高寒草甸 15 种植物种子发芽的比较研究

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摘要：对高寒草甸 15 种植物种子的发芽进行了比较实验研究。结果显示，冷湿层化、温度变幅及光照条件能够提高或者降低多数高寒草甸植物种子发芽率。其中，13 种植物对层化、11 种对光照条件、14 种对温度变幅处理有显著性响应。15 种植物中，有 14 种对单一因子或因子组合有反应，仅藏蒿草种子发芽对设定的因子或因子组合没有响应。根据不同植物种子对不同处理及其组合的发芽反应可将植物种子划分为不同的反应类型，通过对种子进行冷湿层化处理，可以部分或者全部地替代某些植物种子发芽对光、温需求。探明植物种子在特定环境因子组合条件下的发芽表现，对通过种子恢复退化草甸是至关重要的。

关键词：高寒草甸；冷湿层化；发芽率；萌发生态位；恢复生态学

A comparative researches on seed germination of 15 plant species from alpine meadow

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Abstract: Germination test of 15 alpine plant species showed that stratification, temperature fluctuation and light conditions could improve or decrease germination percentage of the most of alpine meadow plant species. In which, 13 plant species responded to stratification significantly, 11 species responded to light conditions, and 14 plant species responded to temperature fluctuations. Of all the 15 plant species, single factor or combinations of factors had significant effects on germination of 14 plant species. *Aster flaccidus* is the only species that did not response to any factor or combination of factors. Herein seeds of alpine plant species could be categorized to different response types according to their germination performance under different conditions. Study is essential to understand the germination behavior of plant species under specific conditions for the restoration of degraded alpine meadow communities from seed regeneration.

Key words: alpine meadow; cold-wet stratification; germination rate; germination niche; restoration ecology

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Germination of many plant species require specific microsites[1～7], in which light, nitrogen concentration[8～11], temperature fluctuation[1,12], and cold wet stratification[13,14] are the main factors. Dormancy breaking of plant seeds usually depends on the above factors or combination of them, which furthermore determines the strategy and diversity of plant species in plant communities[15～19]. Recent field experiments showed that responses of seedling emergence to ecological factors are species-specific[7,19]. The lack of factors or uncompleted combination of factors is the key constraint in germination for plant species establishment and the dormant seeds experience various unfavorable conditions before germination[20～23]. It is well known that different plant species seeds have their own capability to detect whether some factors are suitable for their

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germination. Only when the factors meet their requirements they can germinate, hence escapes from germinating under unfavorable conditions[3,4,17,18,21,24].

Germination of seeds in seed bank or introduced from other parts is the key for successful establishment of degraded plant vegetation, but little is known about the requirement for germination of alpine plant species. Some evidences revealed that the regeneration of plant species in grassland is mainly dependent on vegetative reproduction compared to seed germination[20], and seeds experience various fates[23]. Some investigations revealed that some plant species only found on specific sites, such as disturbed area, or in dense vegetation[20]. So plant species can be categorized into gap and non-gap plant species, or classified as pioneer and climax plant species. The classification represents only the two extreme points of a series of response types in continuum in the environment, and the other responsive types between the two extreme points are neglected[20]. The main aim of this study is to test the effects of stratification, light and fluctuating temperature on seed germination and to compare the different requirement of cold wet stratification, light and temperature fluctuations of alpine plant species. According to the response of plant species to the main factor and its interaction with other factors, we try to classify the plant species into some functional response types.

1 Materials and methods

The seeds were collected at Haibei Alpine Meadow Ecosysytem Research Station, which is located at a large valley oriented NW-SE surrounded by the Qilian Mountains with N latitude 37°29′～37°45′ and E longitude 101°12′～101°23′, with an altitude around 2900～3500 meters. The climate type is continental monsoon, with an annual rainfall ranges from 426 to 860 mm. The mean annual temperature is −1.7℃, with maximum 23.7℃ in July and minimum −37.1℃ in January. Seeds of *Elymus nutans*, *Ptilagrostis dichotoma*, *Elshotzia densa*, *Aconitum gymnandrum*, *Aster flaccidus*, *Notopterygium forbesii*, *Morina chinensis*, *Festuca ovina*, *Gueldenstaedtia diversifolia*, *Pedicularis kansuensis*, *Oxytropis kansuensis*, *Astragalus polycladus*, *Plantago depressa*, *Kobresia schoenoides* and *Koeleria cristata* were used to test germination response under different controlled conditions. The plant seeds were collected during the period of late September and early October in 2001, on the alpine meadow, Haibei Research Station of Alpine Meadow Ecosystem, Northwest Plateau Institute, Chinese Academy of Sciences.

Among these species, *A. gymnandrum*, *E. densa* and *P. depressa* were mainly found on disturbed soil, *N. forbesii* and *M. chinensis* found in meadow as spare species, *G. diversifolia* mainly grow on sunny slopes, rarely found in close vegetation. *P. kansuensis* and *O. kansuensis* widely spread in the meadow, in which *O. kansuensis* even became landscape species in Autumn. *K. schoenoides* mainly distributed in lower and moist and even areas, but was not found on the drier slope. *E. nutans*, *F. ovina*, *K. cristata* and *A. polycladus* widely spread in the meadow, in which *E. nutans* even became landscape species in the Autumn. *A. flaccidus* distributed in both meadow and arable lands.

Table 1 Life form, seed size and distribution area of the 15 alpine plant species

Species	Family	Seed size (g/1000seeds)	Life form	Habitats distribution
Elymus nutans	Gramineae	2.950	Perennial grass	Common
Ptilagrostis dichotoma	Gramineae	1.650	Perennial grass	Disturbed
Elshotzia densa	Labiatae	0.950	Annual forb	Disturbed
Aconitum gymnandrum	Ranunculaceae	0.725	Annual forb	Disturbed
Aster flaccidus	Compositae	0.475	Perennial forb	Common
Notopterygium forbesii	Umbelliferae	1.500	Perennial forb	Spare
Morina chinensis	Dipsacaceae	4.200	Perennial forb	Spare
Festuca ovina	Gramineae	0.925	Perennial grass	Common
Gueldenstaedtia diversifolia	Leguminosae	1.800	Perennial legume	Hill
Pedicularis kansuensis	Scrophulariaceae	0.500	Annual forb	Common
Oxytropis kansuensis	Leguminosae	1.050	Perennial legume	Common
Astragalus polycladus	Leguminosae	1.250	Perennial legume	Common
Plantago depressa	Plantaginaceae	0.240	Perennial forb	Disturbed
Kobresia schoenoides	Cyperaceae	0.500	Perennial herb	Common
Koeleria cristata	Gramineae	0.190	Perennial grass	Spare

The experiment with three factors and two levels for each factor was carried out. The three factors are stratification, light conditions and temperature fluctuations.

In the stratification treatments, batches of 20 seeds of each species were placed in 9-cm petri dishes on double layer of filter paper and moistened with distilled water. The petri dishes were sealed with parafilm during stratification for protecting water from loss, and were wrapped in black bags and stored in light-impermeable boxes within the incubators for 32 days at 4℃. For the non-stratified seeds, seeds have been stored in room temperatures until germination tests started.

In the light treatments, seeds were exposed to 12h of light per day in incubators equipped with warm white fluorescent light providing a photon flux density of approximately 20 $\mu mol/(m^2s)$ and an R:FR-ratio of about 10.2. Seeds in darkness treatments were kept in the petri dishes under dim green light. Petri dishes intended for darkness treatments were covered immediately with black bags within wooden boxes, and black plastics were used to cover the boxes.

In the temperature treatment, half of seeds were put in incubators with a temperature fluctuation of 5～12℃ and another half were put in incubators with a temperature fluctuation of 12～22℃. Lowest and highest temperatures of each temperature fluctuation (i. e. 5～12℃ & 12～22℃) matched with dark and light cycle respectively. So there were 8 combinations of factors as treatment, with each treatment five replications. The germinated seeds were counted and removed every second day. In the darkness treatments, seeds germinated were counted and removed under dim green light. Tests were terminated after a week without any further germination, so the experiment took 37 days from April 3 to May 9.

The data were analyzed with SPSS. Here we only analyzed the effects of stratification, light and temperature on the germination of each species. The data used for statistical analysis were arcsin transformed[7].

2 Results and analysis

2.1 Effects of stratification

Germination of 13 plant species responsded to stratification significantly except *A. flaccidus* and *A. polycladus*, but stratification showed negative effects on germination for *E. nutans* and *P. dichotoma*. Germination of seeds of other 11 plant species could be increased through stratification (Table 2). For *K. schoenoides*, although stratification could increase its germination percentage, higher germination only occurred within the combination of stratification, light and higher temperature fluctuation (73%). Under other combination of the factors, germination percentage was less than 3% or did not germinate at all (Table 2). Intensely requirements for stratification showed that they only germinate next year after natural stratification through winter and spring in the field, especially the seeds that were sowed in close vegetation (personal communication). In the following tables the species are abbreviated to first two letters of their botanical names.

Response to stratification for seed germination could be categorized into 4 types. The germination of plant species in type Ⅰ did not respond to both stratification and its interaction with light and/or temperature significantly. Plant species belonging to this group were *A. flaccidus* and *A. polycladus*. Germination of these two plant species was not affected by stratification and its interaction with light and/or temperature. Type Ⅱ suggested that seed germination in it did not respond to stratification, but responded to its interaction with light and/or temperature fluctuation, but no species belonged to this type among the 15 plant species. Type Ⅲ was that germination was affected only by stratification, but not by its interaction with light and/or temperature fluctuation, *E. nutans* was the only species that belongs to this type.

For type Ⅳ, both stratification and its interaction with light and/or temperature had significant effects on seed germination, 11 plant species belonged to this functional response type. Germination of *P. dichotoma* responded to stratification and its interaction with light negatively, showing that its germination did not require stratification and light. Stratification and its interaction with temperature fluctuation had strong effects on germination of *E. densa* and *A. gymnandrum*, and the latter one had an apparent requirement for lower temperature fluctuation under light when seeds were not stratified and under darkness when seeds were stratified. Stratification and its interaction with light had significant effects on germination of *N. forbesii*, showing that stratification can replace the requirements for light. For germination of *M. chinensis*, stratification and its interaction with temperature fluctuation had significant effects. And stratification could replace the requirements for temperature for dormancy breaking of *M. chinensis*. Stratification and its interaction with light and temperature fluctuation had strong effects on germination of *F. ovina* and *K. cristata*, meant that dormancy breaking requirements for both light and temperature could be replaced by stratification partly or completely. Germination of *G.*

diversifolia responded significantly to stratification and its interaction with temperature fluctuation significantly. Germination of stratified seeds of *P. kansuensis* significantly responded to stratification and its interaction with temperature fluctuation, and stratification could partly replace the requirements for higher temperature fluctuation. For *O. kansuensis* and *P. drepressa*, Stratification and its interaction with light and temperature imposed significant effects on their germination, and stratification could replace the requirements of germination for light and higher temperature fluctuation. For *K. schoenoides*, although stratification and its interaction with light and temperature fluctuation had strong effects on seed germination, only under the combination of stratification, light and higher temperature fluctuation, could K. schoenoides germinate better than other combinations of factors.

Table 2　Germination rate (%) of 15 alpine plant species under conditions with- and without stratification, light or darkness and two temperature fluctuation regimes

S	L	T	ELNU	PTDI	ELDE	ACGY	ASFL	NOFO	MOCH	FEOV	GUDI	PEKA	OXKA	ASPO	PLDE	KOSC	KOCR
1	1	1	88.0	73.3	14.0	0.0	68.0	1.0	0.0	48.0	3.0	28.2	0.0	10.9	6.0	0.0	14.0
1	1	2	83.3	81.7	8.0	0.0	69.0	4.0	4.0	73.2	2.0	22.2	0.0	8.0	66.3	0.0	26.0
1	2	1	93.0	68.8	4.0	12.0	64.4	1.0	0.0	48.0	4.1	34.0	6.0	15.2	27.0	0.0	39.3
1	2	2	97.0	78.0	8.0	0.0	66.3	28.7	3.0	92.1	4.0	37.0	9.0	13.8	97.9	3.0	73.0
2	1	1	75.3	81.7	10.0	6.4	63.5	33.0	21.0	98.9	0	49.0	7.0	9.0	39.0	0.0	74.0
2	1	2	69.0	72.1	15.0	0.0	72.8	67.0	8.7	95.0	7.0	22.6	8.0	13.0	95.0	1.0	78.0
2	2	1	82.0	28.8	12.0	1.0	71.1	30.5	9.9	95.0	5.1	12.3	8.2	14.5	34.4	1.0	73.1
2	2	2	76.8	65.2	50.0	40.8	55.6	66.3	17.0	95.0	13.0	77.1	11.9	21.0	91.0	73.2	80.0
Factors			ANOVA summary, significance of *F*-value														
S			0.000	0.008	0.000	0.000	0.781	0.000	0.000	0.000	0.020	0.012	0.001	0.319	0.001	0.000	0.000
L			0.001	0.000	0.185	0.000	0.293	0.025	0.549	0.369	0.003	0.010	0.009	0.035	0.003	0.000	0.000
T			0.402	0.031	0.012	0.390	0.779	0.000	0.278	0.000	0.011	0.009	0.374	0.328	0.000	0.000	0.000
S×L			0.135	0.004	0.000	0.129	0.892	0.008	0.958	0.020	0.123	0.714	0.012	0.584	0.000	0.000	0.000
S×T			0.427	0.924	0.005	0.000	0.521	0.483	0.041	0.000	0.005	0.002	0.930	0.163	0.226	0.000	0.026
L×T			0.451	0.008	0.001	0.001	0.109	0.012	0.084	0.018	0.434	0.000	0.476	0.719	0.435	0.000	0.216
S×L×T			0.368	0.010	0.307	0.000	0.080	0.017	0.026	0.390	0.308	0.000	0.790	0.678	0.291	0.000	0.483

Note: S_1 = without stratification, S_2 = with stratification, L_1 = darkness, L_2 = light, T_1 = lower temperature fluctuation 5～12℃, T_2 = higher temperature fluctuation 12～25℃; For *F*-values, data were arcsin transformed

2.2 Effects of light

Germination of 11 plant species responded to light significantly, in which light condition inhibited germination of *P. dichotoma* (Table 2). *E. nutans* had a higher germination percentage under all the situations, but its germination was higher in light than that in darkness significantly. *A. gymnandrum* did germinate under darkness without stratification, non-stratified seeds of *N. forbesii* had a higher germination percentage under combination of light and higher temperature fluctuation, but for the stratified seeds, light had no effects on germination. Germination of *G. diversifolia*, *P. kansuensis*, *O. kansuensis*, *A. polycladus*, *P. depressa*, *K. schoenoides* and *K. cristata* were higher in light than in darkness. Non-stratified seeds of *A. gymnandrum*, *O. kansuensis* and *K. schoenoides* even did not germinate in darkness. Requirements for light for dormancy breaking revealed that their germination in nature require light, and sward gaps provided by various ways may meet their requirements for light and/or temperature. But some species could be inhibited by light, such as *P. dichotoma* (Milberg & Andersson 1998).

The response of seed germination to light could be categorized into 4 functional response types (Table 2). In type Ⅰ, germination of seeds did not respond to light and its interaction with stratification and temperature fluctuation significantly, Plant species belonging to this type are *A. flaccidus* and *M. chinensis*. In type Ⅱ, germination of seeds did not respond to light significantly, but to the interaction with stratification and/or temperature fluctuation, *E. densa* and *F. ovina* belonged to this type. In type Ⅲ, light had important effects on germination, but its interaction with stratification and temperature had no significant effects on germination, *E. nutans*, *G. diversifolia* and *A. polycladus* belongs to this type.

In type Ⅳ, germination of plant seeds responded to both light and its interaction with stratification and /or temperature significantly. For *P. dichotoma*, light and its interaction with temperature fluctuation played significant effects on germination, in which light showed its negative effects, and higher temperature could partly alleviate the negative effects of light. Germination of *A. gymnandrum* also responded to light and temperature fluctuation significantly. Light and its interaction with stratification and temperature fluctuation could significantly increase germination of *N. forbesii* and *K. schoenoides*. Light and its interaction with temperature fluctuation could significantly increase germination of *P. kansuensis*. Light and its interaction with stratification imposed strong effects on germination of *O. kansuensis*, *P. depressa* and *K. cristata*, stratification could partly or completely eliminate their germination requirement for light.

2.3 Effects of temperature

Temperature played an important role in regulating germination of plant species (Probert 2000). Germination of 9 plant species responded to temperature significantly, they are *P. dichotoma*, *E. densa*, *N. forbesii*, *F. ovina*, *G. diversifolia*, *P. kansuensis*, *P. depressa*, *K. schoenoides* and *K. cristata*. Higher temperature fluctuation increased germination percentage of 8 species but failed for *P. dichotoma*.

Germination response to temperature fluctuation and its interaction with light and stratification could also be categorized into 4 types (Table 2). Type Ⅰ, temperature fluctuation and its interaction both with stratification and light did not impose significant effects of germination. Plant species belonged to this type were *E. nutans*, *A. flaccidus*, *O. kansuensis* and *A. polycladus*. In the type Ⅱ, temperature fluctuation had no significant impacts on seed germination, but the interaction of temperature fluctuation with light or stratification had significant impacts on seed germination. And *A. gymnandrum* and *M. chinensis* belongs to this type. In the type Ⅲ, temperature fluctuation had significant effects, but the interaction with light and stratification had no effect on seed germination, and only *P. depressa* belongs to this type.

In the type Ⅳ, both temperature and it interaction with light and/or stratification imposed significant effects on seed germination. For *P. dichotoma*, temperature fluctuation has positive effects on its germination, but the interaction of temperature fluctuation and light imposed negative effects on germination.

Temperature fluctuation and its interaction with the other two factors had positive effects on germination of *E. densa* and *F. ovina*. But for *F. ovina*, the effects of temperature fluctuation on seed germination disappeared under stratification, means that stratification could replace requirement of *F. ovina* for light and higher temperature fluctuation.

For *N. forbesii*, both temperature fluctuation and its interaction with light had positive effects on seed germination, means that temperature fluctuation and light could partly be replaced by each other. Germination of *G. diversifolia* responded to both temperature fluctuation and its interaction with stratification, showed that stratification could partly replace requirement for higher temperature, but in darkness under lower temperature fluctuation, stratified seeds could not germinate. Both temperature fluctuation and its interaction with stratification played significant effects on seed germination of *K. cristata*, and stratification could replace the requirement for higher temperature fluctuation.

For *P. kansuensis*, temperature fluctuations and its interaction with stratification and light played significant effects on seed germination. For the stratified seeds, higher temperature fluctuation decreased germination percentage in darkness, and increased germination percentage in light. For *K. schoenoides*, though temperature fluctuation and its interaction with stratification and light played significant effects on seed germination, yet only under the combination of stratification, light and higher temperature fluctuation, *K. schoenoides* could reach a higher germination percentage.

3 Discussion

Stratification could impose positive, neutral or negative effects on seed germination[13,14]. Stratification significantly increased germination of *M. chinensis*, *N. forbesii* and *F. ovina* etc., and decreased germination of *E. nutans* and *P. dichotoma*. This situation does not occur in genus of *Carex*[14], but occur in annual plant species[13]. Perhaps the process of stratification reduced physiological activity of *E. nutans* and *P. dichotoma*. Stratification can replace the requirements for higher temperature and/or light for some species germination[17,22], e.g. *O. kansuensis* and *K. cristata*. However positive effects of stratification to some species have not been documented in field experiment[7].

Seed germinations of most of plant species required suitable light and temperature fluctuation, especially for smaller seeds[2,11,12,20], and could replace each other on some plant species[7,13,25]. *A. gymnandrum* and *P. depressa* generally distributed in gaps disturbed by different ways, this phenomenon may relate to their requirements for light or higher temperature fluctuation, or we consider them as gap plant species[20]. However, degree of germination response to the main factors or combinations of factors varied among different plant species. So in the field we usually found that plant species show great variation in their distribution.

Requirements for higher temperature fluctuation means that seed usually geminate in warm summer, and almost no germination occurs in spring and autumn. Comparatively speaking, the seeds germinate well in lower temperature fluctuation, perhaps they would germinate just after shedding from parents' plant, for example in autumn or spring, for the species that germinate in autumn, the seedlings may suffer cold weather after emergence. Higher requirements for stratification for germination, seeds usually germinate in spring, similar results are found in other studies[7,14]. To meet requirements for breaking seed dormancy and seed germination is prerequisite for successful establishment.

As described above, there are species-specific requirements among plant species for seed germination, such as light, temperature fluctuation and cold-wet stratification and their possible interactions. The results showed that germination of seeds of different plant species is corresponding to their own germination niche and/or overlap of germination niche[18]. Three main factors in the study were included, we believe that there would be more germination response type if more factors were considered[22].

Restoration of degraded vegetation is partly dependent on seed bank in the soil and seed rain from standing plants[15,18]. It is difficult to restore degraded grassland in practice, the reason may be: (1) Lack of available seeds or propagules, both in seed bank and in neighboring field because of seed dispersal limitation[19]; (2) Lack of 'safe sites' which provide seeds and seedlings with essential nitrogen, phosphorus and potassium etc. [4,20,26].

As mentioned above, breaking of seeds dormancy of most plant species in alpine meadow require specific factor or combination of factors[17,22,27], and in few cases, for some species the factors can replace each other. For example, seed germination of *O. kansuensis* require light condition for germination without stratification, but stratification could replace the effects of light on seed germination, implied that pretreatments of seeds of some plant species for artificial sowing in practice might be required.

4 Conclusion

Germination niche or requirements for germination, varied among plant species in alpine meadow community. The results revealed that different species have different dormancy mechanisms underlying. Germination performance could be limited by single factor or combination of factors, for some species, stratification could replace requirements for light and/or temperature fluctuation. Germination of some plant species was usually lower than other species, no matter what factor or combination of factors are, such as *G. diversifolia*, *O. kansuensis* and *A. polycladus*, their germination possibly controlled by other factors, e. g. seed hardness, nitrogen concentration etc., perhaps scarification is needed for breaking legume seed dormancy. Stratification, light and higher temperature are not always provoking germination for all the species. Plant species could be categorized into different functional response types according to their response to single main factor or interaction of different factors. Environmental variation and heterogeneity of alpine meadow on temporal and spatial scale not only determine the patters and structure of plant biodiversity, but also determine seed germination behavior and germinating time. Germination could be improved or inhibited through alteration of environment conditions or by seed treatment prior to sowing.

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