

Comparing the relationship between seed germination and temperature for *Stipa* species on the Tibetan Plateau

Shihai Yang, Xiong Li, Yunqiang Yang, Xin Yin, and Yongping Yang

Abstract: Alpine steppe grasslands dominated by *Stipa* species (Poaceae) on the Tibetan Plateau are important model ecosystems. Here, we present data on seed germination of three typical *Stipa* species (*Stipa purpurea* Griseb., *Stipa glareosa* P.A.Smirn., and *Stipa capillacea* Keng) from the northern core region of the Tibetan Plateau. We carried out laboratory investigations of germination behavior under both constant and alternating temperatures. Germination varied significantly with temperature. Under constant temperature, we found that temperature and species, but not their interaction, had significant effects on seed germination. Under alternating temperatures, species had a significant effect on seed germination, whereas the effects of alternating temperature and the interaction between species and alternating temperature were not significant. In addition, light and the interaction of light and species had no significant effect on seed germination; however, species had a significant effect, implying that *Stipa* species on the Tibetan Plateau are not inhibited by light. Base temperatures of *S. glareosa*, *S. purpurea*, and *S. capillacea* were 1.0 °C, 0.1 °C, and -1.4 °C, respectively, with corresponding thermal times at suboptimal temperatures of 233 °C-day, 154 °C-day, and 263.2 °C-day. Our results suggest that *Stipa* seed germination characteristics are adaptations to a harsh environment and are species-specific.

Key words: alpine steppe, seed germination, cardinal temperature, thermal time, *Stipa* species, Tibetan Plateau.

Résumé : Les prairies de la steppe alpine du Plateau tibétain dominées par *Stipa* (Poaceae) constituent des écosystèmes modèles importants. Les auteurs présentent ici des données de la germination de trois espèces de *Stipa* typiques (*Stipa purpurea* Griseb., *Stipa glareosa* P.A.Smirn. et *Stipa capillacea* Keng) de la région nord du Plateau tibétain. Ils ont réalisé des recherches en laboratoire du comportement germinatif sous des températures constantes et alternées. La germination variait de manière significative en fonction de la température. Sous une température constante, la température et l'espèce, mais pas leur interaction, exerçaient en effet significatif sur la germination des graines. Sous des températures alternées, l'espèce exerçait un effet significatif sur la germination des graines, alors que les effets de températures alternées et l'interaction entre l'espèce et les températures alternées n'étaient pas significatifs. De plus, la lumière et l'interaction entre la lumière et l'espèce n'avaient pas d'effet significatif sur la germination des graines; toutefois, l'espèce exerçait un effet significatif, qui implique que les espèces de *Stipa* du Plateau tibétain ne sont pas inhibées par la lumière. Les températures de base de *S. glareosa*, *S. purpurea* et *S. capillacea* étaient de -1.0 °C, 0.1 °C et -1.4 °C, respectivement, correspondant à des temps thermiques à des températures sous-optimales de 233 °C-jour, 154 °C-jour et 263.2 °C-jour. Les données des auteurs suggèrent que les caractéristiques de la germination de *Stipa* sont le résultat d'adaptations à un environnement hostile et qu'elles sont spécifiques à l'espèce. [Traduit par la Rédaction]

Mots-clés : steppe alpine, germination des graines, température cardinale, temps thermique, espèces de *Stipa*, Plateau tibétain.

Introduction

Seed germination, a central component of plant life history, is essential to plant reproductive success (Bliss 1958; Billings and Mooney 1968; Baskin and Baskin 1988, 1998; Schütz 2002; Bu et al. 2009). Various environmental factors affect germination, with temperature, light, and water availability generally having the greatest influence (Guterman 1974; Thompson et al. 1977; Boeken et al. 2004; Tobe et al. 2005; Kettenring et al. 2006; Zhang et al.

2006; Qu et al. 2008; Ronnenberg et al. 2007, 2008; Hamasha and Hensen 2009; Luna and Moreno 2009; Giménez-Benavides and Milla 2013). These factors have fundamental roles in natural selection of strategies that reduce mortality and increase the probability of successful establishment (Schütz 2002; Tobe et al. 2005). Temperature requirements are very important determinants of species distributions; they limit plants to regions having thermal amplitudes compatible with their germination and growth re-

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quirements (Baskin and Baskin 1988; Fenner 2000; Bewley et al. 2013).

Angus et al. (1980) were the first to use thermal time to quantify the important relationship between plant development and temperature. Thermal time is now frequently used to integrate more complex biological processes in poikilothermic species, with practical and ecological implications. Thermal time has also been used to analyze the effect of temperature under non-limiting moisture conditions in various stages in the life cycle and growth of many species (Garcia-Huidobro et al. 1982). Thermal time accumulation requires cardinal temperatures, comprising base (T_b), optimum (T_o), and maximum temperatures (T_c), to be defined for each developmental phase of a species (Fenner 2000). Thermal time and associated cardinal temperatures can be used to precisely predict sowing and seedling emergence times (Covell et al. 1986; Moot et al. 2000; Lonati et al. 2009; Nori et al. 2013).

Stipa alpine steppe, a type of vegetation dominated by *Stipa purpurea* Griseb., *Stipa glareosa* P.A.Smirn., and *Stipa capillacea* Keng (Poaceae), is widespread on the Tibetan Plateau (Guo and Sun 1982; Wu 1983; Lu and Wu 1996; Miehe et al. 2009, 2011; Harris 2010). The alpine steppe grasslands support grazing rangeland, biodiversity, and ecosystem stability. Several studies have been undertaken to elucidate the genetic diversity (Liu et al. 2009, 2011a; Hensen et al. 2010), geographical distribution (Guo and Sun 1982; Wang 1988; Lu and Wu 1996), community classification (Yue et al. 2011), and ecophysiology (Zaka et al. 2002) of *Stipa* species. To our knowledge, however, data concerning species of *Stipa* on the Tibetan Plateau are still limited.

In the present study, we carried out a laboratory investigation of germination of three *Stipa* species that are typical of the Tibetan Plateau alpine steppe region. We specifically addressed the following questions: (1) What are the cardinal temperatures and thermal-time temperatures for germination? (2) How does germination of the three *Stipa* species differ at constant versus alternating temperature? and (3) Does light affect germination? Data obtained from this germination study can be used to predict sowing times at similar sites for the restoration of alpine steppe communities.

Materials and methods

Plant materials

Stipa purpurea is a dominant species of the alpine steppe of the Tibetan Plateau. The species is endemic to the Tibetan Plateau and the Pamir Mountains of central Asia, where it grows at altitudes of 1900–5150 m a.s.l. (Guo and Sun 1982; Lu and Wu 1996). *Stipa purpurea* is a perennial herb that flowers and sets seeds from July to October, and can also grow clonally by tillering (Liu et al. 2011a). Panicles are open, up to 15 cm long, and purple. The awns are deciduous, plumose throughout, and bigenicate (Wu 1983). *Stipa purpurea* plays an important role in soil and water conservation on the plateau, and is also a major pasture grass for livestock and wild herbivores.

Stipa glareosa is a perennial herb with very high levels of protein and fiber. It inhabits very dry alpine desert steppe at altitudes of 4000–5000 m a.s.l. throughout most of the western Tibetan Plateau. Awns are deciduous, hairy throughout, and unigeniculate. *Stipa glareosa* flowers and sets seeds from May to October (Wu 1983).

Stipa capillacea is widespread at 3000–4000 m a.s.l. in the alpine meadow–steppe zone of the eastern Tibetan Plateau, where it yields good forage when young. Its panicles are narrow, with their bases enclosed by the expanded uppermost leaf sheath. Awns are deciduous, scabrid, and bigenicate. *Stipa capillacea* flowers and set seeds from July to September (Wu 1983).

Seeds of *S. purpurea*, *S. glareosa*, and *S. capillacea* were collected from alpine steppe, alpine desert steppe, and alpine meadow–steppe vegetation, respectively. We selected mature seeds by vi-

sual observation in the field from August to September 2013. The collected seeds were stored at a low temperature (15 °C) and a low relative humidity (30%) for 2 weeks prior to their use in germination tests. Caryopses of each species were cleared by hand and the awns were removed.

Laboratory experiments

Germination tests were performed with four replicates of 25 seeds per Petri dish on 1% agarose medium. Seeds were surface-sterilized for 2 min with 1% sodium hypochlorite and then rinsed with tap water. Experiments were carried out in incubators at a relative humidity of 50% for 28 days at either a constant temperature of 5, 10, 15, 20, 25, or 30 °C or at alternating temperatures of 15 and 5 °C, 20 and 10 °C, or 25 and 15 °C. The daily photoperiod was 12 h (light) – 12 h (dark). The alternating temperature regimes relative to 10, 15, or 20 °C at constant temperature were consistent with local air temperatures during the growing season. The light source consisted of white fluorescent tubes with a mean photon flux density of 120 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. In addition, we compared the effects of the 12 h (light) – 12 h (dark) cycle and of continuous complete darkness (Petri dishes covered with aluminum foil) on seed germination of the three species at 15 °C.

Germination was checked at 12 h intervals and was considered complete when no additional seeds germinated. To detect germination, plates were examined with green light under dark conditions. Seeds were considered to have germinated if protruding coleorhiza were observed.

Data analysis

A two-way fixed effects analysis of variance (ANOVA) ($P < 0.05$) was performed to evaluate the effects of constant temperature, species, and their interaction on seed germination. ANOVAs were similarly applied to test the effects of alternating temperature, species, and their interaction, as well as the effects of light, species, and their interaction, on seed germination. Duncan's multiple range test was used to compare means of germination percentages between treatments when significant differences were found. All tests were carried out using SPSS version 16.0 for Windows (IBM, Chicago, Illinois, USA), and all figures were drawn with OriginPro 8.0 (OriginLab, Northampton, Massachusetts, USA).

For thermal time model construction, germination time courses of all four replicates within a given temperature were combined and modeled using the Chapman 3-parameter function in SigmaPlot (Qiu et al. 2006). To determine cardinal temperatures (T_b , T_o , and T_c) and thermal-time requirements for germination at suboptimal and supraoptimal temperatures, we plotted germination data for each species as the reciprocal of germination rate ($1/t_{50}$, where t_{50} is the time to 50% germination) versus incubation temperature (T). When actual germination did not reach 50%, we fitted cumulative germination percentage over time to a sigmoidal simulation to predict the median percentile. Germination rates of subpopulations were calculated from the reciprocal of their germination times (t_g). For each subpopulation, the slope of the linear regression line corresponded to the reciprocal of the thermal-time requirement.

Results

Effect of temperature and species on germination

Under constant temperature conditions, final germination percentages of the three *Stipa* species were significantly affected by temperature and species, but not their interaction (Table 1; Fig. 1).

Germination percentages increased with temperature, with a maximum value of 70% observed in *S. capillacea* at 15 °C, and maximum values of 61% in *S. glareosa* at 20 °C and 87% in *S. purpurea* at 20 °C. Species also had a significant effect on germination percentage along a given temperature gradient; in particular, *S. purpurea* and *S. capillacea* had higher germination percentages than *S. glareosa* at 15 and 20 °C.

Table 1. Two-way ANOVA of the effects of constant temperature (CT), species (S), and their interaction on seed germination percentage of *Stipa* species.

Source of variation	Type III sum of squares	df	Mean square	F	Significance
CT	34764.225	5	6952.845	34.522	0.000
S	5238.775	2	2619.388	13.006	0.000
CT×S	3295.901	10	329.59	1.636	0.121
Error	10875.673	54	201.401		
Corrected total	54174.574	71			

Fig. 1. Effect of constant temperature and species on *Stipa* species seed germination percentage (mean ± SE). Different letters above bars indicate significant difference at $\alpha = 0.05$. SG, *S. glareosa*; SP, *S. purpurea*; SC, *S. capillacea*.

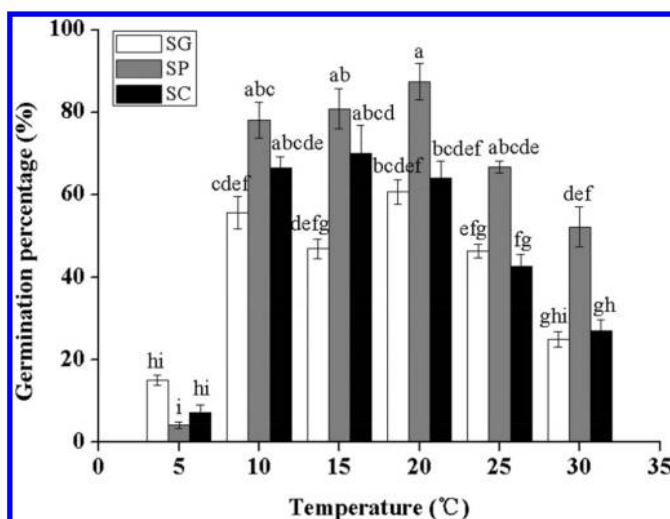


Table 2. Two-way ANOVA of the effects of alternating temperature (AT), species (S), and their interaction on seed germination percentage of *Stipa* species.

Source of variation	Type III sum of squares	df	Mean square	F	Significance
AT	679.164	2	339.582	2.451	0.105
S	5433.943	2	2716.972	19.61	0.000
AT×S	621.079	4	155.27	1.121	0.367
Error	3740.853	27	138.55		
Corrected total	10475.039	35			

Under alternating temperatures, final germination percentages of the three *Stipa* species were not significantly affected by temperature or the interaction of temperature and species, with significant differences only observed within species (Table 2; Fig. 2). At alternating 20 and 10 °C, *S. purpurea* had the highest germination percentage (83%) followed by *S. capillacea* and *S. glareosa* with germination percentages of 73% and 47%, respectively.

Effect of light and species on germination

We examined the effect of light and species on germination at 15 °C. While light and the interaction of light and species had no significant effect on germination percentage, species had a significant effect (Table 3; Fig. 3). Of the three species, *S. purpurea* exhibited the highest germination percentages under both light and dark conditions: 81% and 82%, respectively. Germination percentages were 70% and 64% in *S. capillacea* and 56% and 59% in *S. glareosa* under light and dark conditions, respectively.

Fig. 2. Effect of alternating temperature and species on *Stipa* species seed germination percentage (mean ± SE). Different letters above bars indicate significant difference at $\alpha = 0.05$. SG, *S. glareosa*; SP, *S. purpurea*; SC, *S. capillacea*.

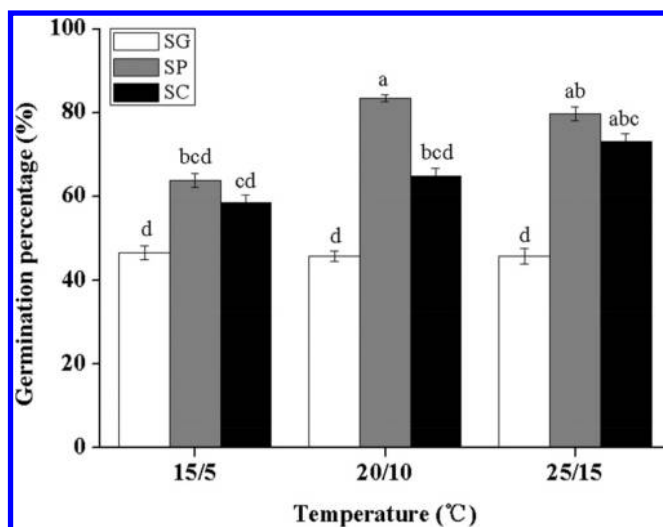
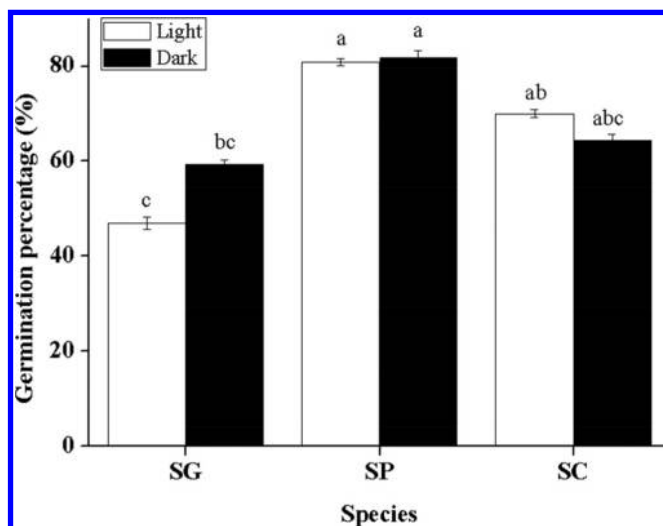


Table 3. Two-way ANOVA of the effects of light (L), species (S), and their interaction on seed germination percentage of *Stipa* species.

Source	Type III sum of squares	df	Mean square	F	Significance
L	38.813	1	38.813	0.224	0.641
S	3174.389	2	1587.195	9.179	0.002
L×S	337.873	2	168.936	0.977	0.396
Error	3112.55	18	172.919		
Corrected total	6663.625	23			

Fig. 3. Effect of light and species on *Stipa* species seed germination percentage (mean ± SE). Different letters above bars indicate significant difference at $\alpha = 0.05$. SG, *S. glareosa*; SP, *S. purpurea*; SC, *S. capillacea*.



Cardinal temperature and thermal time

Seed germination of the three *Stipa* species in response to temperature was well described by the thermal-time model at both suboptimal and supraoptimal temperatures (Table 4; Fig. 4). Cardinal temperatures (T_b , T_o , and T_c) of *S. glareosa*, *S. purpurea*, and *S. capillacea* were -1.0, 22.0, and 32.8 °C; 0.1, 20.3, and 31.5 °C; and

Table 4. Estimation of temperature threshold value with a linear regression of seed germination rate $1/t_{50}$ as a function of temperature in three *Stipa* species.

Species	T_b (°C)	T_o (°C)	T_c (°C)	Regression equation	R^2	δ	$\theta_{T(50)}$ (°C-day)
<i>S. glareosa</i>	-1.0	22.0	32.8	$y = 0.0043x + 0.0041$	0.95	2.37	233
				$y = -0.0092x + 0.3017$	1	2.04	108.7
<i>S. purpurea</i>	0.1	20.3	31.5	$y = 0.0065x - 0.0009$	0.94	2.19	154
				$y = -0.0117x + 0.3686$	1	1.93	85.5
<i>S. capillacea</i>	-1.4	15.6	25.3	$y = 0.0038x + 0.0054$	1	2.42	263.2
				$y = -0.0021x + 0.0532$	0.96	1.92	82.6

Note: t_{50} , time to 50% germination; T_b , base cardinal temperature; T_o , optimum cardinal temperature; T_c , maximum cardinal temperature; $\theta_{T(50)}$, thermal time.

-1.4, 15.6, and 25.3 °C, respectively. At suboptimal temperatures, thermal times ($\theta_{T(50)}$) for *S. glareosa*, *S. purpurea*, and *S. capillacea* were 233 °C-day, 154 °C-day, and 263.2 °C-day, respectively. At supraoptimal temperatures, $\theta_{T(50)}$ values for *S. glareosa*, *S. purpurea*, and *S. capillacea* were 109 °C-day, 85 °C-day, and 83 °C-day, respectively.

Discussion

Constant and alternating temperature effects on seed germination

Our analysis revealed the three *Stipa* species were able to germinate over a wide range of temperatures. Seeds germinated at all tested temperatures, both constant and alternating, indicating that different thermal regimes were suitable for germination. We found constant temperature and species had significant effects on seed germination. Because the three studied *Stipa* species grow in different geographical regions, their germination was somewhat limited by temperature. On the Tibetan Plateau, species distribution of *Stipa* is strongly influenced by the presence of a horizontal precipitation gradient extending from the eastern region to the western margin. However, meadow steppe dominated by *S. capillacea* is located in the eastern region, desert steppe dominated by *S. glareosa* occupies the western region, whereas alpine steppe dominated by *S. purpurea* is situated between these two regions. Temperature is thus positively correlated with *Stipa* species distribution. Our results are consistent with other reported studies of seed germination at constant temperatures (Ronnenberg et al. 2008; Lonati et al. 2009; Nori et al. 2013). Seed germination is also physiologically important, as delayed germination protects against high temperatures (Chiu et al. 2012; Bewley et al. 2013; Tan et al. 2013). In this study, we also confirmed high temperatures inhibit seed germination.

Diurnal fluctuations in temperature also may accelerate or initiate germination, with the effectiveness of this stimulus varying according to the amplitude of the fluctuation (Thompson et al. 1977). We found optimum alternating temperature regimes for germination of *S. purpurea*, *S. glareosa*, and *S. capillacea* were 20 and 10 °C, 15 and 5 °C, and 25 and 15 °C, respectively. These findings imply seed germination in *Stipa* is somewhat dependent on alternating temperature (Thompson et al. 1977; Baskin and Baskin 1998). Ronnenberg et al. (2007) reported seeds of five mountain steppe species from central Asia germinated best under warm to high temperatures (20 and 10 °C, 32 and 20 °C) and cooler temperatures of 8 and 4 °C deferred germination but did not inhibit it. Hamasha and Hensen (2009) also found that seed germination of four Jordanian *Stipa* species (*S. capensis*, *S. parviflora*, *S. arabica*, and *S. lagascae*) responded well to three different alternating temperature regimes (8 and 4 °C, 20 and 10 °C, 32 and 20 °C). Although variations among populations from different regions were species-specific, the authors observed populations with the highest seed germination rates were always of arid and Saharan Mediterranean origin. In that study, seed germination was thus found to be negatively correlated with annual precipitation. Finally, Liu et al. (2013) have proposed seed germination of perennials on the Tibetan Plateau is significantly promoted by alternating temperatures of both 5 and 25 °C and 10 and 20 °C.

Thermal-time requirements

The use of cardinal temperatures allowed us to calculate a single, easily transferable coefficient for thermal-time accumulation under suboptimal and supraoptimal temperatures. Base temperatures of *Stipa* species were below freezing. The thermal-time model provided us with new insights into the effects of suboptimal and supraoptimal temperatures on seed germination. A significantly higher thermal requirement implies that seed germination under such conditions is a very slow process (Hu et al. 2013). Some authors have reported basal temperatures of 0–4 °C in temperate zones (Angus et al. 1980; Moot et al. 2000). Hu et al. (2012) reported that the cardinal temperatures (T_b , T_o , and T_c) of four *Vicia* species along the eastern margin of the Tibetan Plateau were as follows: 0.43 °C, 19.64 °C, and 30.53 °C for *V. angustifolia*; 3.29 °C, 19.84 °C, and 37.17 °C for *V. amoena*; 2.44 °C, 20.09 °C, and 37.37 °C for *V. unijuga*; and -0.48 °C, 16.05 °C, and 31.66 °C for *V. sativa* 'Lanjian 3'. Liu et al. (2011b) found the mean base temperature of 12 Asteraceae species was 0 °C and of *Senecio diversipinnus* was -1.38 °C. Wei et al. (2009) used thermal-time and hydrothermal-time models to quantify the effects of temperature and water potential on seed germination. They found *Cryptantha minima*, an endangered annual species adapted to prairie sand dunes of Canada, had a base temperature of -3.9 °C for germination. However, the lowest base temperature in our study was -1.4 °C in *S. capillacea*. The highest base temperature, 0.1 °C, was recorded for *S. purpurea*, while the base temperature of *S. glareosa* was found to be -1.0 °C. Low base temperatures allow seeds to accumulate heat when temperatures are low, resulting in early germination and seedling recruitment following snowmelt in winter or spring (Wei et al. 2009).

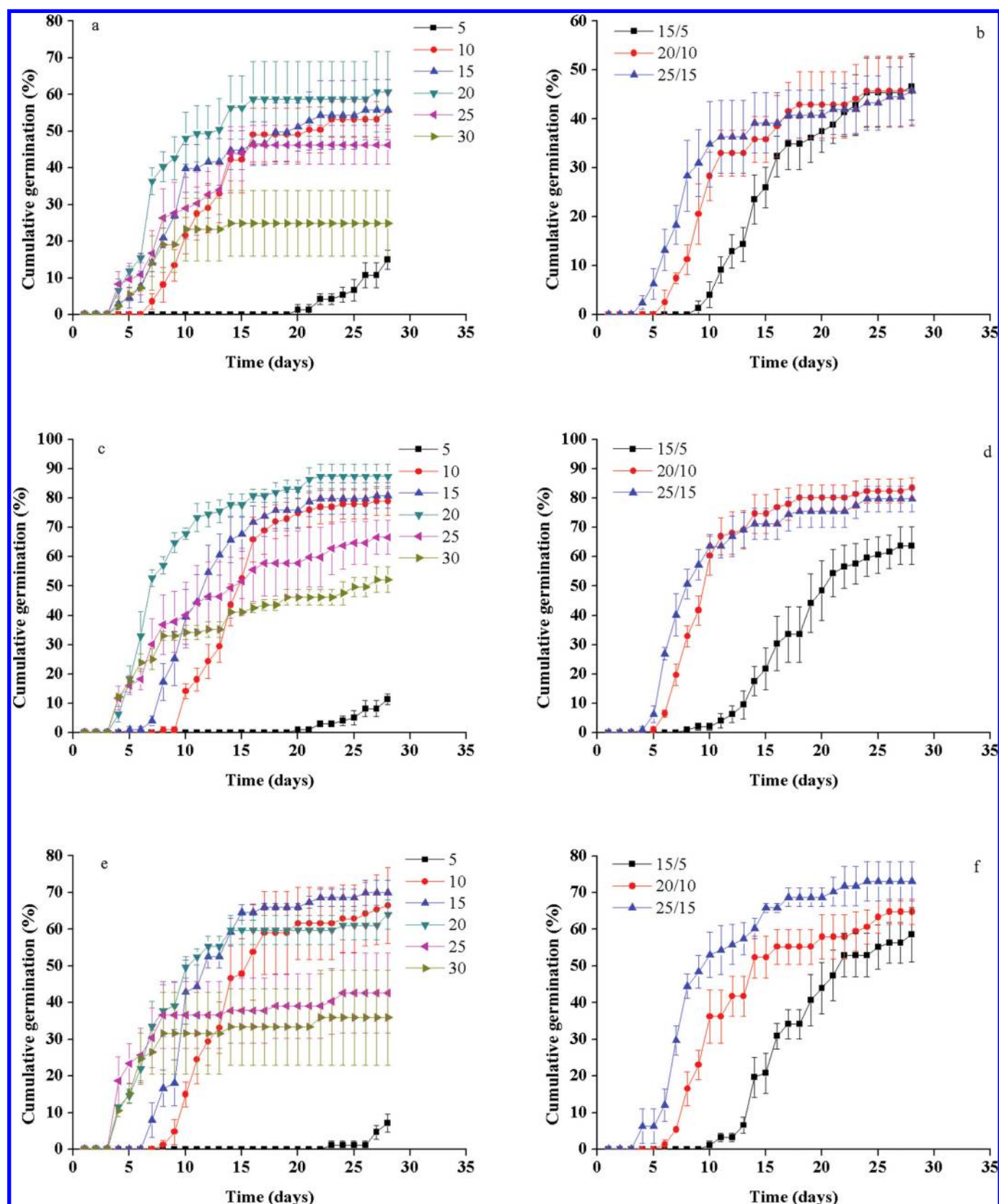
Effect of light on seed germination

We investigated the effect of light on seed germination of the three *Stipa* species under a constant temperature of 15 °C. Light had an insignificant effect on seed germination. We therefore conclude that *Stipa* seeds buried in soil, such as by rodent burrowing, soil disturbance, wind, or grazing animals (Fenner 2000; Fenner and Thompson 2005; Luna and Moreno 2009), can still germinate in deep permafrost layers of the Tibetan Plateau during winter and early spring. Moisture in the soil can be absorbed by seeds, thereby facilitating seedling recruitment in the alpine steppe region.

Implications for alpine steppe restoration

Information on cardinal temperatures and thermal times is necessary to accurately predict sowing times for alpine steppe restoration. The base temperatures of the three *Stipa* species examined in this study were coincident with mean air temperature in April (data not shown). Soil temperatures may be higher than air temperatures because of water heat capacity. On the Tibetan Plateau, soil begins to thaw and deep permafrost melts in April, which allows *Stipa* seeds to absorb water and accumulate heat for germination. In spring, the ability of seeds to germinate at low temperatures helps seedlings fully exploit available soil moisture from melted snow, while in autumn, seeds dropped on the soil

Fig. 4. Cumulative germination of (a, b) *Stipa glareosa*, (c, d) *Stipa purpurea*, and (e, f) *Stipa capillacea* at (a, c, e) constant and (b, d, f) alternating temperatures.



surface are buried by wind and the trampling of grazing livestock. Viable seeds in transient and permanent soil banks support timely recruitment of the aboveground plant community, thereby stabilizing the alpine steppe ecosystem.

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