storage is known to allow after-ripening and to break physiological as well as physical seed dormancy (Gutterman, 1993; Baskin and Baskin, 1998). Thus, we cannot infer the dormancy status from these types of studies with any certainty. Nevertheless, non-dormancy is known for a number of Central Asian species, while evidence of some type of dormancy is more rarely described (Table 7). Physical dormancy was reported for *Ammopiptanthus nanus*, and is possibly present also in *Leymus chinensis*. The perennial *Polygonaceae* species *Calligonum* spp. and *Atraphaxis bracteata* are described as showing unspecified complex dormancy mechanisms (Tobe *et al.*, 2001; Ren and Tao, 2003). There is also evidence of physiological dormancy in the latter species, as well as in the perennial grasses *Leymus racemosus* and *Psammochloa villosa* (Table 7). Perennial species categorized in Table 7 as having seed dormancy grow mostly in true deserts (cf. Hilbig, 1995), except for *Leymus chinensis*, which is a steppe species. This is consistent with previous records of seed dormancy in other cold deserts (Gutterman, 1993; Baskin and Baskin, 1998). However, non-dormancy remains the most commonly reported strategy (Table 7). Thus, although Central Asian plants show a wide variety of germination strategies, the majority of species seem to have at most conditional physiological dormancy, confirming our observations.

Germination strategies of different growth forms

In the present study, the magnitude of dormancy varied among growth forms. Fresh seeds of perennial species germinated readily, but short-lived species behaved differently. Only *Salsola collina* germinated with high final percentages, while most other species apparently had delayed germination. Unspecified dormancy was previously described for the short-lived *Setaria viridis* and *Tragus berteronianus* (Liu *et al.*, 2003). Most other short-lived species, such as *Agriophyllum squarrosum* and *Bassia dasyphylla*, are known to produce non-dormant seeds (Table 7). However, most species tested by other authors are annuals of continental Asian deserts. There, the climate is seasonal but unpredictable, in the sense that quantity and timing of precipitation varies tremendously between summers. As seeds would be expected to take full advantage of the relatively rare and unpredictable periods, when moisture and temperature conditions are suitable for germination and establishment, non-dormancy would be a mechanism to ensure regeneration (e.g. *Agriophyllum squarrosum*; Wang *et al.*, 1998).

In contrast, most short-lived species in our dataset have wider Eurasian ranges (e.g. *Chenopodium album*, *C. vulvaria*), or an exclusively montane distribution

(*Axyris hybrida*) (Table 3). Their habitats experience generally moister conditions that allow germination during most of the year. In such cases, where thermal conditions are unfavourable in winter but suitable in spring, physiological dormancy is a common phenomenon (Gutterman, 1993; Baskin and Baskin, 1998). Moreover, many species accumulate persistent seed banks, although this does not seem to be closely linked to dormancy status (Thompson *et al.*, 2003).

Perennial species, on the other hand, do not depend on successful germination in any given year, or on being able to establish a persistent seed bank, as they can survive by vegetative growth for extended periods, even if sexual reproduction ceases totally (Wesche *et al.*, 2005c). Sexual recruitment appears to be rare in perennials of Central Asian steppes and deserts. In our study region, there have been no seedlings of the dominant perennials *Agropyron cristatum*, *Stipa gobica* and *Artemisia frigida* in most years; and only unusually moist conditions, such as those of 2003, allow for seedling emergence and establishment. A similar pattern was described in a long-term study in desert steppes 50 km north of the study region, where *Stipa gobica* successfully re-seeds at mean intervals of 7–10 years (Lavrenko and Karamysheva, 1993). Seeds of the dune-grass *Psammochloa villosa* require unusually wet years (>400 mm) for germination and establishment at the Ordos Plateau (Huang *et al.*, 2004b), and seedlings of *Cleistogenes squarrosa* are rare in Inner Mongolian grasslands, where there is a mean annual precipitation well above 300 mm (Liang *et al.*, 2002). In southern Mongolian deserts, seedling establishment of the dominant woody perennials, *Haloxyton ammodendron* and *Iljinia regelii*, is estimated to occur only every 50 years (Gunin *et al.*, 2003). As a consequence, many species survive by extensive clonal growth (Song *et al.*, 2002; Bruelheide *et al.*, 2003).

Thus, both available data and theoretical considerations support our observation that germination strategies differ with respect to growth form, but also among different biogeographical elements.

Effect of frost treatment

Dispersal occurs late in most of the species tested here (Table 3), so temperature requirements for germination are not met, and seeds subsequently have to pass through the winter. Our frost treatment experiment showed that effects of freezing on germination are limited (Fig. 2). Overall germination and viability were hardly changed in perennial species; the prime exceptions being *Stipa glareosa*, *S. krylovii* and *Ulmus pumila*, where frost treatment had detrimental effects. Among those tested, the elm (*Ulmus* sp.) has the earliest dispersal time, and the *Stipa* species (feather

grasses) also complete dispersal well before autumn. Germination in summer may be expected in these cases, and both elm and feather grasses were observed germinating *in situ* during summer, provided moisture levels were high enough (Wesche and Ronnenberg, unpublished data). Under such conditions, seedlings, as opposed to seeds, need to be resistant to the impact of deep frosts.

Short-lived species depend largely on passing the winter as seeds, and have to be tolerant to freezing. Viability was not affected in 4 of the 8 short-lived species tested, and remained above 50% in the remaining ones (Table 5). We applied a relatively simple approach for drying seeds, so loss of viability in the latter species might be related to moisture that remained in the seeds, turning to ice at low temperatures. In the field, these losses should be lower as seeds are slowly exposed to the progressively drier and colder conditions of autumn (Table 2).

Dry seeds are expected to be physiologically inactive (Baskin and Baskin, 1998), and germination of perennials was not positively affected. Seeds of short-lived species tested here were also dried before freezing, yet germination increased in most species; this increase was independent of changes in viability (Table 5). This is not easily explained, as physiological dormancy is not known to be influenced by dry freezing, while physical dormancy is unlikely in the families tested here. However, dry storage is known to affect dormancy through after-ripening, and cycles of wet and dry conditions can also affect germination or dormancy status in seeds with non-deep physiological dormancy (Baskin and Baskin, 1998). More detailed data are needed, but final germination remained well below 50% in most species (the main exception again being *Salsola collina*, where fresh seeds germinated well), indicating that the dormancy was not fully broken in the other species.

Controls of germination in situ

Our study provides evidence that physiological dormancy is common among short-lived species (except for *Salsola collina*, Table 5). Widespread weeds, such as *Chenopodium album*, are known for having physiological dormancy, and the same is true for *Pedicularis* species (Baskin and Baskin, 1998). Climatic conditions that allow cold stratification are limited in the study region, as seasonal temperature changes occur rather quickly, with spring and autumn being relatively dry. However, periods needed for stratification may be short in our species, and short spells of rain or snow (very rare in the region), may theoretically be sufficient. Moreover, recurrent drying and wetting of seeds in May and early June may also affect dormancy status.

Even without dormancy, or with at most conditional dormancy, germination is nonetheless controlled. Many montane species are non-dormant (Baskin and Baskin, 1998), but remain quiescent, as the growth period is too short to allow germination directly after dispersal. In seasonal grasslands, late dispersing species also often have non-dormant seeds that do not germinate until the following spring, when temperature conditions become suitable for germination (Washitani and Masuda, 1990). Central Asian species appear to follow a similar strategy. Reduced germination at low temperatures is a widespread strategy in Central Asian drylands (Table 7). All five shrubs tested by Tobe *et al.* (2001) needed at least 10°C for germination, with optimum values between 15 and 25°C. In *Artemisia sphaerocephala*, optimum germination at temperatures of 15–25°C, plus strongly reduced germination below 5°C, ensures germination in spring (dispersal in September to October) (Huang and Gutterman, 1999). A similarly reduced germination at low temperatures (5–10°C) was confirmed for North American collections of *Halogeton glomeratus*, a Eurasian (including western Central Asian) annual, that became a widespread neophytic species in the Great Basin (Khan *et al.*, 2001). There, plants also showed similar temperature requirements with a sensitivity to low temperatures, which is in contrast to species from southern Asia/Pakistan, for example (Khan and Ungar, 1996; Khan *et al.*, 2001). Preliminary studies on the species set of our study also showed low germination at temperature regimes of 4°C darkness/8°C light (Table 4). In southern Mongolia, temperatures drop below that level as early as mid-September, while dispersal of most species starts in August (Table 3), and often continues until October (e.g. *Artemisia frigida*, *Eurotia ceratoides* and *Salsola collina*). This is generally also typical for other species of Central Asian drylands (Table 7). Thus, seeds that are dispersed in late summer, or even autumn, would not meet the temperature requirements for germination, which would be delayed until the following spring. This pattern is inferred also in other studies that provide information on the topic (e.g. *Agriophyllum squarrosum*, *Caragana intermedia* and *Haloxyylon ammodendron*, Table 7).

However, seeds of species with early dispersal in July/August—such as *Ulmus pumila*, *Stipa glareosa*, *Stipa gobica* and *Arenaria meyeri* (Table 3) – also do not have any dormancy and may well germinate directly after dispersal. Under favourable conditions, seedlings might be able to establish permanently before winter. If not, the given year's seed yield might be lost. But as these species are perennial, successful recruitment may be delayed until a sequence of seasons more suitable for germination occurs. This would most probably include an unusually dry summer, preventing germination in July/August,

followed by a moist spring and summer (an example is the period 2002–2003 in the study region). Such a seasonal combination has been rare in the steppes studied here (Lavrenko and Karamysheva, 1993), but is much more common than in the drier deserts, where several perennial species are characterized by seed dormancy (*Atraphaxis bracteata*, *Psammochloa villosa*, Table 7).

At present, most restoration schemes in northern China concentrate on heavily desertified steppes, and therefore employ pioneer species of early successional stages. Non-dormant, short-lived species dominate in soil seed banks (Zeng *et al.*, 2003; Bai *et al.*, 2004), but also germinate well after artificial sowing if they are covered by 1–2 cm of soil. Several perennial pioneer species can be sown in a similar manner (Nie and Zheng, 2005). Once they have become established, further restoration could aim at grassland species, which are preferred pastures for livestock keeping. Our results indicate that most species of such grass-dominated steppes could also be used directly without any dormancy-breaking treatment. The appropriate time of sowing would depend upon local climatic conditions. In Middle Asia, where drylands receive winter precipitation, sowing of seeds for restoration purposes is recommended for January to March (Mukhammedov *et al.*, 1999); but by that time, neither temperature nor moisture availability would be sufficient in Central Asia. There, germination under natural conditions occurs in spring, rather than directly after dispersal in late summer or autumn (with the possible exception of *Stipa* spp. and *Ulmus pumila*, see above). Moreover, as frosts may have a negative impact on seed viability, we suggest that artificial sowing should take place in spring. Considering that the rains in southern Mongolia commence mainly in May, by which time temperature requirements for germination are also met, a suitable time for sowing would be the end of April or early May.

Further studies are clearly needed on this issue, but our results confirmed that data from other regions, such as North America, should be adopted with care for the physiognomically similar, yet physiologically different, vegetation of Central Asia.

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